



**The Society of  
Vertebrate Paleontology  
80<sup>th</sup> Annual Meeting · Virtual 2020**  
October 12-16 2020

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**Meeting Program and Abstracts**



# THANK YOU TO THIS YEAR'S MEETING SPONSORS!

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## THANK YOU TO OUR COMMITTEE

Thank you to the committee members whose efforts ensured an SVP meeting experience during this unusual year! We'd like to extend an extra special thanks to our Program Committee Co-Chairs, Paul Barrett and Patricia Holroyd, for the additional effort required in restructuring the program format to fit the virtual nature of this year's meeting.



### 2020 Program Committee

Paul Barrett, <i>Co-Chair</i>	Sebastian Groh
Patricia Holroyd, <i>Co-Chair</i>	Thomas Halliday
Kenneth Angielczyk ( <i>ex officio</i> )	Amber MacKenzie
Victoria Arbour	Philip Mannion
Kirstin Brink	Josh Miller ( <i>ex officio</i> )
Jonah Choiniere	Jess Miller-Camp
Mark Clementz	Alison Murray
Larisa DeSantis ( <i>ex officio</i> )	Jennifer Olori
Julia Desojo	Catalina Pimiento
Jaelyn Eberle	Kristen Prufrock
Dana Ehret ( <i>ex officio</i> )	Kaye Reed
Susan Evans	Vanessa Rhue ( <i>ex officio</i> )
Alistair Evans	Gabi Sobral ( <i>ex officio</i> )
Andrew Farke	

### 2020 Virtual Planning Committee

Paul Barrett	Jessica Theodor
Larisa DeSantis	Mark Uhen
Patricia Holroyd	Ted Vlamis
Emily Rayfield	Lindsay Zanno

### 2020 Host Committee

*Special thanks to Bianca Neale for designing our 2020 Virtual Meeting logo.*

Joshua Miller, <i>Co-Chair</i>	Brenda Hunda
Glenn Storrs, <i>Co-Chair</i>	Takuya Konishi
Carlton Brett	Julie Reizner
Jonathan Calede	Cameron Schwalbach
Brooke Crowley	

# WELCOME TO VIRTUAL!

Dear Delegates,

As we departed from Brisbane in October 2019, who could have predicted that I would be delivering this message to welcome you to not only the 80th SVP Annual Meeting but the first virtual annual meeting event? But this is where we are in October 2020. In times of such uncertainty and global unease, it is my pleasure to still be able to welcome you to the SVP annual meeting and the opportunity for us to connect and share our interest and enthusiasm for vertebrate paleontology.

Speaking on behalf of all those involved in organising the meeting, we're delighted that you've chosen to attend this year, despite the obvious differences in format and engagement a virtual platform necessitates. And to those of you presenting posters or talks, delivering a workshop, contributing to diversity or student and postdoc sessions, or working behind the scenes, thank you. We appreciate the time and effort that goes in to producing a presentation, delivering a workshop or a platform event under normal circumstances and therefore recognise the additional commitment involved in such challenging times.

The impact of this year will reverberate for many more. Yet as scientists and those interested in vertebrate life and past environments, more than ever we have a key role to play in understanding the interplay between climates, environments and vertebrate evolution over geological timescales. As a professional scientific society, we also bear the responsibility for addressing and subverting racial inequality in our discipline and amplifying the voices and sharing the perspectives, personal and scientific, of traditionally underrepresented groups. I'm excited that the meeting presents the opportunity for us to showcase our current research, and also to outline and promote some of the new initiatives SVP is taking to address structural inequality and diversity within vertebrate paleontology, yet there is still much to do.

2020 has been an exceptional year: a global pandemic, racial inequality, and manmade global climate disasters. Labs have been closed, museum collections inaccessible, fieldwork postponed or cancelled. These continuing events will be represented in the talks and posters you view, and your interactions with other meeting attendees. Do exercise empathy during your interactions on the site and appreciate that despite current circumstances, we are still able to participate and enjoy new developments and ideas in the science of vertebrate paleontology and the issues that affect our field. And with that, I welcome you, and hope that you enjoy the 80th annual meeting, 1st virtual meeting, of the Society of Vertebrate Paleontology.



**Emily Rayfield**  
SVP President

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# GENERAL INFORMATION

*All meeting activities will be accessed through the SVP Virtual Meeting platform unless otherwise noted.*

## EXHIBIT HOURS

Virtual Exhibit Hall is open for viewing information throughout the meeting between Sunday, October 11 through Saturday, October 17th. Live engagement with exhibits is scheduled to occur between Tuesday, October 13 through Friday, October 16 during the following hours:

### **TUESDAY, OCTOBER 13,**

12:00pm – 1:00pm EDT

### **WEDNESDAY, OCTOBER 14,**

10:30am – 11:30am EDT

### **THURSDAY, OCTOBER 15,**

11:30am – 12:30pm EDT

### **FRIDAY, OCTOBER 16,**

11:30am – 12:30pm EDT

There are three key components to the 2020 SVP Virtual Meeting:

**Pre-recorded talks and posters,** grouped into themes, available for viewing 24/7 Sunday 11 – Saturday 17 October.

**Asynchronous moderated Q&A** associated with each presentation available Mon 12 – Fri 16 October. Leave a question and presenters will get back to you in their own time.

### **Live content:**

workshops, live networking sessions linked to themes, diversity and student-postdoc events, Mon 12 – Fri 16 October.

## SVP 2020 VIRTUAL FORMAT - A DIFFERENT EXPERIENCE!

Our virtual-only format necessitated changes to the structure of the SVP Program this year, but this has offered us opportunities to program content in novel ways. For example, the lack of a fixed talk and poster schedule allows you to engage with presentations in personally customized ways at the times most convenient to you, without the need to choose between competing presentations at fixed times. To exploit these changes and to offer members a different experience, we made an early decision to rely less on traditional taxon-based sessions and to explore other ways to bring members of the SVP community together. In addition to taxonomic sessions for some popular groups (e.g., dinosaurs, mammals), we also unified presentations by theme, which either reflect work in a particular sub-discipline (e.g., biomechanics) or a broader research topic (e.g., the application of novel quantitative methods to evolutionary questions). As a result, many sessions represent a mix of taxa and timescales: we hope you like this new approach.

These live networking sessions map to the main session themes in the Program, but a few themed sessions share the same live session. We have allocated time based on the number of presentations allotted to each theme. In doing this, we have also tried to ensure that the members of the many small sub-communities that make up SVP each get a dedicated time in which to interact in real time with each other and to pose questions to the presenters.

Other elements of the Program will be familiar, with sessions dedicated to Symposium, Romer Prize, Preparator's, and Education & Outreach presentations. Colbert Prize presentations have been allocated to the most relevant themed sessions and their status as a prize nominee is noted in the Program & Abstracts volume.

## SVP SESSION THEMES

Anatomical & Developmental Explorations of the Mammalian Skull	Macroecology & Macroevolution
Biomechanics & Functional Morphology	Mammalian Skeletal Morphology
Bird Biology & Evolution	Marine Mammals
Cenozoic Herpetology Collections	Marine Reptile Diversity & Biology
Dinosaur Systematics, Diversity & Ecology	Mesozoic & Early Cenozoic Mammalian Evolution
Education & Outreach	Mesozoic Herpetology
Evolution & Biology of Non-Avian Theropods	Paleozoic Tetrapods & Lissamphibians
Fishes & Chondrichthyans: Evolution & Distribution	Permo-Triassic Tetrapods
Holocene & Pleistocene Mammalian Macroecology and Faunal Studies	Preparators
Late Cenozoic Mammalian Macroecology & Macroevolution	Quantitative Methods
	Romer Prize
	Symposium: Paleoneurology
	Symposium: Dietary Reconstruction
	Taphonomy & Stratigraphy

All session themes are allocated their own live networking session, except for the following themes which have been combined into the following networking sessions: Mammalian Skeletal Morphology and Marine Mammals; Mesozoic Herpetology and Cenozoic Herpetology; Education & Outreach and Collections.

### THE ALFRED SHERWOOD ROMER PRIZE SESSION

Hear from new voices in paleontology on Tuesday, October 13, from 10:00am to 12:00pm EDT. Sixteen abstracts were chosen for presentation during this session in recognition of outstanding scientific contributions in vertebrate paleontology by predoctoral students.

### EDUCATION & OUTREACH POSTER SESSION

Learn from your colleagues' education outreach successes by visiting the Education & Outreach theme page, and participate in the live networking session on Friday, October 16, from 4:00pm to 4:45pm EDT.

### EDWIN H. AND MARGARET M. COLBERT PRIZE POSTER SESSION

This year, the posters selected for the Edwin H. and Margaret M. Colbert Prize Poster Session have been integrated into the session themes listed above. Wherever these special posters are listed, whether on the virtual platform, in the abstract volume or the author listing, you will find them highlighted as a "Colbert Poster Prize" candidate. View the posters from which the 2020 Edwin H. and Margaret M. Colbert Prize winner will be chosen. These students offer fresh viewpoints in Vertebrate Paleontology.

### PREPARATORS' SESSION

Join this live networking session on Wednesday, October 14, from 1:30pm to 2:15pm EDT for presentations on current issues in paleontological preparation, ranging from field and lab techniques to specimen curation and exhibition design.

# GENERAL INFORMATION

## SOCIAL MEDIA GUIDELINES

Follow SVP and comment about the upcoming Annual Meeting using hashtag #2020SVP. Please follow these social media guidelines before you tweet (or blog, or Facebook, or Instagram...)

The Society of Vertebrate Paleontology encourages open discussion on social media and other outlets at our annual meeting. In order to find a balance between embracing social media and protecting authors' work, we set forth the following guidelines:

- SVP has an embargo in place on discussing presentations until the beginning of the talk or poster session. This year the embargo will be lifted once the virtual platform goes live. Please do not discuss presentations until this time if you do not have the authors' permission to do so.
- This embargo exists to protect the authors. As an author, you have permission to break your own embargo or permit someone else to do the same. This includes discussing your own presentation online, posting slides or posters, etc. However, to protect yourself, make sure you are aware of any potential future publisher's policies about early dissemination of work.
- Do not photograph or video tape a talk or poster without the authors' express permission. Never post any images or video without the authors' permission.
- While the default assumption is to allow open discussion of SVP presentations on social media, please respect any request by an author to not disseminate the contents of their talk.

We want to thank everyone for following these basic guidelines for online posts of all kinds. As a reminder, the official hashtag of the meeting is #2020SVP. We look forward to seeing your thoughts and discussion online!

## CITING AN ABSTRACT IN THE 2020 SVP PROGRAM AND ABSTRACTS BOOK

This Program and Abstracts Book is an official supplement to the online version of the *Journal of Vertebrate Paleontology*. The citation format for an abstract printed in this book is: *Journal of Vertebrate Paleontology*, Program and Abstracts, 2020, <insert page number here>.

## SVP CODE OF CONDUCT (REVISED, 2020)

SVP is committed to equity, diversity, inclusion, and accessibility and to providing a safe, productive, and welcoming environment for all meeting participants and SVP staff. We value the presentations and attendance of diverse scientists from a range of backgrounds and experiences and commit to maintaining a harassment-free environment for everyone. Accordingly, we require that all participants, including, but not limited to, attendees, presenters, volunteers, exhibitors, SVP staff, and service providers abide by this SVP Meeting Code of Conduct. This Code of Conduct applies to all SVP meeting-related events (both online and in person), including those sponsored by organizations other than SVP but held in conjunction with SVP events outside of the Annual Meeting virtual environment.

## EXPECTED BEHAVIOR

- Treat one another with respect, consideration, and dignity regardless of gender, gender identity and expression, sexual orientation, marital or parental status, age, immigration status, disability, neurodiverse status, physical appearance, body size, race, ethnicity, nationality, religious affiliation, socioeconomic background, educational background, career stage, or military service.
- Questions and discussions should be respectful and constructive and focus on ideas rather than individuals.
- Comments or behaviors that may reasonably



be assumed to have the effect of creating, contributing to, or maintaining an environment that is hostile toward or damaging to a person or group are prohibited, no matter whether they are made directly (e.g., in person or directly online) or indirectly (e.g., via social media).

- Do not use legal intoxicants to the extent that your ability to act professionally and follow this Code of Conduct is compromised.
- Do not take or disseminate photographs, recordings, or reproductions of materials presented as part of the Annual Meeting without express permission of the author(s).
- Obey the rules and policies of any SVP-contracted facilities or services utilized during the meeting or anywhere your SVP badge/affiliation is on display.

Anyone requested to stop unacceptable behavior is expected to comply immediately.

Retaliation against any individual who reports harassment or assists in an investigation will not be tolerated and is also subject to disciplinary action.

### **HOW CAN I REPORT A COMPLAINT?**

Complaints of harassment or retaliation should be e-mailed to [safeSVP@vertpaleo.org](mailto:safeSVP@vertpaleo.org). If you witness a crime or behavior that is an immediate threat to public safety, make sure you are safe and then call emergency services (e.g., 911 in the USA).

### **HOW ARE REPORTS HANDLED?**

Complaints will be handled by the Vice President and reported to the President and the Executive Director. If any of these individuals should be the subject of the complaint, the other SVP officers will be notified. The VP or other officers designated by the President, the President and Past President will determine whether the matter requires additional investigation. Investigations will be carried out by the VP and an impartial investigator, who may interview the alleged offender

and any relevant witnesses.

Investigations will be reported to the President and Past President who will recommend appropriate action, including, where advisable, consultation with legal counsel. Confidentiality will be maintained to the extent that it does not compromise the rights of others or the need to conduct an adequate investigation and to the extent allowed by law. The determination will be promptly communicated to the complainant and alleged offender. SVP reserves the right to take preliminary action to protect our members, including removing an attendee from the event pending full investigation and resolution of the complaint.

### **CONSEQUENCES**

In the Society's sole discretion, sanctions may include, but are not limited to, a written warning, ejection from the meeting environment, reporting to the offender's home institution and other penalties without refund of any applicable registration fees or other costs. Repeat offense or especially serious offenses may result in bans from future meetings or revocation of membership in SVP. If the determination is made to terminate the membership of any person, the applicable provisions of the Bylaws, including procedural requirements, will be followed.

### **APPEAL**

An individual who has been sanctioned under this Code may submit a written appeal to the SVP Executive Committee and may be granted at the discretion of the Executive Committee. Any questions regarding the Code or its execution should be directed to a member of the Executive Committee.

# SPECIAL EVENTS

## ANNUAL BUSINESS MEETING

This live session will be held on Wednesday, October 14, from 4:30pm to 5:30pm EDT.

## 2020 SVP AWARDS CEREMONY

Due to the virtual format this year, we have decided to forego the traditional live Awards Banquet in favor of a prerecorded ceremony that will both honor our 2020 Awardees as well as our esteemed colleagues who have departed this past year. The prerecorded Awards Ceremony will be available on the virtual platform beginning on Saturday, October 17 at 12pm EDT. It will also be available on the SVP website after the virtual meeting concludes.

## DIVERSITY SESSIONS

This year, we will be offering four 30-minute diversity sessions on distinct topics each day beginning Tuesday, October 13 through Friday, October 16. We have varied the times that these sessions are offered in order to reach attendees in as many time zones as possible. See below for the schedule of sessions:

### TUESDAY, OCTOBER 13 12:30PM - 1:00PM EDT

*Racial and Ethnic Minorities*

### WEDNESDAY, OCTOBER 14 6:00PM - 6:30PM EDT

*LGBTQ+*

### THURSDAY, OCTOBER 15 11:00AM - 11:30AM EDT

*Neurodiversity/Disability*

### FRIDAY, OCTOBER 16 6:00PM - 6:30PM EDT

*Mental Health*

## STUDENT AND POSTDOC ROUNDTABLE EXCHANGE SESSIONS

This year, we will be offering four 30-minute Student and Postdoc Roundtable Exchange sessions from Tuesday, October 13 through Friday, October 16. These will be offered in a panel format with three 10-minute panels offered within each 30-minute session. We have varied the times that these sessions are offered in order to reach attendees in as many time zones as possible. See below for the schedule of sessions:

### TUESDAY, OCTOBER 13 6:00PM - 6:30PM EDT

- Science Communication, Virtual Networking and Social Media
- *Getting into Graduate School*
- *Meet the SVP Leadership*

### WEDNESDAY, OCTOBER 14 10:00AM - 10:30AM EDT

- *Applying for Grants and SVP Awards*
- *Field Work*
- *Maintaining a Work/Life Balance and Having a Family in 2020*

### THURSDAY, OCTOBER 15 6:00PM - 6:30PM EDT

- *Teaching Online*
- *Landing a Postdoc*
- *Academic Jobs*

### FRIDAY, OCTOBER 16 11:00AM - 11:30AM EDT

- *Working at and Visiting Museums*
- *Paleontology Consulting*
- *Fossil Preparation*

# EXHIBITORS



## GEORGE MASON UNIVERSITY - PALEOBIOLOGY DATABASE

The Paleobiology Database (PBDB) is a non-governmental, non-profit public resource for paleontological data. It has been organized and operated by a multi-disciplinary, multi-institutional, international group of paleobiological researchers. Its purpose is to provide global, collection-based occurrence and taxonomic data for organisms of all geological ages, as well data services to allow easy access to data for independent development of analytical tools, visualization software, and applications of all types. The Database's broader goal is to encourage and enable data-driven collaborative efforts that address large-scale paleobiological questions

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- Texture Based Classification for isolating specimens from matrix



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Our major subject areas include African, African American, Asian, cultural, Jewish and Holocaust, Middle East, Russian and East European, women's and gender studies; anthropology, film, history, bioethics, music, paleontology, philanthropy, philosophy, and religion. We also feature an extensive regional publishing program under our Quarry Books imprint. We are one of the largest public university presses, as measured by titles and income level.



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**VISIT THE EXHIBITS  
SUNDAY, OCTOBER 11—  
SATURDAY, OCTOBER 17**



Disclaimer – Participation in the Exhibits Program does not constitute an endorsement by the Society of Vertebrate Paleontology (SVP) of the claims, products or services offered.

Note: All sales of fossils are prohibited at the SVP Annual Meeting. Casts are acceptable.

# PROGRAM AT A GLANCE

Day	Start	End	Title	Live or Asynchronous
Sun Oct 11	7:00 AM EDT		Launch of virtual platform online, including Welcome Message from the President, asynchronous pre-recorded posters, talks, exhibits	Asynchronous
Mon Oct 12	1:00 PM EDT	3:00 PM EDT	Workshop #2 "Filling the Expectation Gap: Paleontologists as teaching professors—Professional development for paleontologists working outside of research-intensive universities"	Live but external to SVP Platform (pre-registered only)
Mon Oct 12	2:00 PM EDT	4:00 PM EDT	Workshop #1 "Active and Inquiry-Based Learning Strategies for Field and Classroom Educators"	Live but external to SVP Platform (pre-registered only)
Mon Oct 12	4:00 PM EDT	6:00 PM EDT	Workshop #3 "Movement and Paleontology: Integrating Movement Arts to Explore and Communicate Paleontology"	Live but external to SVP Platform (pre-registered only)
Mon Oct 12	5:00 PM EDT	7:00 PM EDT	Workshop #4 "Screening of the New Documentary, We Believe in Dinosaurs"	Live but external to SVP Platform (pre-registered only)
Tues Oct 13			Virtual platform online, including asynchronous pre-recorded posters, talks, exhibits	Asynchronous
Tues Oct 13	10:00 AM EDT	12:00 PM EDT	Romer Prize: Live Q&A	Live
Tues Oct 13	12:00 PM EDT	1:00 PM EDT	Visit with Exhibitors	Live
Tues Oct 13	12:30 PM EDT	1:00 PM EDT	Diversity Session #1: "Racial and Ethnic Minorities"	Live (recording will be posted to site)
Tues Oct 13	1:00 PM EDT	2:00 PM EDT	Fishes & Chondrichthyans: Evolution and Distribution <b>Networking Session</b>	Live
Tues Oct 13	2:00 PM EDT	2:30 PM EDT	Paleozoic Tetrapods & Lissamphibians <b>Networking Session</b>	Live
Tues Oct 13	2:30 PM EDT	3:00 PM EDT	BREAK	
Tues Oct 13	3:00 PM EDT	4:00 PM EDT	Symposium: New Geochemical and Dental Wear Approaches to Reconstruct the Diet, Ecology, and Physiology of Fossil Vertebrates <b>Networking Session</b>	Live
Tues Oct 13	4:00 PM EDT	4:45 PM EDT	Evolution and Biology of Non-Avian Theropods <b>Networking Session</b>	Live
Tues Oct 13	4:45 PM EDT	6:00 PM EDT	BREAK	
Tues Oct 13	6:00 PM EDT	6:30 PM EDT	Student & Post Doc Session #1: "Science Communication, Virtual Networking, and Social Media; Getting into Graduate School; Meet the SVP Leadership"	Live (recording will be posted to site)
Tues Oct 13	6:30 PM EDT	7:00 PM EDT	BREAK	
Tues Oct 13	7:00 PM EDT	7:45 PM EDT	Mammalian Skeletal Morphology & Marine Mammals <b>Networking Session</b>	Live
Wed Oct 14			Virtual platform online, including asynchronous pre-recorded posters, talks, exhibits	Asynchronous
Wed Oct 14	10:00 AM EDT	10:30 AM EDT	Student & Post Doc Session #2: "Applying for Grants and SVP Awards; Field Work; Maintaining a Work/Life Balance and Having a Family in 2020"	Live (recording will be posted to site)
Wed Oct 14	10:30 AM EDT	11:30 AM EDT	Visit with Exhibitors	Live
Wed Oct 14	11:30 AM EDT	12:15 PM EDT	Permo-Triassic Tetrapods <b>Networking Session</b>	Live
Wed Oct 14	12:15 PM EDT	12:45 PM EDT	Bird Biology and Evolution <b>Networking Session</b>	Live
Wed Oct 14	12:45 PM EDT	1:30 PM EDT	BREAK	
Wed Oct 14	1:30 PM EDT	2:15 PM EDT	Preparators' <b>Networking Session</b>	Live
Wed Oct 14	2:15 PM EDT	3:15 PM EDT	Late Cenozoic Mammalian Macroecology and Macroevolution <b>Networking Session</b>	Live

# PROGRAM AT A GLANCE

Wed Oct 14	3:15 PM EDT	3:30 PM EDT	BREAK	
Wed Oct 14	3:30 PM EDT	4:15 PM EDT	Mesozoic & Early Cenozoic Mammalian Evolution <b>Networking Session</b>	Live
Wed Oct 14	4:15 PM EDT	4:30 PM EDT	BREAK	
Wed Oct 14	4:30 PM EDT	5:30 PM EDT	Annual Business Meeting	Live
Wed Oct 14	5:30 PM EDT	6:00 PM EDT	BREAK	
Wed Oct 14	6:00 PM EDT	6:30 PM EDT	Diversity Session #2 "LGBTQ+"	Live (recording will be posted to site)
Thurs Oct 15		n/a	Virtual platform online, including asynchronous pre-recorded posters, talks, exhibits	Asynchronous
Thurs Oct 15	10:00 AM EDT	11:00 AM EDT	Symposium: Frontiers in Paleoneurology and Neurosensory Evolution <b>Networking Session</b>	Live
Thurs Oct 15	11:00 AM EDT	11:30 AM EDT	Diversity Session #3: "Neurodiversity/Disability"	Live (recording will be posted to site)
Thurs Oct 15	11:30 AM EDT	12:30 PM EDT	Visit with Exhibitors	Live
Thurs Oct 15	12:30 PM EDT	1:00 PM EDT	BREAK	
Thurs Oct 15	1:00 PM EDT	2:00 PM EDT	Anatomical & Developmental Explorations of the Mammalian Skull <b>Networking Session</b>	Live
Thurs Oct 15	2:00 PM EDT	2:45 PM EDT	Macroecology & Macroevolution <b>Networking Session</b>	Live
Thurs Oct 15	2:45 PM EDT	3:00 PM EDT	BREAK	
Thurs Oct 15	3:00 PM EDT	3:30 PM EDT	Marine Reptile Diversity and Biology <b>Networking Session</b>	Live
Thurs Oct 15	3:30 PM EDT	4:30 PM EDT	Mesozoic Herpetology & Cenozoic Herpetology <b>Networking Session</b>	Live
Thurs Oct 15	4:30 PM EDT	6:00 PM EDT	BREAK	
Thurs Oct 15	6:00 PM EDT	6:30 PM EDT	Student & Post Doc Session #3: "Teaching Online; Landing a Postdoc; Academic Jobs"	Live (recording will be posted to site)
Thurs Oct 15	6:30 PM EDT	8:00 PM EDT	BREAK	
Thurs Oct 15	8:00 PM EDT	9:00 PM EDT	Holocene and Pleistocene Mammalian Macroecology and Faunal Studies <b>Networking Session</b>	Live
Fri Oct 16		n/a	Virtual platform online, including asynchronous pre-recorded posters, talks, exhibits	Asynchronous
Fri Oct 16	10:00 AM EDT	11:00 AM EDT	Biomechanics & Functional Morphology <b>Networking Session</b>	Live
Fri Oct 16	11:00 AM EDT	11:30 AM EDT	Student & Post Doc Session #4: "Working at and Visiting Museums; Paleontology Consulting; Fossil Preparation"	Live (recording will be posted to site)
Fri Oct 16	11:30 AM EDT	12:30 PM EDT	Visit with Exhibitors	Live
Fri Oct 16	12:30 PM EDT	1:00 PM EDT	BREAK	
Fri Oct 16	1:00 PM EDT	1:45 PM EDT	Taphonomy and Stratigraphy <b>Networking Session</b>	Live
Fri Oct 16	1:45 PM EDT	2:30 PM EDT	Quantitative Methods <b>Networking Session</b>	Live
Fri Oct 16	2:30 PM EDT	3:00 PM EDT	BREAK	
Fri Oct 16	3:00 PM EDT	4:00 PM EDT	Dinosaur Systematics, Diversity and Ecology <b>Networking Session</b>	Live
Fri Oct 16	4:00 PM EDT	4:45 PM EDT	Education & Outreach and Collections <b>Networking Session</b>	Live
Fri Oct 16	4:45 PM EDT	6:00 PM EDT	BREAK	
Fri Oct 16	6:00 PM EDT	6:30 PM EDT	Diversity Session #4: "Mental Health"	Live (recording will be posted to site)
Fri Oct 16	6:30 PM EDT		Site is closed to online Q&A	
Sat Oct 17			Virtual platform online, including asynchronous pre-recorded posters, talks, exhibits (content available for viewing only; no online Q&A)	Asynchronous
Sat Oct 17	12:00 PM EDT		2020 SVP Awards Ceremony - recording available on platform	Asynchronous
Sat Oct 17	12:00 AM EDT		Platform closes down completely at midnight EDT	

A 3D rendered image of a skull, likely a primate or similar mammal, showing the jawbone and teeth. The bones are segmented and color-coded: the upper jawbone is grey, the lower jawbone is light grey, and the individual teeth and jaw joints are colored in various shades including blue, purple, pink, red, orange, yellow, green, and cyan. The rendering is highly detailed, showing the texture of the bone and the sharp edges of the teeth.

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Courtesy of David Jacobs, SARCHI, Animal Evolution & Systematics -  
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S C I E N T I F I C

## List of Authors and Abstract Titles in Chronological Session Order

TUESDAY, OCTOBER 13, 2020, 10:00AM EDT-12:00PM EDT  
ROMER PRIZE: LIVE Q&A

### TALKS

**K. Chapelle** ONTOGENY OF THE EARLY JURASSIC DINOSAUR *MASSOSPONDYLUS CARINATUS* AND ITS IMPLICATIONS FOR SAUROPODOMORPH EVOLUTION

**A.A. Chiarenza** COMBINING EARTH SYSTEM AND ECOLOGICAL MODELLING REVEALS THE CLIMATIC DRIVERS BEHIND MESOZOIC DINOSAUR DISTRIBUTION AND EXTINCTION

**E. Coombs** CRANIAL MORPHOLOGY IN WHALES: A STUDY SPANNING THE EVOLUTIONARY HISTORY AND DIVERSITY OF THE CETACEAN SKULL

**B.V. Dickson** THE ORIGIN AND EVOLUTION OF TERRESTRIAL LOCOMOTION: FUNCTIONAL ADAPTIVE LANDSCAPES OF THE TETRAPOD HUMERUS ACROSS THE WATER-LAND TRANSITION

**S.J. ElShafie** DO BODY SIZE CHANGES IN LOCAL REPTILE ASSEMBLAGES CORRESPOND TO LOCAL OR GLOBAL TEMPERATURES ON DEEP TIME SCALES?

**N. Fox** COMMUNITY ECOLOGY AND STABLE ISOTOPE ECOLOGY OF SMALL MAMMAL FOSSILS REFLECT REGIONAL CLIMATE CHANGE PATTERNS AT RANCHO LA BREA, LOS ANGELES, CALIFORNIA, U.S.A.

**C. Griffin** 'RECAPITULATION' OF ANCESTRAL STATES ACROSS THE EARLY ONTOGENY IN THE AVIAN PELVIS IS DRIVEN BY PERSISTENT MODULARITY IN THE ARCHOSAURIAN HINDLIMB

**J.K. Lungmus** EVOLUTIONARY RATE ANALYSIS REVEALS DYNAMIC AND VARIABLE PATTERNING OF FORELIMB EVOLUTION ACROSS THE DEEP HISTORY OF SYNAPSIDA

**Z.S. Morris** FOSSIL EVIDENCE INDICATES ANCIENT ORIGIN OF THE CROCODYLIAN CRANIAL DEVELOPMENTAL PROGRAM

**M. Qvarnström** FOOD WEB ANALYSIS OF EARLY MESOZOIC ECOSYSTEMS SHED NEW LIGHT ON EARLY DINOSAUR EVOLUTION

**T. Raven** UNTANGLING THE MODE AND TEMPO OF ARMORED DINOSAUR MACROEVOLUTION

**K. Sellers** JAW MUSCLES, JAW JOINTS, AND THE STEPWISE ACQUISITION OF HIGH BITE FORCE PERFORMANCE OF MODERN CROCODYLIA

**R. Takasaki** EVOLUTIONARY HISTORY OF ARCHOSAUR GASTROLITH USES

**M. Whitney** HISTOLOGICAL INSIGHTS INTO MAMMALIAN DENTAL EVOLUTION FROM THE DENTITIONS OF NON-MAMMALIAN SYNAPSIDA

**J. Wiemann** FOSSIL BIOMOLECULES REVEAL THE PHYSIOLOGY AND PALEOBIOLOGY OF EXTINCT AMNIOTES

**C.B. Withnell** A PALEOBIOGEOGRAPHIC HYPOTHESIS OF ARVICOLINE RODENT ORIGINATION AND DISPERSAL USING THE FIRST TIME-CALIBRATED PHYLOGENY FOR THE CLADE

**TUESDAY, OCTOBER 13, 2020, 1:00PM EDT-2:00PM EDT**  
**FISHES & CHONDRICHTHYANS: EVOLUTION AND DISTRIBUTION NETWORKING SESSION**

**POSTERS**

**O. Afanassieva, A. Bakaev, I. Kogan** ON THE HISTOLOGY OF TREMATASPIDIFORMES (AGNATHA) AND DISCORDICHTHYIFORMES (GNATHOSTOMATA), LOWER VERTEBRATES FROM THE PALEOZOIC OF RUSSIA

**J.G. Allen, K. Shimada** CASTING A FISHNET INTO THE LATE CRETACEOUS WESTERN INTERIOR SEAWAY—MARINE VERTEBRATES IN A UNIQUE BONEBED FROM THE NIOBRARA CHALK OF WESTERN KANSAS, U.S.A.

**E.L. Bernard, D.J. Ward, C.J. Underwood** THE OLDEST ASSOCIATED REMAINS OF THE CRETACEOUS SHARK *SCAPANORHYNCHUS*; A NEW ACQUISITION FROM THE LEBANON

**K. Claeson, S. Ngasala, M.D. Gottfried, E. Roberts, P.M. O'Connor, N.J. Stevens** A NEW ASSEMBLAGE OF LUNGFISHES (DIPNOI: LEPIDOSIRENIDAE) FROM THE LATE OLIGOCENE NSUNGWE FORMATION, RUKWA RIFT BASIN, SOUTHWESTERN TANZANIA

**J.A. Díaz-Cruz, S. Giles, H. Beckett, J. Alvarado-Ortega** A REDESCRIPTION OF *CIMOLICHTHYS LEWESIENSIS* LEIDY, 1857 (AULOPIFORMES: CIMOLICHTHYIDAE) BASED ON COMPUTED TOMOGRAPHY WITH COMMENTS ON ITS PHYLOGENETIC POSITION

**C.J. Duffin, D.J. Ward, B. Lauer, R. Lauer** THE HOLOCEPHALIAN FAUNAS OF THE LATE JURASSIC LITHOGRAPHIC LIMESTONES OF SW GERMANY

**D.J. Ehret, S. Ballwanz** THE CENOZOIC RECORD OF THE OTODONTID SHARKS (LAMNIFORMES, OTODONTIDAE) IN NEW JERSEY, U.S.A.

**M.D. Gottfried, A. Jerve, O. Bremer, E. Roberts, P. Dirks, S. Ostrowski** A MALVINOKAFFRIC HOLOCEPHALAN FROM THE EARLY DEVONIAN OF THE FALKLAND ISLANDS (ISLAS MALVINAS)

**N.R. Hartnett, N.E. Campione, P.R. Bell, T. Brougham, E.T. Smith** LUNGFISH TOOTH PLATES AS A TEST CASE FOR POST-DEVONIAN DIPNOAN PHYLOGENY: AN AUSTRALIAN EXAMPLE

**J.M. Hodnett, D.K. Elliott, R. Toomey, R. Olson, J. Wood, V. Santucci** THE LATE MISSISSIPPIAN (VISEAN) CHONDRICHTHYAN ASSEMBLAGE FROM THE JOPPA MEMBER OF THE STE. GENEVIEVE FORMATION AT MAMMOTH CAVE NATIONAL PARK, KENTUCKY

**J.C. Hoeflich, J.I. Bloch** SYSTEMATICS AND BIOGEOGRAPHY OF NEW FOSSIL WRASSES FROM THE LATE MIOCENE OF FLORIDA

**W. Itano** THE HOLOTYPE OF THE PALEOZOIC CHONDRICHTHYAN *PSEPHODUS MINUTUS* IS A GASTROPOD STEINKERN

**M.E. Jobbins, M. Rücklin, T. Argyriou, C. Klug** A LARGE MIDDLE DEVONIAN EUBRACHYTHORACID 'PLACODERM' (ARTHRODIRA) FROM NORTHERN GONDWANA

**D.R. Kirkpatrick, D.J. Cicimurri** PRELIMINARY ANALYSIS OF THREE LATE CRETACEOUS MARINE VERTEBRATE ASSEMBLAGES FROM THE PEEDEE FORMATION AT ALLISONS FERRY, CAINS LANDING, AND BURCHES FERRY, FLORENCE COUNTY, SOUTH CAROLINA

**J. Liston, A.E. Maltese** DUE NORTH: NORTHERN EXPOSURES OF PACHYCORMIDS EXTEND THE BIOGEOGRAPHICAL RANGE OF PACHYCORMIDS IN THE LOWER JURASSIC AND UPPER CRETACEOUS

**H. Maisch, M.A. Becker, K. Shimada** CHONDRICHTHYANS AND OSTEICHTHYANS FROM A TURONIAN–CONIACIAN LAG DEPOSIT BETWEEN THE TOCITO SANDSTONE AND MULATTO TONGUE (MANCOS SHALE), SANDOVAL COUNTY, NEW MEXICO, U.S.A. WITH COMMENTS ON CORRELATIVE LAGS IN THE WESTERN INTERIOR SEAWAY

**H.S. Miller, H.M. Avrahami, L.E. Zanno** DENTAL PATHOLOGY IN CHONDRICHTHYES REPRESENTS FIRST DOCUMENTATION OF GEMINATION OUTSIDE MAMMALIA

**A. Miller, R. Boessenecker** BABY MEGASHARK DO DO DO DO: AN OLIGOCENE *CARCHAROCLES ANGUSTIDENS* NURSERY FROM SOUTH CAROLINA

**R. Shell, C. Ciampaglio** COMPOSITION OF MARINE FISH COMMUNITIES DURING THE EARLY PERMIAN PERIOD IN CENTRAL NORTH AMERICA

**K. Shimada, R. Hacker** A NEW EDENTULOUS ICHTHYODECTIFORM FISH (OSTEICHTHYES: ACTINOPTERYGII) FROM THE UPPER CRETACEOUS OF TEXAS, U.S.A., AND ITS SYSTEMATIC POSITION

**D.J. Ward, C.J. Duffin, A. Ward** ARE SPIRAL BROMALITES ENTEROSPIRAE OR COPROLITES? A BRIEF REVIEW WITH SOME ADDITIONAL EVIDENCE

**M.B. Willson, B.L. Matzen** INITIAL DESCRIPTION AND IDENTIFICATION OF LARGEST KNOWN LONGNOSE GAR, *LEPISOSTEUS BEMISI* (HOLOSTEI:LEPISOSTEIFORMES), FROM THE EARLY EOCENE FOSSIL BUTTE MEMBER OF THE GREEN RIVER FORMATION, WYOMING, U.S.A.

**C.D. Wilson, C. Mansky, J. Anderson** NEW ACTINOPTERYGIANS FROM THE TOURNAISIAN OF BLUE BEACH, NOVA SCOTIA **COLBERT PRIZE ENTRY**

## TALKS

**J. Andrews, M. Friedman** THREE-DIMENSIONAL MORPHOMETRY OF OTOLITHS AS A TOOL FOR QUANTIFYING HABITAT AND LOCOMOTOR DIVERSITY IN MODERN AND FOSSIL TELEOSTS

**A. Capobianco, M. Friedman** A LONG-SNOUDED MARINE BONYTONGUE (TELEOSTEI: OSTEOGLOSSIDAE) FROM THE EARLY EOCENE OF MOROCCO: GLIMPSE INTO THE UNDERAPPRECIATED DIVERSITY OF AN EARLY PALEOGENE MARINE RADIATION OF PREDATORY FISHES

**A.M. Caron, V. Venkataraman, M.I. Coates** RAISING ENDOCRANIAL DATA: A NEW CARBONIFEROUS ACTINOPTERYGIAN AND REVISION OF *KANSASIELLA EATONI*

**M.I. Coates, L. Frey, K. Tietjen, M. Rücklin, C. Klug** A NEW SYMMORIIIFORM FROM THE LATE DEVONIAN OF MOROCCO: NOVEL JAW FUNCTION IN ANCIENT SHARKS

**X. Cui, Q. Qu, P. Andreev, M. Zhu, M. Friedman** NEW DATA ON *GUALEPIS ELEGANS* (CHONDRICHTHYES) FROM THE LOCHKOVIAN (LOWER DEVONIAN) OF QIJING, YUNNAN, SOUTHWESTERN CHINA

**S. El-Sayed, M. Friedman, T. Anan, M. Faris, H. Sallam** DIVERSE MARINE FISH ASSEMBLAGES INHABITED THE PALEOTROPICS DURING THE PALEOCENE-EOCENE THERMAL MAXIMUM

**R.T. Figueroa, M. Friedman** THE DEVONIAN LOST WORLD: THE FIRST ACTINOPTERYGIAN OCCURRENCE FROM THE MALVINOKAFFRIC REALM

**S. Henderson, S. Giles** MORPHOLOGICAL DIVERSITY IN AN ACTINOPTERYGIAN FISH FOLLOWING THE END-DEVONIAN MASS EXTINCTION

**J. Li, Z. Sun, C. Gilles, D. Jiang** A NEW CHONDRICHTHYAN FAUNA FROM THE ZHUGANPO MEMBER OF THE FALANG FORMATION AT NIMAIGU SECTION, GUIZHOU PROVINCE, SOUTH CHINA

**J. Liu** POTENTIAL UTILITY OF QUANTITATIVE BODY SHAPE ANALYSIS IN TAXONOMY OF EOCENE CYPRINIFORMS AND IMPLICATIONS FOR EVOLUTION

**A. López-Arbarello, E.E. Maxwell** REGIONALIZATION OF THE VERTEBRAL COLUMN IN RAY-FINNED FISHES

**T. Miyashita** A NEW LOOK AT FOSSIL HAGFISHES AND THE EVOLUTION OF DIVERGENT CYCLOSTOME CHARACTERS

**L. Schnetz, R.J. Butler, M.I. Coates, I.J. Sansom** SKELETAL AND SOFT TISSUE COMPLETENESS OF THE ACANTHODIAN FOSSIL RECORD THROUGH TIME

**J. Stack, M.D. Gottfried** A PERMIAN (ROADIAN) RAY-FINNED FISH (ACTINOPTERYGII) FROM THE MINNEKAHTA LIMESTONE OF SOUTH DAKOTA, U.S.A.

**T.A. Stewart, J.B. Lemberg, E.B. Daeschler, N.H. Shubin** THE PECTORAL FIN OF A NEW LATE DEVONIAN ELPISTOSTEGALIAN SPECIMEN FROM ELLESMERE ISLAND

**M.S. Torres Ladeira, L. Frey, M.I. Coates, M. Ginter, C. Klug** A NEW CLADOSELACHID CHONDRICHTHYAN FROM THE FAMENNIAN OF MOROCCO

**L. Wretman, J. Liston, B. Kear** FIRST RECORD OF AN EDENTULOUS SUSPENSION-FEEDING PACHYCORMIFORM FISH FROM THE LOWER CRETACEOUS OF AUSTRALIA

**TUESDAY, OCTOBER 13, 2020, 2:00PM EDT-2:30PM EDT  
PALEOZOIC TETRAPODS & LISSAMPHIBIANS NETWORKING SESSION**

**POSTERS**

**A.M. Báez, P. Muzzopappa** SIGNIFICANT NEW PIPIMORPH REMAINS (AMPHIBIA, ANURA) FROM THE CENOMANIAN CANDELEROS FORMATION OF NORTHWESTERN PATAGONIA, ARGENTINA

**J. Driebergen** A POSSIBLE TRANSITIONAL SPECIES TO A FROG YOU'VE NEVER HEARD OF: WHERE DID *RHINOPHRYNUS* GO FOR 30 MILLION YEARS?

**T. Ikeda, H. Ota** ON THE TAXONOMIC STATUS OF FRAGMENTARY FOSSIL ANURANS FOUND FROM THE LOWER CRETACEOUS OHYAMASHIMO FORMATION OF THE SASAYAMA GROUP, HYOGO, JAPAN

**TALKS**

**G.R. Adams, H.C. Maddin** AN UPDATED DESCRIPTION OF *CALLIGENETHLON WATSONI* BASED ON COMPUTED TOMOGRAPHY AND THE RESULTING IMPLICATIONS FOR THE TAXONOMY OF THE GENUS *CALLIGENETHLON*

**T. Arbez, A. Mann, J.B. Atkins, H.C. Maddin** NEW INSIGHTS ON THE TEMNOSPONDYL FAUNA FROM JOGGINS FOSSIL CLIFFS WITH DISCUSSION OF EARLY TEMNOSPONDYL RELATIONSHIPS

**B.M. Gee, J. Bevitt, R. Reisz** NEUROCRANIAL ONTOGENY IN EARLY PERMIAN DISSOROPHOIDS: SURPRISING OSSIFICATIONS AND SURPRISING IMMATUREITY

**J. Jia, J. Gardner, J. Anderson, J. Jiang, K. Gao** PATTERNS OF CAUDOSACRAL VERTEBRAE WITH REFERENCE TO THE EVOLUTION OF FERTILIZATION MODES IN SALAMANDERS (AMPHIBIA: CAUDATA)

**J.B. Lemberg, T.A. Stewart, E.B. Daeschler, N.H. Shubin** TOMOGRAPHY OF A TANTALIZINGLY TINY *TIKTAALIK*-LIKE TAXON

**D. Marjanović, M. Jansen** A COMPLETE, THREE-DIMENSIONAL EARLY PERMIAN AĪSTOPOD (TETRAPODOMORPHA) ILLUMINATES THE PHYLOGENY, ONTOGENY AND TERRESTRIALIZATION OF EARLY LIMBED AND LIMBLESS VERTEBRATES

**B. Otoo, J. Bolt, E. Lombard, M.I. Coates, K. Angielczyk** A NEW RECONSTRUCTION OF WHATCHEERIA AND THE ECOMORPHOLOGICAL DISPARITY OF EARLY TETRAPODS

**M.C. Vallejo-Pareja, J.I. Bloch, D.C. Blackburn** THE UNEXPECTED PRESENCE OF A CARIBBEAN FROG IN THE LATE OLIGOCENE OF FLORIDA

**TUESDAY, OCTOBER 13, 2020, 3:00PM EDT-4:00PM EDT**

**SYMPOSIUM: NEW GEOCHEMICAL AND DENTAL WEAR APPROACHES TO RECONSTRUCT THE DIET, ECOLOGY, AND PHYSIOLOGY OF FOSSIL VERTEBRATES**

### **POSTERS**

**T.E. Cerling, S. Bernasconi, L. Hofstetter, M. V. Jaggi, F. Wyss, C. Rudolf von Rohr, M. Clauss** CH<sub>4</sub>/CO<sub>2</sub> RATIOS AND ISOTOPE ENRICHMENT BETWEEN DIET AND BREATH IN MAMMALS

**M. Harrington, C. Widga** VERTEBRATE MOBILITY WITHIN STRONTIUM ISOSCAPES: A FRAMEWORK FOR ACCURATE, INFORMATIVE, AND VISUAL MAPPING

**F. Lugli, A. Nava, L. Bondioli, C. Dean, S. Benazzi, W. Müller** DETECTING THE INTRODUCTION OF NON-BREASTMILK FOOD IN INFANTS' DIET THROUGH HISTOLOGICALLY-DEFINED LA-(MC)-ICPMS ANALYSES OF DECIDUOUS DENTAL ENAMEL

**M.P. Mellett, B. Kligman, A.D. Marsh, W. Parker, S.J. Nesbitt, M.R. Stocker** DENTAL MICROWEAR ANALYSIS OF TWO NEW SPECIES OF TRILOPHOSAURID FROM THE CHINLE FORMATION (ARIZONA) REVEALS DIVERSITY OF HERBIVOROUS DIETS WITHIN THE CLADE

**M.A. Purnell, N. Adams, J. Bestwick** NICHE PARTITIONING AND SUBTLE DIETARY SHIFTS— TESTING THE SENSITIVITY OF MULTIVARIATE MICROWEAR TEXTURE ANALYSIS

**C. Tarnig, L. Hu, O. Mwebi, T.E. Cerling, D. Fernandez** MAGNESIUM STABLE ISOTOPE RATIOS OF EAST AFRICAN LARGE MAMMALS

**H. Vonhof, T. Tütken, J.N. Leichliter, T. Luedecke, G. Haug** HIGH-PRECISION STABLE ISOTOPE ANALYSIS OF STRUCTURAL CARBONATE IN < 100 MG TOOTH ENAMEL SAMPLES BY CONTINUOUS-FLOW MASS SPECTROMETRY.

**K. Weber, D.E. Winkler, M. Weber, J. Fröbisch, T.M. Kaiser, T. Tütken** PERMIAN TERRESTRIAL VERTEBRATE FOOD WEBS: A COMBINED DENTAL WEAR AND ISOTOPE APPROACH

### **TALKS**

**N. Bourgon, K. Jaouen, A. Bacon, E. Dufour, F. Demeter, L.L. Shackelford, V. Souksavatdy, J. Hublin, T. Tütken** ZN ISOTOPES AS A DIETARY AND TROPHIC PROXY IN FOSSIL TEETH: VARIABILITY IN LATE PLEISTOCENE SOUTHEAST ASIAN FOOD WEBS

- M. Brenning, F. Longstaffe, D. Fraser** DEVELOPING CARIBOU ANTLERS AS ECOLOGICAL INDICATORS USING STABLE ISOTOPE ANALYSIS
- M. Brown, K.T. Uno, G. Merceron, J. Boisserie** CARBON ISOTOPE ANALYSIS OF CERCOPITHECIDAE FROM THE SHUNGURA FORMATION, 3.3 MA–1.2 MA: DIET DURING THE TRANSITION BETWEEN DOMINANT SPECIES OF *THEROPITHECUS* IN THE TURKANA BASIN
- M. Clementz, L.N. Cooper, J. Thewissen** COMPOSITIONAL ANALYSIS OF MODERN AND FOSSIL BONE USING RAMAN SPECTROSCOPY (1064 NM)
- B. Crowley, S. Cooke** AN INITIAL INVESTIGATION OF NICHE PARTITIONING AMONG HISPANIOLA'S RECENT RODENT RADIATION USING STABLE ISOTOPES
- L. DeSantis, R. Feranec, J. Southon, W.J. Binder, J. Cohen, A. Farrell, E. Lindsey, J. Meachen, F.R. O'Keefe, G. Takeuchi** MORE TOOLS AND ISOTOPES ARE BETTER THAN ONE: CLARIFYING THE ECOLOGY OF ANCIENT MAMMALS AT RANCHO LA BREA AND BEYOND
- D.R. Green, T.M. Smith, M. Arora, C. Austin** TRACE METAL COMPOSITIONS IN FORMING TEETH REFLECT BOTH MINERALIZATION AND DIET
- S.W. Hixon, E.A. Smith, B. Crowley, G. Perry, L.M. Rakotozafy, J. Randrianasy, J.F. Ranaivoarisoa, K.G. Douglass, D. Kennett, S. Newsome** INSIGHT ON TROPHIC LEVEL ESTIMATION THROUGH AMINO ACID  $\Delta^{15}\text{N}$  VALUES FROM MADAGASCAN MEGAFUNA
- F.M. Holwerda, J. Bestwick, M.A. Purnell, A.S. Schulp** MASHERS, GNASHERS, OR UNDERWATER SLASHERS? MOSASAUR MICROWEAR AND GEOCHEMISTRY EXPLORED AMONGST TWO DIFFERENT MOSASAUR COMMUNITIES IN THE LATE CRETACEOUS OF THE NETHERLANDS AND CANADA
- M.I. Hullot** A MULTI-PROXY APPROACH TO RECONSTRUCT THE PALEOECOLOGY OF THE RHINOCEROTIDAE (MAMMALIA, PERISSODACTYLA) FROM THE EARLY MIOCENE BÉON 1 LOCALITY, MONTRÉAL-DU-GERS, SW FRANCE
- E. Jarochowska, B.O. Shirley, M. Grohgan, I. Leonhard, F.M. Holwerda** STRONTIUM CONTENT AND ISOTOPES REVEAL ECOLOGICAL NICHE COMPLEXITY IN NORTH AFRICAN CRETACEOUS DINOSAURS
- Y. Kimura, K.E. Yamada, I. Casanovas-Vilar, T. Cerling, A. Seki, N. Suzuki** BREATH AND TOOTH ENAMEL OF SMALL MAMMALS FROM FEEDING-CONTROLLED EXPERIMENTS FOR STABLE CARBON ISOTOPES
- J. Leichliter, T. Luedecke, N. Duprey, D.E. Winkler, M. Clauss, T. Tütken, A. Martínez-García** MEASURING NITROGEN ISOTOPES IN TOOTH ENAMEL: A NOVEL METHOD FOR CHARACTERIZING TROPHIC POSITION IN FOSSIL ECOSYSTEMS
- N. Löffler, J. Fiebig, A. Mulch, T. Tütken, B.C. Schmidt, A.C. Conrad, U. Wacker, A.S. Schulp, M.E. Böttcher** APPLYING REFINED CLUMPED AND OXYGEN ISOTOPE TEMPERATURE CALIBRATIONS TO TEETH FROM *T. REX* AND *C. MEGALODON*
- M. Louail, S. Ferchaud, A. Souron, A.E. Walker, G. Merceron** DISCRIMINATING DENTAL MICROWEAR TEXTURES OF DIFFERENT SEED EATERS: PERSPECTIVES FROM A CONTROLLED FEEDING STUDY WITH PIGS

**T. Luedecke, J.N. Leichliter, N. Duprey, D. Stratford, H. Vonhof, M. Bamford, G. Haug, A. Martínez-García** FIRST ENAMEL NITROGEN ISOTOPE DATA OF EARLY HOMININS: TROPHIC LEVEL RECONSTRUCTION OF *AUSTRALOPITHECUS* IN THE EARLY PLEISTOCENE (STERKFONTAIN MEMBER 4, SOUTH AFRICA)

**R.H. Madden, B.A. Buchholz, J.B. Lemberg, J.P. Parkes, R.E. Dunn** EXQUISITE COMPLEXITIES: RADIOCARBON BOMB-PULSE CHRONOMETRY OF ENAMEL MINERALIZATION AND TOOTH WEAR RATE VARIATION IN INSULAR OVICAPRINES FROM THE SOUTH PACIFIC

**G. Merceron, E. Berlioz, H. Vonhof, D.R. Green, M. Garel, N. Bourgon, T. Tütken** GROUND TRUTHING DENTAL ECOLOGICAL PROXIES ON A MODERN ALPINE COMMUNITY OF SYMPATRIC RUMINANTS

**S.M. Moran, B.J. MacFadden** AGGREGATION OF STABLE ISOTOPES WITHIN MUSEUM SPECIMEN DATA ELUCIDATES THE HYPERGRAZER NICHE IN PLEISTOCENE MAMMALS OF FLORIDA

**A.S. Schulp, T.J. Giltaij, F.M. Holwerda** DIET AND RESOURCE PARTITIONING IN MOSASAURS - THE NECESSITY OF A MULTI-PROXY APPROACH

**K.T. Uno, G. Merceron, M. Brown, F. Guy, L. Hlusko, J. Martin, V. Balter, A. Souron, J. Boisserie** COMBINING FOSSIL ENAMEL STABLE ISOTOPES AND DENTAL MICROWEAR TEXTURE ANALYSIS TO ASSESS DIETARY NICHE-PARTITIONING AMONG PRIMATES (CERCOPITHECIDAE AND HOMINIDAE) FROM THE LOWER OMO VALLEY, ETHIOPIA

**M. Weber, T. Tacail, F. Lugli, M. Clauss, T. Tütken** ASSESSING THE VARIABILITY OF CA AND SR ISOTOPES IN VERTEBRATE SOFT- AND HARD-TISSUES—IMPLICATIONS FOR RECONSTRUCTING DIET AND PROVENANCE

**D.E. Winkler, M. Clauss, E. Schulz-Kornas, T.M. Kaiser, D. Codron, J.N. Leichliter, K. Weber, M. Weber, T. Tütken** IMPROVING DIETARY RECONSTRUCTION USING DENTAL MICROWEAR TEXTURE ANALYSIS COMBINED WITH STABLE ISOTOPE ANALYSIS - FROM EXPERIMENTAL TO FOSSIL APPLICATION

**TUESDAY, OCTOBER 13, 2020, 4:00PM EDT-4:45PM EDT  
EVOLUTION AND BIOLOGY OF NON-AVIAN THEROPODS NETWORKING SESSION**

**POSTERS**

**K. Brink** DESCRIPTION OF NEW TOOTH PATHOLOGIES IN *TYRANNOSAURUS REX*

**C.D. Brownstein** REEVALUATION OF DINOSAUR MATERIAL FROM THE ATLANTIC COASTAL PLAIN ILLUMINATES A BIZARRE NEW ASSEMBLAGE

**R. Bykowski, J.O. Farlow** USING 2D GEOMETRIC MORPHOMETRICS AND LINEAR DISCRIMINANT ANALYSIS TO CLASSIFY DINOSAUR FOOTPRINTS FROM THE LOWER JURASSIC EAST BERLIN FORMATION, DINOSAUR STATE PARK, ROCKY HILL, CONNECTICUT

**T.D. Carr, J.C. Sedlmayr** JUVENILE TYRANNOSAURID FRONTAL FROM THE TWO MEDICINE FORMATION (CAMPANIAN, LATE CRETACEOUS) SHOWS ONTOGENETIC RECAPITULATION OF PHYLOGENETIC CHARACTER ACQUISITION

**T. Chinzorig, G. Philips, T.M. Cullen, J. Lamb, P.L. Larson, R. Rolke, L.E. Zanno** ORNITHOMIMOSAUR SPECIMENS FROM THE UPPER CRETACEOUS EUTAW FORMATION (SANTONIAN) OF MISSISSIPPI: NEW DATA ON APPALACHIAN THEROPOD DINOSAURS

**J.E. Diepenbrock** QUANTITATIVE HETERODONTY IN *ALLOSAURUS*: PALEOECOLOGICAL IMPLICATIONS OF SHED TEETH

**A.A. Farke, M. Letteau Stallings, W. Andrews** NEW VERTEBRATE LOCALITIES AND BIOSTRATIGRAPHIC INTERPRETATIONS OF THE MESAVERDE FORMATION (CAMPANIAN, LATE CRETACEOUS) IN NORTHWESTERN WYOMING

**A.R. Fiorillo, A. Chiarenza, R. Tykoski, P.J. McCarthy, P. Flaig** ON THE SIGNIFICANCE OF THE FIRST NON-DENTAL REMAINS OF A DROMAEOSAURIDAE (DINOSAURIA: THEROPODA) FROM ARCTIC ALASKA

**E. Isasmendi, A. Torices, J. Canudo, X. Pereda-Suberbiola** PALEOBIODIVERSITY OF THEROPOD DINOSAURS FROM THE UPPER CRETACEOUS LAÑO SITE, NORTHERN IBERIAN PENINSULA

**E.D. Johnson-Ransom, P. Gignac, G.M. Erickson, E. Snively** SIZE-EQUALIZED FINITE ELEMENT MODELS OF ADULT *TYRANNOSAURUS REX* CRANIA SUGGEST LOWER STRAIN LEVELS THAN JUVENILES IN ASSOCIATION WITH THE ONTOGENETIC SHIFT TO EXTREME OSTEOPHAGY **COLBERT PRIZE ENTRY**

**W. Kassab, M. AbdelGawad, G. Abu El-Kheir** THEROPOD AND BIRD TRACKS IN THE NUBIA SANDSTONE, EASTERN DESERT, EGYPT

**D. Maranga, R. Reisz, D. Evans** DETAILED MORPHOLOGY OF THE SKULL AND DENTITION IN A NEW, EXCEPTIONALLY PRESERVED SPECIMEN OF *MICRORAPTOR* (THEROPODA: DROMAEOSAURIDAE) FROM THE EARLY CRETACEOUS OF CHINA

**E. Snively, N. Longrich, D.E. Barta, H. Woodward, D.M. Cooper, M.M. Burns, L. Surring, P.J. Currie** GROWTH AND REMODELING IN AN ONTOGENETIC SERIES OF *GORGOSAURUS LIBRATUS* (DINOSAUR PROVINCIAL PARK, ALBERTA) METATARSALS REVEALED THROUGH 3D VASCULAR HISTOLOGY

**R.S. Sombathy, M. D'Emic** BONE HISTOLOGY REVEALS EXTREME GROWTH VARIATION IN THE THEROPOD DINOSAUR *ALLOSAURUS* ACROSS ITS GEOGRAPHIC RANGE **COLBERT PRIZE ENTRY**

**C. Sullivan, P.R. Bell, N.E. Campione, R. Sissons, F. Fanti, D.W. Larson, M.J. Vavrek, G.F. Funston** CAENAGNATHID (THEROPODA: OVIRAPTOROSAURIA) DINOSAUR SPECIMENS FROM THE UPPER CRETACEOUS WAPITI FORMATION OF NORTHERN ALBERTA

**H.E. Rivera-Sylva, R. Guzmán-Gutierrez, R. Zapata-Jaime, J. García-de la Garza, R. Guajardo-Guajardo, H. Porras-Múzquiz, M. Galicia-Chávez** NEW DINOSAUR LOCALITIES FROM THE OLMOS FORMATION (CAMPANIAN–MAASTRICHTAN) IN NORTHERN COAHUILA

**K. Tanaka, O.U. Anvarov, A. Ahmedshaev, Y. Kobayashi** A LARGE NEOVENATORID (DINOSAURIA: THEROPODA) FROM THE UPPER CRETACEOUS BISSEKTY FORMATION (TURONIAN), UZBEKISTAN

**J.P. Wilson, W.J. Freimuth** NEW MANUAL UNGUALS OF THE ALVAREZSAURID THEROPOD DINOSAUR FROM THE HELL CREEK FORMATION, MONTANA, AND THE ONTOGENETIC DEVELOPMENT OF THE FUNCTIONAL ALVAREZSAURID HAND CLAW

## **TALKS**

**T.M. Cullen, D.W. Larson, L.E. Zanno, P.J. Currie, D. Evans** THEROPOD BIODIVERSITY PATTERNS IN THE DINOSAUR PARK FORMATION (LATE CRETACEOUS: CAMPANIAN) OF ALBERTA REVEALED THROUGH MORPHOMETRICS AND BIOSTRATIGRAPHY

**A.J. Fitch, D.M. Lovelace, M.R. Stocker** THE OLDEST DINOSAUR FROM THE NORTHERN HEMISPHERE AND THE ORIGINS OF THEROPODA

**G.F. Funston, M.J. Powers, S.A. Whitebone, S. Brusatte, J. Scannella, J.R. Horner, P.J. Currie** BABY TYRANNOSAUR BONES FROM THE LATE CRETACEOUS OF WESTERN NORTH AMERICA

**J. Hedge, P.J. Makovicky, R. Cifelli, L.E. Zanno** NEW DATA ON THE OOASSEMBLAGE OF THE CENOMANIAN-AGE MUSSENTUCHIT MEMBER, CEDAR MOUNTAIN FORMATION, UTAH

**T.R. Holtz** TAXONOMIC DIVERSITY, GUILD STRUCTURE, AND ONTOGENETIC NICHE SHIFTS IN THEROPOD CARNIVORE COMMUNITIES: IMPLICATIONS FOR PALEOECOLOGY AND LIFE HISTORY STRATEGIES IN TYRANT DINOSAURS

**E.M. Jevnikar, L.E. Zanno, T.A. Gates** DECOUPLED RATES OF BODY SIZE EVOLUTION AND DENTAL MORPHOLOGY IN THEROPOD DINOSAURS

**J.P. Nassif, R.C. Ridgely, L. Witmer** RECONSTRUCTING THE MIDDLE-EAR SOUND-CONDUCTION APPARATUS IN COELUROSAURIA IN THE TRANSITION TO BIRDS

**T.R. Pascucci, M. D'Emic, A.H. Turner** OSTEOHISTOLOGY OF THE EARLY CRETACEOUS THEROPOD *DEINONYCHUS ANTIRRHOPUS*

**Z. Qin, Q. Zhao, J.N. Choiniere, M.J. Benton, X. Xu** COMPARATIVE OSTEOHISTOLOGY OF ALVAREZSAURS INFORMS HYPOTHESES FOR THEIR BODY SIZE EVOLUTION

**K.M. Schroeder, S.K. Lyons, F.A. Smith** MIND THE GAP: THE IMPACT OF JUVENILE MEGATHEROPODS ON DINOSAUR BODY SIZE DISTRIBUTIONS AND GLOBAL DIVERSITY

**J.T. Voris, D.K. Zelenitsky, F. Therrien** ONTOGENETIC VARIATION BETWEEN *GORGOSAURUS LIBRATUS* AND *DASPLETOSAURUS TOROSUS* (THEROPODA: TYRANNOSAURIDAE) AND TAXONOMIC IDENTIFICATION OF JUVENILE TYRANNOSAURIDS

**TUESDAY, OCTOBER 13, 2020, 7:00PM EDT-7:45PM EDT**  
**MAMMALIAN SKELETAL MORPHOLOGY & MARINE MAMMALS NETWORKING SESSION**

### **MAMMALIAN SKELETAL MORPHOLOGY**

#### **POSTERS**

**E.A. Buchholtz, C. Siege** STERNAL STRUCTURE PREDICTS FEEDING STYLE IN MYSTICETE CETACEANS

**R.A. Edie, A.E. Kort, P. D. Polly** SHAPE GRADIENT ACROSS THE LUMBAR VERTEBRAE REFLECTS LOCOMOTOR STYLE IN MAMMALS

**A. Grass** FOSSIL SLOTH CLAW CURVATURE AND BONY CORE TO SHEATH RATIOS PREDISPOSED A SUSPENSORY LIFESTYLE

**T. Htun, D.R. Prothero, J. Hoffman, S. Lukowski** HOW DID MASTODONS GROW? ONTOGENETIC LONG BONE GROWTH IN THE AMERICAN MASTODONS

**S. Kubica, M.S. Springer** ANCESTRAL STATE RECONSTRUCTION OF MAMMALIAN VERTEBRAL COUNTS

**T.E. Lancaster** MORPHOLOGICAL GROUPING AND BODY MASS PREDICTION MODELS

**A. McGrath, A. Wyss** PHYLOGENETIC AND ECOMORPHOLOGICAL SIGNAL IN NOTOUNGULATE AND LITOPTERN (MAMMALIA) TARSALS FROM THE EARLY MIOCENE SANTA CRUZ FORMATION (ARGENTINA)

**F. Mizuno** THE HIP BONE TELLS US MAMMALIAN HINDLIMB POSTURE WHILE SUPPORTING BODY MASS

**S.K. Pevsner, D. Grossnickle, Z. Luo** EVOLUTIONARY DIVERSIFICATION OF MARSUPIAL LIMBS IS MORE STRONGLY INFLUENCED BY FUNCTIONAL LOCOMOTOR MODES THAN BY DEVELOPMENTAL CONSTRAINTS

**R. Russell, C. Jacquemetton, B. Hupka, A. Drexler, K. Ralls, B. van Valkenburgh** CAN TOOL USAGE IMPACT MORPHOLOGY? AN INTERSPECIFIC ANALYSIS OF OTTERS

**N. Solounias, L.R. Yohe** FIVE IN TWO: PENTADACTYLLY IN GIRAFFIDAE

**A.M. Tantash, J. Caledo** THE COEVOLUTION (OR LACK THEREOF) OF BODY MASS AND LOCOMOTION IN RODENTS

### TALKS

**P. Bishop, A. Falisse, F. De Grootte, J. Hutchinson** DYNAMIC OPTIMIZATION AND SIMULATION OF JUMPING BIOMECHANICS AND PERFORMANCE IN EXTANT AND EXTINCT TERRESTRIAL VERTEBRATES

**Z.T. Calamari, A.J. Ragni** MORPHOLOGICAL CORRELATES OF KNUCKLE-WALKING: ASSESSING CARPAL CONVERGENCE TO UNDERSTAND THE ORIGINS OF HUMAN BIPEDALISM

**D. Grossnickle, M. Chen, J. Wauer, S.K. Pevsner, L.N. Weaver, Q. Meng, D. Liu, Y. Zhang, Z. Luo** SKELETAL ADAPTATIONS IN EXTANT AND FOSSIL GLIDING MAMMALS EXEMPLIFY MANY-TO-ONE MAPPING OF FORM TO FUNCTION, NOT CONVERGENCE

**A. Houssaye, F. Martin, C. Etienne, J. Boisserie, F. Lihoreau** THE ECOLOGY OF FOSSIL HIPPOPOTAMOIDS (MAMMALIA, CETARTIODACTYLA) EXAMINED IN THE LIGHT OF THE MICROANATOMY OF THEIR LONG BONES

**B. Kilbourne** FUNCTIONAL ANATOMY OF THE MUSTELID HINDLIMB SKELETON AND THE POTENTIAL INFLUENCE OF CLIMBING AND SWIMMING LOCOMOTOR HABITS ON MORPHOLOGICAL DIVERSIFICATION

**W.N. McLaughlin, N. Weldon, E.B. Davis** STATISTICAL CLUSTERING ANALYSIS OF MAMMALIAN POSTCRANIAL MORPHOLOGY REVEALS POSSIBLE SEXUAL DIMORPHISM RATHER THAN SPECIES-LEVEL DIVERSITY IN THE PALAEOERYCIDAE

**K. Tate-Jones** THE EVOLUTION OF LOCOMOTOR ECOLOGY IN BASAL ODOBENIDS (MAMMALIA, CARNIVORA)

### MARINE MAMMALS

### POSTERS

**M. AbdelGawad, S. Hassan, I. Abd El-Gaied, Y. Salama, G. AbdelGawad** A NEW DISCOVERY OF SIRENIA FROM THE LATE EOCENE IN BENI SUEF DISTRICT, NORTH EASTERN DESERT, EGYPT

**L. Dewaele, C. de Muizon, S. Everaert** CLEANING UP THE RECORD OF FOSSIL SEALS (MAMMALIA, PHOCIDAE) FROM THE NORTH SEA BASIN: TAXONOMY AND TIMING

**S.J. Godfrey, J. Nance, N. Riker** *CARCHAROCLES*-BITTEN SPERM WHALE TOOTH FROM THE COASTAL EASTERN UNITED STATES

**A. Gohar, M.S. Antar, R. Boessenecker, S. El-Sayed, H. Sallam** A NEW PROTOCETID WHALE (CETACEA, ARCHAEOCETI) FROM THE MIDDLE EOCENE OF THE FAYUM DEPRESSION IN EGYPT SHEDS NEW LIGHT ON RAPTORIAL FEEDING ECOLOGY IN ANCIENT WHALES

**S. Grantham, R. Boessenecker** LONGIROSTRINE NEARLY HOMODONT DOLPHIN FROM THE LATE OLIGOCENE OF SOUTH CAROLINA: THE ORIGIN OF EURHINODELPHINIDAE AND AFFINITIES OF '*PHOCA*' *MODESTA* AND '*PHOCA*' *DEBILIS*

**Z. Guo, N. Kohno** NEW KENTRIODONTIDS (CETACEA, ODONTOCETI) FROM THE MIDDLE MIOCENE OF THE WESTERN NORTH PACIFIC AND A REVISION OF KENTRIODONTID PHYLOGENY

**A. Kawatani, N. Kohno** RECOGNITION OF THE DEEP-DIVING CETACEAN FAUNA FROM THE MIDDLE MIOCENE OF THE WESTERN NORTH PACIFIC

**A. Lanzetti, J. Gatesy, R. Meredith, M. Springer, M.R. McGowen** EVOLUTION OF DENTITION IN THE PHYLOGENY OF BEAKED WHALES (ZIPHIIDAE, ODONTOCETI): THE CASE OF THE TASMAN'S BEAKED WHALE

**S. McLeod, J. Hook** A FOSSIL RIGHT WHALE FROM THE LATE MIOCENE MARINE DIATOMITES NEAR LOMPOC, SANTA BARBARA COUNTY, CALIFORNIA, U.S.A.

**M.D. Nelson, M.D. Uhen** TAXONOMIC REVISION OF THE PACIFIC RECORD OF THE SQUALODONTIDAE (CETACEA, ODONTOCETI)

## **TALKS**

**R. Boessenecker, J. Geisler** REAPPRAISAL OF THE ENIGMATIC EARLY ODONTOCETE *XENOROPHUS SLOANII*: FUNCTIONAL MORPHOLOGY, ONTOGENY, AND VARIATION REVEALED BY NEW FOSSILS FROM THE OLIGOCENE ASHLEY FORMATION OF SOUTH CAROLINA

**C.M. Peredo, N. Pyenson** PALATAL FORAMINA IN STEM WHALES AND TERRESTRIAL ARTIODACTYLS OBFUSCATE THEIR POTENTIAL FOR INFERRING BALEEN IN STEM MYSTICETES

**M.D. Uhen** FIRST CONFIRMED BASILOSAURID ARCHAEOCETES FROM THE NORTH PACIFIC

**WEDNESDAY, OCTOBER 14, 2020, 11:30AM EDT-12:15PM EDT  
PERMO-TRIASSIC TETRAPODS NETWORKING SESSION**

## **POSTERS**

**B.H. Breithaupt, N.A. Matthews, P.A. Gensler, C.R. Dunn, S.G. Lucas** PHOTOGRAMMETRIC ICHNOLOGY OF A PERMIAN ICHNOLAGERSTÄTTE: PREHISTORIC TRACKWAYS NATIONAL MONUMENT, NEW MEXICO

**D. Foffa, P.M. Barrett, R.J. Butler, S.J. Nesbitt, S. Walsh, S. Brusatte, N. Fraser** NEW INFORMATION ON THE LATE TRIASSIC REPTILE *SCLEROMOCHLUS TAYLORI* FROM  $\mu$ CT DATA

**G. Goncalves, C.A. Sidor** CLAW & ORDER: SPECIAL VICTIMS UNIT – UNDERSTANDING DREPANOSAURIFORM DIVERSITY WITHIN THE SONSELA MEMBER OF THE CHINLE FORMATION AT PETRIFIED FOREST NATIONAL PARK

**E. Keeble, W. Parker, S.J. Nesbitt, M.R. Stocker, J.R. Hutchinson** INSIGHT INTO THE OSTEOLOGY OF AN EARLY AETOSAURIAN ARCHOSAUR FROM MICRO-CT SCANNING

**A.D. Marsh, W. Parker, C.V. Beightol, C.A. Sidor** APOMORPHY-BASED IDENTIFICATION OF RECENTLY COLLECTED DINOSAUROMORPH FOSSILS FROM PETRIFIED FOREST NATIONAL PARK (UPPER TRIASSIC, CHINLE FORMATION)

**D. Oberg, C. Suarez, J.N. Choiniere** COMMUNITY RESPONSE TO THE END TRIASSIC MASS EXTINCTION IN THE ELLIOT FORMATION OF SOUTH AFRICA AND LESOTHO

**E. Patellos, B. Kligman, A.D. Marsh, M.R. Stocker, W. Parker, S.J. Nesbitt** CHARACTERIZATION OF DENTAL VARIATION IN A SMALL AZENDOHAURID FROM THE CHINLE FORMATION (UPPER TRIASSIC) OF ARIZONA INDICATES THE ABUNDANCE OF AZENDOHAURIDS IN ADAMANIAN BIOZONE ASSEMBLAGES

**R.C. Price** NEW SPECIMENS OF THE ARCHOSAURIFORM *VANCLEVEA CAMPI* FROM THE UPPER TRIASSIC (RHETIAN) REDONDA FORMATION OF EASTERN NEW MEXICO INDICATES *VANCLEVEA CAMPI* WAS AN APEX PREDATOR

**W.A. Reyes, W. Parker, A.D. Marsh** CRANIAL ANALYSIS OF AETOSAURIA BASED ON THE CRANIAL ANATOMY AND DENTITION OF *TYPOTHORAX COCCINARUM* (ARCHOSAURIA: PSEUDOSUCHIA) FROM THE UPPER TRIASSIC CHINLE FORMATION OF NORTHERN ARIZONA

**B.J. Small, A. Huttenlocker, A.C. Henrici, R. Douglass, S. Voigt, D. Rasmussen** FIRST OCCURRENCE OF THE PALEOZOIC VERTEBRATE ICHNOTAXON *ICHNIOTHERIUM COTTAE* FROM THE TYPE SECTION OF THE CUTLER FORMATION: EVIDENCE FOR UPLAND HABITAT PREFERENCE BY DIADECTIDS (REPTILIOMORPHA)

**M.P. Sodano, B. Kligman, M.R. Stocker, A.D. Marsh, W. Parker, A.C. Pritchard, S.J. Nesbitt** UNIQUE INTERNAL AND EXTERNAL MORPHOLOGIES OF MANUAL UNGUALS OF DREPANOSAURIFORMS HELP IDENTIFY ISOLATED SKELETAL ELEMENTS AND GEOGRAPHIC DISTRIBUTION OF THE CLADE IN THE WESTERN UNITED STATES DURING THE LATE TRIASSIC AND BEYOND **COLBERT PRIZE ENTRY**

**M. Wright, T. Cavanaugh, S.E. Pierce** ESTIMATING BODY MASS IN NON-MAMMALIAN SYNAPSIDS: A TALE OF TWO METHODS

**E. Ziesemer** SIZE DOES NOT CORRELATE WITH MATURITY IN A SAMPLE OF ADULT SPECIMENS OF THE PHYTOSAUR *RUTIODON CAROLINENSIS*

## **TALKS**

**D.E. Barta** PHYTOSAURS (REPTILIA: ARCHOSAURIFORMES) FROM THE UPPER TRIASSIC STRATA OF THE DRY CIMARRON VALLEY, WESTERN OKLAHOMA AND NORTHEASTERN NEW MEXICO, U.S.A.

**B.B. Britt, A. Jackson, A.M. Horn, B.C. Theurer, D. Chure, G.F. Engelmann, R.D. Schetz** DREPANOSAURS: WEIRD TO THE BONE

**J.N. Choiniere, R.B. Benson, J. Botha, P.M. Barrett, E. Bordy, K. Chapelle, K. Dollman, C. Suarez, P.A. Viglietti, L. Sciscio, R. J. Butler** TAXONOMICALLY RICH LATE TRIASSIC FAUNAS FROM SOUTH AFRICA'S LOWERMOST ELLIOT FORMATION

**A. Duhamel, J. Benoit, B.S. Rubidge, M.O. Day** RECOGNISING JUVENILES: AN ONTOGENETIC STUDY OF THE ENIGMATIC BIARMOSUCHIA (SYNAPSIDA: THERAPSIDA) USING CT SCANNING.

**D.K. Hoffman, J. Hancox, S.J. Nesbitt** A DIVERSE EARLY TRIASSIC ARCHOSAUFOMORPH TOOTH ASSEMBLAGE FROM THE BURGERSDORP FORMATION OF SOUTH AFRICA

**A. Huttenlocker, C.A. Sidor** A BASAL NONMAMMALIAFORM CYNODONT FROM THE LATE PERMIAN OF ZAMBIA: NEW EVIDENCE FOR THE ORIGIN OF MAMMAL-LIKE CRANIAL-POSTCRANIAL NEUROMECHANICAL COORDINATION

**K.M. Jenkins, P.J. Lewis, J.N. Choiniere, B.S. Bhullar** THE PHYLOGENETIC PLACEMENT OF AN ENIGMATIC REPTILE FROM THE EARLY TRIASSIC TRANSANTARCTIC MOUNTAINS

**C.F. Kammerer, K. Angielczyk, B.R. Peacock, C.A. Sidor, R.M. Smith, S. Tolan, P.A. Viglietti** NEW LATE PERMIAN DICYNODONTOIDS (SYNAPSIDA: ANOMODONTIA) FROM THE UPPER MADUMABISA MUDSTONE FORMATION (LUANGWA BASIN, ZAMBIA)

**D.E. Korneisel, J.B. Atkins, H.C. Maddin** FATE MAPPING THE SKULL-NECK BOUNDARY OF MODERN AMPHIBIANS AND IMPLICATIONS FOR NECK DEVELOPMENT IN EARLY TETRAPOD EVOLUTION

**Z.T. Kulik, C.A. Sidor** BODY SIZE AND PALEOLATITUDE IN *LYSTROSAURUS*: DID BERGMANN'S RULE APPLY DURING THE EARLY TRIASSIC?

**L.M. Marilao, Z.T. Kulik, C.A. Sidor** NEOMORPHIC OSSIFICATIONS: HISTOLOGICAL INSIGHT INTO THE PREPARIETAL OF DICYNODONT THERAPSID

**B.R. Peacock, K. Angielczyk, C.F. Kammerer, J.K. Lungmus, J. McIntosh, C.A. Sidor, R.M. Smith, S. Tolan, P.A. Viglietti, M. Whitney** A NEW STRATIGRAPHIC FRAMEWORK FOR THE PERMO-TRIASSIC STRATA OF THE MID-LUANGWA BASIN, ZAMBIA: UPPER PERMIAN TURNOVER AND MIDDLE-UPPER TRIASSIC VERTEBRATE ASSEMBLAGES

**A.C. Pritchard, H. Sues, R. Reisz, D. Scott** OSTEOLOGY AND PHYLOGENETIC AFFINITIES OF THE EARLY GLIDING REPTILE *WEIGELTISAURUS JAEKELI*

**T.M. Scheyer, F. Miedema, W. Wang, C. Li, S. Spiekman, V. Fernandez, J.J. Reumer** STANDARD OSTEOLOGICAL AND VIRTUAL 3D ANATOMICAL RE-INVESTIGATION OF *MACROCNEMUS* (TANYSTROPHEIDAE, ARCHOSAUFOMORPHA), A RARE MIDDLE TRIASSIC TERRESTRIAL REPTILE WITH A TETHYS-WIDE DISTRIBUTION

**C.A. Sidor, B.M. Gee, Z.T. Kulik, P.J. Makovicky, J. McIntosh, N.D. Smith, R.M. Smith, N.J. Tabor, M. Whitney** THE FIRST VERTEBRATE ASSEMBLAGE FROM THE MIDDLE FREMOUW FORMATION (TRIASSIC) OF ANTARCTICA.

**R.M. Smith** NEONATE AGGREGATION IN THE PERMIAN THERAPSID *DICTODON*: EVIDENCE FOR A REPRODUCTIVE FUNCTION FOR BURROWS?

**N.D. Smith, P.J. Makovicky, C.A. Sidor, W.R. Hammer** A KANNEMEYERIFORM (SYNAPSIDA: DICYNODONTIA) OCCIPITAL PLATE FROM THE MIDDLE TRIASSIC UPPER FREMOUW FORMATION OF ANTARCTICA

**S. Spiekman** REMARKABLE NICHE PARTITIONING IN THE EXTRAORDINARILY LONG-NECKED TRIASSIC ARCHOSAUFOMORPH *TANYSTROPHEUS*

**B.C. Theurer, B.B. Britt, D. Chure, G.F. Engelmann, R.D. Scheetz, A. Jackson** SEGMENTED MICRO-CT SCANS OF 3D, ARTICULATED DREPANOSAURID FORELIMBS FROM THE SAINTS AND SINNERS (SS) QUARRY (UPPER TRIASSIC, NUGGET SANDSTONE, NORTHEASTERN UTAH) PROVIDE INFORMATION ON THE UNUSUALLY CONSTRUCTED ARM AND HAND

**P.A. Viglietti, R.B. Benson, R.M. Smith, J. Botha, C.F. Kammerer, Z. Skosan, N. Mtalana, S. Mtungata, P.**

**October, D. Wolvaardt, M. Strong, G. Skinner, K. Angielczyk** A MULTI-INDEX CHARACTERIZATION OF FAUNAL DYNAMICS REVEALS THE NATURE OF SOUTH AFRICA'S LATEST PERMIAN MASS EXTINCTION

**WEDNESDAY, OCTOBER 14, 2020, 12:15PM EDT-12:45PM EDT  
BIRD BIOLOGY AND EVOLUTION NETWORKING SESSION**

## **POSTERS**

**D. Camarena, P. Houde** TAXONOMIC AND ECOLOGICAL ASSOCIATIONS OF THE AVIFAUNA WITHIN THE 8ABC SITE FROM THE EARLY EOCENE CLARKS FORK BASIN, WILLWOOD FORMATION, WYOMING

**S. Choi, M. Hauber, N. Kim, D. Varricchio, Y. Lee** MICROSTRUCTURAL AND CRYSTALLOGRAPHIC EVOLUTION OF PALEOGNATH (AVES) EGGSHELLS

**J.J. El Adli, J.A. Wilson Mantilla, M.S. Antar, P.D. Gingerich** THE OLDEST FOSSIL PELICAN, FROM THE EOCENE OF WADI AL HITAN, EGYPT

**A.L. Hendrix, D.K. Zelenitsky, F. Therrien** A COLLECTION OF *METOOLITHUS NEBRASKENSIS* FRAGMENTS FROM THE CHADRON AND BRULE FORMATIONS OF NORTHWESTERN NEBRASKA

**I. Jordan, B. Drabsch, A. Howells** FROM BONES TO FEATHERS: RECONSTRUCTING THE EXTINCT PLEISTOCENE COUCAL '*CENTROPUS MAXIMUS*'

**T.W. LaBarge, C.L. Organ** A BAYESIAN REANALYSIS OF PHORUSRHACIDAE AND THE EVOLUTION OF GIGANTISM

**C.V. Miller, M. Pittman, T.G. Kaye, X. Wang, X. Zheng** PRESERVED DISASSOCIATED RHAMPHOTHECA OF THE CRETACEOUS EARLY BIRD *CONFUCIUSORNIS* AND ITS IMPLICATIONS FOR RECONSTRUCTION AND EVOLUTIONARY DEVELOPMENT OF AVIALAN BEAKS

## **TALKS**

**J. Benito, J. Jagt, D.J. Field** REINVESTIGATING THE 'MAASTRICHT ICHTHYORNITHINE' FROM THE LATEST CRETACEOUS OF BELGIUM

**A. Chen, R.B. Benson, D.J. Field** PHYLOGENETIC UTILITY OF THE AVIAN PECTORAL GIRDLE AND FORELIMB SKELETON

**D.J. Field, J. Benito, A. Chen, J. Jagt, D. Ksepka** LATE CRETACEOUS NEORNITHINE FROM EUROPE ILLUMINATES CROWN BIRD ORIGINS

**M. Pittman, T.G. Kaye, W.R. Wahl** NON-SEQUENTIAL FLIGHT-PERFORMANCE-RELATED WING MOLTING AROSE EARLY IN AVIALAN EVOLUTION

**T. Stidham, R. Patnaik** PHYLOGENETIC AFFINITIES OF NEW LATE PLIOCENE WATERBIRDS (AVES: AEQUORNITHES) FROM THE SIWALIK HILLS OF INDIA SUPPORT A PLEISTOCENE SHIFT FROM AFRICAN TO ASIAN BIOGEOGRAPHIC AFFINITIES

**Y. Wu, L.M. Chiappe, D.J. Bottjer, A. Bailleul** TOOTH CYCLING AND REPLACEMENT PATTERNS OF CRETACEOUS ORNITHUROMORPH BIRDS

**WEDNESDAY, OCTOBER 14, 2020, 1:30PM EDT-2:15PM EDT  
PREPARATORS NETWORKING SESSION**

**POSTERS**

**A. Behlke** WHEN *GLYPTOTHERIUM* FLIES: RELOCATION OF A MOUNTED SPECIMEN TO A NEW BASE

**S. Boessenecker** SKELETONS IN THE CLOSET: A CURATORIAL CASE STUDY OF THE MACE BROWN MUSEUM OF NATURAL HISTORY, AND OTHER UNIVERSITY NATURAL HISTORY MUSEUMS

**J. Cavigelli, T. Kerr, M. Connely, L.A. Vietti, H. Hoff, C. Hutchen** A TEST OF THE STATE OF THE ART IN 3D COLOR PRINTING

**M. Ferrer Ventura, A. Torices, X. Mas-Barberà, R. San Juan Palacios, P. Navarro-Lorbés** THE USE OF THE TEAS TRIANGLE TO REMOVE AGED MATERIALS APPLIED TO FOSSILS: AGED HYDROGENATED POLYMER (BLUE-TACK®) ON *HYSILOPHODON FOXII* IN IGEA (LA RIOJA, SPAIN)

**R. Lauer, B. Lauer, D.J. Ward, A. Ward, C.J. Duffin** ULTRAVIOLET INDUCED FLUORESCENCE DIGITAL PHOTOGRAPHY AS A DIAGNOSTIC TOOL FOR DISCOVERY, DIGITAL DOCUMENTATION, ANALYSIS AND CURATION OF PALEONTOLOGICAL SPECIMENS

**C. Redman, R. Landstra** REMOVING PAINT FROM A MASTODON THAT WAS ON EXHIBIT FOR 90 YEARS

**C. Sailer, A.B. Heckert** RESTORING OUTREACH, DISPLAY, AND RESEARCH VALUE TO A SPECIMEN OF *TRICERATOPS* FROM THE UPPERMOST CRETACEOUS HELL CREEK FORMATION OF NORTH DAKOTA THROUGH INSTRUCTION IN PREPARATION AND CONSERVATION

**TALKS**

**C. France, R.A. Kaczowski, G.M. Kavich, J.A. Giaccai** EFFECTS OF CONSOLIDANTS (PVAC, PARALOID, BUTVAR, CELLULOSE NITRATE, CYCLODODECANE) ON BONE COLLAGEN AND BIOAPATITE COMPOSITION – CONSIDERATIONS FOR FUTURE CHEMICAL ANALYSES

**J.R. Groenke, D.W. Krause, S. Hoffmann** PREPARATION AND RECONSTRUCTION OF THE TEETH OF *ADALATHERIUM HUI*, A GONDWANATHERIAN MAMMAL FROM THE UPPER CRETACEOUS MAEVARANO FORMATION OF MADAGASCAR

**A.C. Henrici, J. Stokes** RECENT EFFORTS TO DIGITIZE IMAGES IN THE SECTION OF VERTEBRATE PALEONTOLOGY CARNEGIE MUSEUM OF NATURAL HISTORY USING THE VAUGHN PROJECT AS AN EXAMPLE

**J. Hook, S. McLeod** CURATION OF THE MEHRTEN FORMATION

**A. Millhouse, H. Little** IF A SPECIMEN IS ON EXHIBIT DOES IT REALLY EXIST?

**M.E. Smith, B. Kligman, V. Yarborough, A.D. Marsh** SCREENWASHING, MICROPREPARATION, AND MICRO CT: A CASE STUDY OF HOW PREPARATION WORKFLOW FACILITATES RESEARCH ON MICROFOSSIL LOCALITIES AT PETRIFIED FOREST NATIONAL PARK

**WEDNESDAY, OCTOBER 14, 2020, 2:15PM EDT-3:15PM EDT**  
**LATE CENOZOIC MAMMALIAN MACROECOLOGY AND MACROEVOLUTION**  
**NETWORKING SESSION**

**POSTERS**

**M. Bushell, S. Wallace, S. Haugrud** UPDATED POPULATION STRUCTURE OF *TAPIRUS POLKENSIS* AT THE EARLIEST PLIOCENE GRAY FOSSIL SITE, TENNESSEE, BASED ON NEW MNI CALCULATIONS

**A. Claxton, J. Calede** A NEW SPECIES OF *GREGORYMYS* FROM THE ARIKAREEAN OF SOUTH DAKOTA AND THE PHYLOGENETICS OF ENTOPTYCHINAE (MAMMALIA, RODENTIA, GEOMYIDAE)

**S.R. Davison, S.S. Hopkins** A NEW HEMINGFORDIAN LOCALITY FROM THE MASCALL FORMATION, CROOKED RIVER BASIN, OREGON

**N.A. Famoso, J.D. Orcutt** FIRST OCCURRENCES OF *PALAEOGALE* IN THE PACIFIC NORTHWEST, U.S.A.

**F. Hardy** TESTING THE TECTONIC CONTROLS ON PRESERVATION AND MAMMAL SPECIES RICHNESS IN A MIOCENE BASIN FROM SOUTHERN CALIFORNIA

**R.A. Hawkins, M.J. Everhart** MIOCENE FOSSIL OR HOLOCENE ARTIFACT—*AGRIOTHERIUM SCHNEIDERI* MANDIBLE FROM SEDGWICK COUNTY, KANSAS

**M.E. Hunt, J. Calede, E. Jiménez-Hidalgo, A. Claxton** CONTRASTING THE BODY MASS EVOLUTION OF ENTOPTYCHINE AND GEOMYINE GOPHERS

**A.M. Jukar, N.P. Singh, R. Patnaik, K.M. Sharma, N.A. Singh, Y.P. Singh** THE FIRST SPECIMEN OF *DEINOTHERIUM INDICUM* (MAMMALIA, PROBOSCIDEA, DEINOTHERIIDAE) FROM THE LATE MIOCENE OF KUTCH, INDIA

**A.E. Kort, E.J. Hicks, J. Calede, T.M. Smiley** QUANTIFYING INDIVIDUAL VARIATION AND WEAR IN THE EXTINCT POCKET GOPHER *ENTOPTYCHUS* (MAMMALIA, RODENTIA)

**R. López-Antoñanzas, P. Peláez-Campomanes, A. Prieto-Marquez** NEW INSIGHTS INTO THE PHYLOGENY OF EARLY MUROID RODENTS

**J.A. Moretti, E. Johnson** REVISIONS TO THE LATE BLANCAN MAMMALIAN FAUNA FROM ROLAND SPRINGS RANCH LOCALITY 1, SCURRY COUNTY, TEXAS

**M.I. Pardi, L. DeSantis** FLEXIBLE DIETS AMONG GRAZING-ADAPTED HERBIVORES OVER THE PAST SEVEN MILLION YEARS

**A.W. Peng, S.S. Hopkins, E.B. Davis** COMPARISONS OF MORPHOLOGICAL DISPARITY IN MODERN AND MIOCENE NORTH AMERICAN RODENTS **COLBERT PRIZE ENTRY**

**D.R. Prothero** REVIEW OF THE MIOCENE PECCARY *PROSTHENNOPS* (MAMMALIA, TAYASSUIDAE): THE ULTIMATE WASTEBASKET TAXON, AND ITS IMPLICATIONS FOR PALEOBIOLOGICAL DATABASES

**H.P. Puschel, S.L. Shelley, S. Soto-Acuña, J. Alarcón-Muñoz, R. Ugalde, S. Brusatte** THE FIRST MACRACHENIID (MAMMALIA, LITOPTERNA) FROM THE NEOGENE BAHÍA INGLESA FORMATION: ANATOMICAL DESCRIPTION AND COMMENTS ON BODY SIZE IN MACRACHENIID

**W.J. Sanders, E.R. Miller, I. Nengo, G. Semperebon, I. Arney** TAXONOMY AND PALEOECOLOGY OF A REMARKABLY DIVERSE NEW PROBOSCIDEAN ASSEMBLAGE FROM THE TERMINAL EARLY MIOCENE SITE OF BULUK, KENYA

**M.S. Stevens, D.R. Prothero, T. Htun** THE LAST OF THE OREODONTS: A REVIEW OF THE GENUS *USTATOCHOERUS* (MAMMALIA, ARTIODACTYLA, MERYCOIDODONTIDAE)

**Y. Tse, J. Calede** FIRST DETERMINATION OF THE DIETARY ECOLOGY OF TWO OLIGO-MIOCENE-AGED SHREWS, *DOMNINA* AND *PSEUDOTRIMYLUS*, USING GEOMETRIC MORPHOMETRICS

**J. Welch, M. Blua, N. Magone, J. Case** A LATE BLACAN LOCAL FAUNA FROM NORTHERN IDAHO

**C. Widga, W. Von Koenigswald, U. Göhlich, C. Inabinett** RECENT RESEARCH INTO NORTH AMERICAN MIO-PLIOCENE MAMMUTIDAE

**G. Wilbert, J. Cohen, J.A. Frederickson, T.C. Hunt, N. Czaplewski, M. Engel** PALEOECOLOGICAL ANALYSIS OF CARNIVORANS FROM THE OPTIMA LOCAL FAUNA OF OKLAHOMA (MIOCENE; LATE HEMPHILLIAN)

**L.T. Yann, R. Feranec, D. Pagnac, I.D. Browne** A LONGER FUSE FOR THE SPREAD OF C4-DOMINATED ECOSYSTEMS IN NORTH AMERICA

### TALKS

**R. Ahmad, A. Khan, M. Waseem, M. Ameen, G. Roohi** RHINOCEROTIDS AS THE ECOLOGICALLY MOST SUCCESSFUL SIWALIK UNGULATES: ENAMEL HYPOPLASIA BASED IMPLICATION

**J. Calede** CLIMATIC DRIVERS OF BODY SIZE IN LIVING GEOMYIDS AND OLIGOCENE PALEOENVIRONMENTS

**D.A. Croft, B. Saylor, C. Strömberg, R.K. Engelman, A. Catena, A. Deino, L. Gibert, D. Hembree, F. Anaya** PALEOENVIRONMENT AND CHRONOLOGY OF THE LATE MIDDLE MIOCENE (SERRAVALLIAN) MAMMAL SITE OF QUEBRADA HONDA, SOUTHERN BOLIVIA

**M.A. Khan, S.G. Abbas** PROBOSCIDEANS (MAMMALIA) FROM THE MIO-PLIOCENE OF NORTHERN PAKISTAN

**K.M. Loughney, C. Badgley, A. Bahadori, W.E. Holt, E. Rasbury** MAMMAL RICHNESS AND TECTONIC HISTORY OF THE BASIN AND RANGE SINCE 36 MA

**D.M. Reuter, S.S. Hopkins, E.B. Davis** BEYOND MISSING BROWSERS: OLIGO-MIOCENE COMMUNITY STRUCTURE AND FUNCTIONAL DIVERSITY IN THE NORTHWEST

**J. Samuels** MAMMAL COMMUNITY STRUCTURE EVOLUTION IN RESPONSE TO CLIMATE AND HABITAT CHANGES THROUGH THE CENOZOIC OF OREGON

**J. Schap, J. Samuels** ECOMETRIC ESTIMATION OF PRESENT AND PAST CLIMATE OF NORTH AMERICA USING CROWN HEIGHTS OF RODENTS AND LAGOMORPHS

**WEDNESDAY, OCTOBER 14, 2020, 3:30PM EDT-4:15PM EDT  
MESOZOIC AND EARLY CENOZOIC MAMMALIAN EVOLUTION NETWORKING SESSION**

**POSTERS**

**S.F. Al-Ashqar, M.R. Borths, E. Seiffert, S. El-Sayed, M.S. Antar, H. Sallam** A NEARLY COMPLETE CRANIUM OF '*PTERODON*' *SYRTOS* AND THE EVOLUTION OF AFRO-ARABIAN '*PTERODON*' (HYAENODONTA, HYAINAILOURINAE)

**D.K. Anderson** RECENTLY DISCOVERED SPECIMENS OF *ACRITOPARAMYS* AND *FRANIMYS* HIGHLIGHT THE DIFFERENCES BETWEEN THESE TWO GENERA, KNOWN FROM THE EARLY EOCENE OF THE BIGHORN BASIN, WYOMING

**S.C. Anderson, S.L. Shelley, O.C. Bertrand, T.E. Williamson, S. Brusatte** THE OSTEOLOGY OF *GONIACODON*: SHEDDING LIGHT ON THE ENIGMATIC 'TRISODONTIDAE'

**J.J. Eberle, W.A. Clemens, G.M. Erickson, P.S. Druckenmiller** A NEW, TINY, LATE CRETACEOUS GYPSONICTOPID (MAMMALIA, EUTHERIA) FROM THE NORTH SLOPE OF ALASKA

**Y. Gong, Y. Wang, F. Mao, B. Bai, Q. Li, H. Wang** DIETARY RECONSTRUCTION AND PALEOECOLOGY OF EOCENE LOPHIALETIDAE (MAMMALIA, TAPIROIDEA) FROM THE ERLIAN BASIN OF CHINA: EVIDENCE FROM DENTAL MICROWEAR

**T. Harper, G.W. Rougier** MASTICATORY MECHANICS IN *PELIGROTHERIUM*, AN OMNIVOROUS NON-TRIBOSPHENIC MAMMAL FROM SOUTH AMERICA SHOWING CONVERGENCE TO MODERN THERIANS **COLBERT PRIZE ENTRY**

**L.T. Holbrook, C. Li, J. Yang, T. Smith** PHYLOGENETIC POSITION OF *OLBITHERIUM* (MAMMALIA, PERISSODACTYLA) BASED ON NEW MATERIAL FROM THE EARLY EOCENE WUTU FORMATION

**M.F. Jones, K. Beard, M. Salem, J. Jaeger** A LARGE, PREDATORY BAT (CHIROPTERA, PHILISIDAE) FROM THE MIDDLE EOCENE OF LIBYA **COLBERT PRIZE ENTRY**

**Z. Kynigopoulou, S.L. Shelley, T.E. Williamson, S. Brusatte** THE ANATOMY, PALEOBIOLOGY, AND PHYLOGENY OF THE PALEOCENE TAENIODONT *CONORYCTES* **COLBERT PRIZE ENTRY**

**K. Miller, K. Beard** PHYLOGENETIC RECONSTRUCTION OF TWO SPECIES OF PAROMOMYID PLESIADAPIFORMS FROM A UNIQUE, HIGH ARCTIC ECOSYSTEM OF EOCENE CANADA **COLBERT PRIZE ENTRY**

**K. Newton, S. Apesteguía, B. Davis, G.W. Rougier** TOOTH ERUPTION AND MORPHOLOGY IN EARLY MAMMALS: A JUVENILE DRYOLESTOID SKULL FROM THE LATE CRETACEOUS OF SOUTH AMERICA

**V.A. Pérez-Crespo, J. Arroyo-Cabrales, A. Osorio Segura, E. Cienfuegos-Alvarado, F. J. Otero** FOOD HABIT INFERENCES FROM A WHITE RIVER BRONTOTHERE (PERISSODACTYLA, BRONTHOTHERIIDAE, *BRONTOPS* SP.)

**K. Rust, K. Beard** NEW SPECIMENS OF *EKGMOWECHASHALA* FROM THE GERING FORMATION (EARLY ARIKAREAN) OF NEBRASKA

**N. Schottenstein, J. Hunter, M. Hubbe** THE ROLE OF CLIMATE CHANGE ON THE DENTAL EVOLUTION OF LATE PALEOCENE AND EARLY EOCENE *PHENACOLEMUR*

**K.B. Townsend, P. Higgins** SEARCH FOR THE LAST EOCENE HYPERTHERMAL IN THE UINTA BASIN, UTAH, U.S.A.

**T. Tsubamoto, K. Tsogtbaatar, T. Chinzorig, M. Iijima, N. Egi** THE UPDATED VERTEBRATE FAUNA OF THE UPPER EOCENE ERGILIN DZO FORMATION OF MONGOLIA

**L.A. Vietti, S. Wright, S. McKim, M. Clementz, C. Hutchen** THE CRETACEOUS–PALEOGENE FOSSIL MAMMAL PROJECT: DIGITIZING AND SHARING WYOMING'S RARE FOSSIL MAMMAL COLLECTION FOR UNDERSTANDING MAMMAL EXTINCTION AND RECOVERY THROUGH ECOSYSTEM COLLAPSE

**T.C. Wheat, A.J. McGrath, D.A. Croft, A. Wyss, J.J. Flynn** A NEW SPECIES OF *PLEUROSTYLODON* (MAMMALIA, NOTOUNGULATA) FROM THE LATE EOCENE LOS QUEÑES LOCALITY, ANDEAN MAIN RANGE, CENTRAL CHILE

**M.C. Wood, K. Beard, W.J. Sanders** NEW FOSSIL SPECIMENS OF *PALAEOAMASIA KANSUI* AND PHYLOGENETIC REVISION OF EMBRITHOPODA **COLBERT PRIZE ENTRY**

### TALKS

**K. Beard, G. Métais, F. Ocakoğlu, A. Licht** A LUTETIAN OMOMYID PRIMATE FROM THE PONTIDE MICROCONTINENT, NORTH-CENTRAL ANATOLIA: IMPLICATIONS FOR SWEEPSTAKES DISPERSAL OF TERRESTRIAL MAMMALS DURING THE EOCENE

**M.R. Borths, S. Heritage, G. Gunnell, A. Friscia, E. Seiffert** PERSISTENCE OF THE OLDEST HYAENODONT CLADE THROUGH THE EOCENE OF AFRICA

**C.E. Brown, M.S. Cardozo, N. Kuwabara, G.W. Rougier** NEW LATE CRETACEOUS MAMMALS FROM LA COLONIA FORMATION, PATAGONIA, ARGENTINA SUPPORT MULTITUBERCULATE AFFINITIES FOR FERUGLIOTHERIIDS

**B.E. Christison, D. Fraser** TESTING THE COMPETITION HYPOTHESIS: DID COMPETITION WITH CARNIVORAMORPHANS RESULT IN EXTINCTIONS AMONG CREODONTS DURING THE EOCENE IN NORTH AMERICA?

**H.Z. Fulghum, D. Grossnickle, J.A. Schultz, K.R. Jäger, G.P. Wilson** TESTING THE UTILITY OF EXTANT DIDELPHID MARSUPIALS AS MODERN ANALOGS FOR DENTAL FUNCTION IN EARLY TRIBOSPHENIC MAMMALS USING OCCLUSAL FINGERPRINT ANALYSIS

**S. Holpin, S.L. Shelley, O.C. Bertrand, T.E. Williamson, S. Brusatte** THE ANATOMICAL, LOCOMOTORY, AND SENSORY CHARACTERISTICS OF *TETRACLAENODON*, THE EARLIEST PHENACODONTID

**B. Hovatter, D. Grossnickle, G.P. Wilson** TESTING FOR A LATITUDINAL GRADIENT OF MORPHOLOGICAL DIVERSITY IN EARLY PALEOCENE EUTHERIAN MAMMALS FROM NORTH AMERICA

**E. Huang, G.S. Bever** NEW TRICONODONTID (PAN-THERIA, MAMMALIA) FROM THE JURASSIC OF NORTH AMERICA AND CRANIAL-POSTCRANIAL DISPARITY IN THE BODY MASS ESTIMATIONS OF SMALL-BODIED MAMMALS

**J.J. Hughes, J.S. Berv, S.G. Chester, E.J. Sargis, D.J. Field** EVOLUTION OF MAMMALIAN ARBOREALITY AND THE K–PG MASS EXTINCTION

**S.G. Mattingly, K. Beard, P. Coster, M. Salem, Y. Chaimanee, J. Jaeger** A NEW BASAL CARNIVORAFORM FROM THE EARLY OLIGOCENE OF LIBYA: OLDEST KNOWN RECORD OF CARNIVORAMORPHA IN AFRICA

**P.E. Morse, D.M. Boyer, J.I. Bloch** MEASURING THE RELATIVE EFFECTS OF CLIMATE CHANGE AND COMPETITION ON PRIMATE DIET DURING THE PALEOCENE–EOCENE THERMAL MAXIMUM

**P.E. dePolo, S.L. Shelley, T.E. Williamson, J.R. Wible, S. Brusatte** THE CURIOUS CASE OF THE CYRIACOTHERIIDS: AN EVALUATION OF THEIR PHYLOGENETIC POSITION

**A.W. Poust, S. Tomiya** AN EARLY NIMRAVID (CARNIVORAMORPHA) FROM THE EOCENE OF CALIFORNIA REVEALS A RAPID DISPERSAL OF THE HYPERCARNIVOROUS GUILD

**K.R. Selig, M.T. Silcox** PATTERNS OF INTRASPECIFIC VARIATION IN THE DIET OF *MICROSYOPS LATIDENS* (MAMMALIA, PRIMATES) OVER TIME: INSIGHT INTO ECOLOGICAL AND CLIMATIC CHANGE USING DENTAL TOPOGRAPHIC ANALYSIS

**R. Weppe, F. Condamine, C. Blondel, G. Guinot, M.J. Orliac** CAINOTHERIIDAE FROM QUERCY (SW OF FRANCE): DIVERSITY DYNAMICS AND BIOTIC/ABIOTIC INTERACTIONS AROUND THE EOCENE–OLIGOCENE TRANSITION (34–33.5 MA)

**D. Williams, D.A. Burnham, L. Gurche** PRELIMINARY REPORT OF AN ARTICULATED MAMMALIAN HAND FROM THE HELL CREEK FORMATION IN NORTHEASTERN MONTANA

**THURSDAY, OCTOBER 15, 2020, 10:00AM EDT-11:00AM EDT  
SYMPOSIUM: FRONTIERS IN PALEONEUROLOGY AND NEUROSENSORY EVOLUTION  
NETWORKING SESSION**

**POSTERS**

**J. Han, A.C. Morhardt, A.A. Farke** ENDOCRANIAL MORPHOLOGY OF THE NEOCERATOPSIAN DINOSAUR *LEPTOCERATOPS GRACILIS* FROM THE LATE CRETACEOUS HELL CREEK FORMATION, MONTANA, U.S.A.

**F. Knoll, S. Kawabe** THE BRAIN AND INNER EAR OF DERIVED PTEROSAURS HAVE SIMILAR MORPHOMETRICS TO THOSE OF BIRDS

**TALKS**

**R.B. Benson, A. Bjarnason, M. Bronzati, S. Evers, M. Ezcurra, D.J. Field, S. Giles, G. Navalón, S. Walsh, L. Witmer, J. Choiniere, S.J. Nesbitt** EXPLAINING THE STRUCTURE OF SEMICIRCULAR CANALS IN ARCHOSAURS

**O.C. Bertrand, S. Brusatte, S.L. Shelley, J.R. Wible, T.E. Williamson, S.G. Chester, L.T. Holbrook, T.R. Lyson, T. Smith, J. Meng** BRAIN EVOLUTION OF EARLY PLACENTAL MAMMALS: THE IMPACT OF THE END-CRETACEOUS MASS EXTINCTION ON THE NEUROSENSORY SYSTEM OF OUR DISTANT RELATIVES

**S. Brusatte, M.T. Young, J.A. Schwab, L. Witmer, Y. Herrera, S. Walsh, M. McKeown, A. Muir, T.E. Williamson, T.D. Carr** BRAINS, GIANT DINOSAURS, AND SWIMMING CROCODYLOMORPHS: NEUROSENSORY CHANGES DURING MAJOR EVOLUTIONARY TRANSITIONS IN MESOZOIC ARCHOSAURS

**A. Clement, T. Challands, K. Trinajstic, L. Houle, R. Cloutier, J. Long** BRAIN-BRAINCASE RELATIONSHIPS ACROSS THE FISH-TETRAPOD TRANSITION

**H. Dutel, M. Fabbri, G. Navalón, L.B. Porro, D.S. Paredes, P.J. Watson, B.S. Bhullar, M. Fagan, E. Rayfield** DEVELOPMENTAL CONSTRAINTS AND FUNCTIONAL INNOVATIONS DURING THE EVOLUTION OF THE SARCOPTERYGIAN HEAD

**C.M. Early** AN AVIAN CASE STUDY OF INFERRING NEUROANATOMY AND POTENTIAL FUNCTIONAL CAPABILITIES FROM ENDOCAST STRUCTURES

**E.A. Ferrer, M. Salerno, S. Wei, P. Vaska, A. Balanoff** UNRAVELING THE EVOLUTIONARY HISTORY OF THE AVIAN BRAIN THROUGH BEHAVIORAL NEUROIMAGING AND DIFFUSIBLE IODINE-BASED CONTRAST-ENHANCED COMPUTED TOMOGRAPHY

**P. Gignac, A.R. Beyl, M.L. Gold, J. Gray, A.C. Morhardt, R. Stout, D. Vazquez-Sanroman, A. Watanabe, M. Wilson, N.J. Kley** EXTENDING THE ENDOCAST PARADIGM: STANDARD AND CONTRAST-ENHANCED COMPUTED TOMOGRAPHY UNITE PALEONTOLOGICAL AND NEONTOLOGICAL NEUROIMAGING

**M.L. Gold, J.B. Smaers, M. Norell, A. Balanoff** BRAIN REORGANIZATION AT THE ORIGIN OF CROWN BIRDS

**A. Hogan, A. Balanoff, G.S. Bever** PHYLOGENETIC SCALING OF THE OLFACTORY APPARATUS IN CROWN AVES

**S. Kawabe** EFFECTS OF STRUCTURAL CONSTRAINTS OF SKULL ON BRAIN MORPHOLOGY IN BIRDS: A CASE STUDY WITH THE TEMPORAL FOSSA

**E. Lessner, C. Holliday** TRIGEMINAL NERVE BRANCHING PATTERNS REVEAL DIVERSITY AND EVOLUTION OF FACIAL SENSITIVITY AMONG ARCHOSAURS

**J. Schwab, M.T. Young, J.M. Neenan, S. Walsh, Y. Herrera, L. Witmer, C.A. Brochu, J.N. Choiniere, A.H. Turner, S. Brusatte** VESTIBULAR MORPHOLOGY REVEALS ECOMORPHOLOGICAL TRENDS AND ONTOGENETIC CHANGES IN CROCODYLOMORPHS

**G. Sobral** NEUROSENSORY EVOLUTION IN REPTILES AND THE FULL TRANSITION TO LAND

**A.H. Turner, A.R. Beyl, S. Brusatte, P. Gignac, D. Pol, J.A. Schwab, J.B. Smaers, A. Watanabe, E. Wilberg, M.T. Young** ECOMORPHOLOGICAL AND ALLOMETRIC SIGNATURES IN ENDOCRANIAL SHAPE IN CROCODYLOMORPHS

**A. Watanabe, M. Bedell, R. Felice, A. Balanoff** GETTING IT INSIDE YOUR HEAD: A UNIFIED ANALYSIS OF BRAIN AND SKULL EVOLUTION.

**J.D. Wilson, A. Wisniewski, G.S. Bever** NEW INSIGHTS INTO THE NEUROCRANIUM AND INNER EAR OF THE EARLY STEM ARCHOSAUR *TRILOPHOSAURUS BUETTNERI*

**L.R. Yohe, M. Fabbri, M. Hanson, B.S. Bhullar** OLFACTORY GENE EVOLUTION IS UNUSUALLY RAPID ACROSS TETRAPODA AND OUTPACES CHEMOSENSORY PHENOTYPIC CHANGE

**THURSDAY, OCTOBER 15, 2020, 1:00PM EDT-2:00PM EDT  
ANATOMICAL & DEVELOPMENTAL EXPLORATIONS OF THE MAMMALIAN SKULL  
NETWORKING SESSION**

**POSTERS**

**H.E. Ahrens, M. Passero** FIRST COMPLETE ENDOCAST OF AN OXYAENID (*DIPSALIDICTIS KRAUSEI*)

**N. Chatar, V. Fischer, G. Siliceo, M. Antón, J. Morales, M.J. Salesa** MANDIBULAR DISPARITY OF EARLY SABERTOOTHED FELIDS FROM THE LATE MIOCENE OF SPAIN

**L. Fostowicz-Frelik, A.S. Wolniewicz** CT-INFORMED CRANIAL ANATOMY OF *PALAEOLAGUS HAYDENI* (MAMMALIA, LAGOMORPHA) AND ITS BEARING ON THE RECONSTRUCTION OF BASAL LAGOMORPH MORPHOTYPE

**E. Fulwood** A BAYESIAN MULTILEVEL APPROACH TO THE CALCULATION OF ENCEPHALIZATION QUOTIENTS

**T.J. Gaudin, K. Smith, J.R. Wible** OSTEOLOGICAL ANOMALIES IN THE NARIAL ANATOMY OF THE EXTANT TWO-TOED SLOTH *CHOLOEPUS* AND THE HOMOLOGY OF THE INTERNARIAL BAR IN SOME FOSSIL SLOTHS

**C. Janis, B. Figueirido, L. DeSantis, S. Lautenschlager** AN EYE FOR A TOOTH: WAS *THYLACOSMILUS* REALLY A 'MARSUPIAL SABERTOOTH' PREDATOR?

**L. Koper, I. Koretsky, S. Rahmat** THE FUNCTIONAL MORPHOLOGY AND COMPARISONS AMONG THE PINNIPED MIDDLE EAR APPARATUSES

**D.W. Krause, S.G. Chester, S. Hoffmann, T.R. Lyson, L.G. Dougan, H. Petermann, A. Tecza, I.M. Miller** NEW SKULL MATERIAL OF *TAENIOLABIS TAOENSIS* (MULTITUBERCULATA, TAENIOLABIDIDAE): IMPLICATIONS FOR TAENIOLABIDID ANATOMY, PALEOBIOLOGY, AND PHYLOGENETIC RELATIONSHIPS

**V. Naples, M. Haji-Sheikh** A STUDY OF SABERTOOTH CAT CRANIA: NEW CONSIDERATIONS IN THE FUNCTION OF THE SKULL AND MANDIBLE IN *SMILODON FATALIS*

**R.E. Narducci, M.T. Silcox, J.I. Bloch** NEW VIRTUAL CRANIAL ENDOCASTS OF GIANT GROUND SLOTHS: IMPLICATIONS FOR UNDERSTANDING BRAIN EVOLUTION IN FOLIVORA (MAMMALIA, XENARTHRA, PILOSA) **COLBERT PRIZE ENTRY**

**M. Pollak, K. Tate-Jones** STABILIZING SELECTION ON THE VARIABILITY OF SPACING OF *LOBODON CARCINOPHAGA* (CRABEATER SEAL) POSTCANINE TEETH FOR SUCCESSFUL FILTER-FEEDING FORAGING STRATEGIES

**S.V. Robson, J.A. Ludtke, J. Theodor** THE PETROSAL MORPHOLOGY OF THE BASAL OROMERYCID *PROTYLOPUS*

**C.J. Salcido, P.D. Polly** INFLUENCE OF BIOMECHANICS ON THE MANDIBLE SHAPE AMONGST CARNIVOROUS THERIAN MAMMALS

**E.A. Scarpitti, J. Calede** THE MORPHOLOGY OF THE AUDITORY BULLA ENABLES LOCOMOTORY INFERENCES IN EXTINCT RODENTIA

**J. Theodor, S.V. Robson, J.A. Ludtke** PETROSAL MORPHOLOGY OF THE BASAL PROTOCERATID *LEPTOREODON*

## **TALKS**

**R.L. Anemone, H.E. Ahrens, J.W. Crowell, I.K. Lundeen, P.E. Morse, T.R. Yokley** A NEW TILLODONT SKULL WITH EXCEPTIONAL PRESERVATION FROM THE GREAT DIVIDE BASIN, WYOMING

**B.S. Bhullar, A.R. Manafzadeh, J. Miyamae, E.A. Hoffman, E. Brainerd, C. Musinsky, A.W. Crompton** MAMMALIAN CHEWING DEPENDS ON ROLLING OF THE JAW AND DEEP CONSERVATION OF TOOTH FORM AND FUNCTION

**R.K. Engelman** ESTIMATING BODY MASS IN EXTINCT THERIAN MAMMALS USING WIDTH OF THE OCCIPITAL CONDYLES

**A.M. Glass, M.D. Uhen, R.A. Racicot, E. Ekdale** PHYLOGENETIC RELATIONSHIPS BETWEEN CRANIAL AND INNER EAR MORPHOLOGIES OF ODONTOCETES

**A. Goswami, A. Fabre, C. Dowling, E. Noirault** DEVELOPMENTAL CONSTRAINTS, ECOLOGICAL SPECIALIZATION, AND THE EVOLUTION OF THE MAMMAL SKULL AND MANDIBLE

**A. Hartstone-Rose, E.E. Elminowski, A.M. Blume, E. Dickinson** THE CARNIVORAN OSSICLES OF RANCHO LA BREA

**I.K. Lundeen** USING CT SCAN DATA TO DESCRIBE THE WELL-PRESERVED TURBINALS OF THE ADAPIFORM PRIMATE *LEPTADAPIS LEENHARDTI*

**J. Manguot, M.J. Orliac** EVOLUTION OF ENDOCAST MORPHOLOGY IN THE SUBORDER YINPTEROCHIROPTERA (CHIROPTERA): MORPHOLOGICAL SIGNAL AND ENCEPHALIZATION EVOLUTION IN A CLADE REGROUPING ECHOLOCATING AND NON-ECHOLOCATING BATS

**J.G. Napoli, Q. Jiangzuo, T. Liyandja, W. Harcourt-Smith** SPECIALIZATION IS NOT CANALIZATION: DECOUPLING OF ECOLOGICAL AND MORPHOLOGICAL DISPARITY WITHIN EXTANT URSIDAE

**M.J. Orliac, M.J. Mourlam** INTO THE MIDDLE EAR GEARS OF SEMI-AQUATIC ARTIODACTYLS: HIPPOPOTAMIDS VERSUS EARLY CETACEANS

**H. Orlowski, D. Birlenbach, D.L. Fox** LOOKING GIFT HORSES IN THE MOUTH: AN EXAMINATION OF THE INHIBITORY CASCADE IN EQUID EVOLUTION

**B. Wang, C. Badgley, M. Zelditch, E. VanValkenburg** DIET AND JAW DISPARITY IN THE ARTIODACTYL IN RELATION TO CLIMATE AND TOPOGRAPHY

**THURSDAY, OCTOBER 15, 2020, 2:00PM EDT-2:45PM EDT  
MACROECOLOGY & MACROEVOLUTION NETWORKING SESSION**

**POSTERS**

**S. Shimizu, Y. Kobayashi** PATTERNS OF BODY SIZE DISTRIBUTION ALONG PALEOLATITUDE OF EXTINCT ARCHOSAURS DURING THE LATE CRETACEOUS

**O.M. Takano** RAPTOR EVOLUTION IN RESPONSE TO MEGAFUNA EXTINCTION

**TALKS**

**K. Angielczyk, P. Roopnarine, S. Olroyd, C.F. Kammerer, J. Pardo** THE CHANGING ROLES OF INSECT AND TETRAPOD HERBIVORES IN PROMOTING TERRESTRIAL ECOSYSTEM STABILITY FROM THE PENNSYLVANIAN TO THE TRIASSIC

**P.M. Barrett, A.M. Waterson, D.N. Schmidt, P.J. Valdes, C. Yesson, P. Holroyd, M.E. Collinson, A. Farnsworth, D. Nicholson** TURTLE PALEONICHE DYNAMICS PREDICT RANGE SHIFTS IN A WARMING WORLD

**C.A. Brochu, A.B. Adams, S.K. Drumheller, J. Miller-Camp, M. Rubin** THE INTERPLAY BETWEEN REGIONAL AND GLOBAL CLIMATIC TRENDS IN CROCODYLIFORM FAUNAL CHANGE

**T.W. Dudgeon, Z. Landry, W. Callahan, C. Mehling, S. Ballwanz** ECOLOGICAL NICHE MODELING SUPPORTS FOSSIL EVIDENCE FOR AN APPALACHIAN POPULATION OF NEOCHORISTODERES

**P.L. Godoy, F.C. Montefeltro, M. Bronzati, H. Larsson, R.J. Butler, A.H. Turner** THE INFLUENCE OF ECOLOGICAL TRANSITIONS ON DIFFERENT SKELETAL REGIONS OF CROCODYLIFORMS

**P. Houde, E. Braun, L. Zhou** DEEP-TIME DEMOGRAPHIC INFERENCE SUGGESTS K-PG ECOLOGICAL RELEASE AS DRIVER OF NEOAVIAN ADAPTIVE RADIATION

**M. Kouvari, P. Mannion, A. Goswami** MACROEVOLUTIONARY PATTERNS AND THE APPEARANCE OF THE MODERN-DAY LATITUDINAL BIODIVERSITY GRADIENT IN SOUTH AMERICAN TERRESTRIAL EUTHERIAN MAMMALS

**S. Maidment, R.I. Mansergh, C.D. Dean, R.J. Butler** BIODIVERSITY PATTERNS, FAUNAL ENDEMISM, AND THE DINOSAURIAN FOSSIL RECORD IN THE LATE CRETACEOUS WESTERN INTERIOR, U.S.A.

**K. Melstrom** THE INFLUENCE OF ECOLOGY ON CROCODYLOMORPH SUCCESS THROUGH MASS EXTINCTIONS

**A.K. Parker, J. Head** ECOMETRIC MODELLING OF TURTLE BODY SIZE DISTRIBUTIONS: HOW TURTLES PREDICT PALEOTEMPERATURE

**R.A. Rivero Vega, M. Friedman** PATTERNS IN RATES OF DISCRETE-CHARACTER AND BODY-SHAPE EVOLUTION: ARE 'LIVING FOSSILS' ALIKE?

**C.H. Woolley, J.R. Thompson, Y. Wu, D.J. Bottjer, N.D. Smith** CAN A FRAGMENTED PAST BE TRUSTED? ASSESSING BIAS AND PHYLOGENETIC SIGNAL IN THE SQUAMATE FOSSIL RECORD

**T.C. Wyenberg-Henzler, J. Mallon** COMPETITION AND TAPHONOMY IN THE STRUCTURING OF LATE CRETACEOUS DINOSAUR COMMUNITIES IN NORTH AMERICA

**THURSDAY, OCTOBER 15, 2020, 3:00PM EDT-3:30PM EDT  
MARINE REPTILE DIVERSITY AND BIOLOGY NETWORKING SESSION**

**POSTERS**

**D.J. Morgan, L. Witmer** CONVERGENCE AND CONSTRAINT IN NEUROVASCULAR EVOLUTION IN THE SECONDARILY AQUATIC/MARINE SAUROPSID CLADES SAUROPTERYGIA AND MOSASAUROIDEA **COLBERT PRIZE ENTRY**

**TALKS**

**E. Armour Smith, F.R. O'Keefe** REVISION OF THE GENUS *STYXOSAURUS* AND RELATIONSHIPS OF THE LATE CRETACEOUS ELASMOSAURIDS (PLESIOSAURIA, SAUROPTERYGIA) OF THE WESTERN INTERIOR SEAWAY

**C.I. Bowman, M.T. Young, J.A. Schwab, L. Witmer, S. Walsh, Y. Herrera, S. Brusatte** EVOLUTION OF THE NEUROVASCULAR SYSTEM WITHIN THE SNOOTS OF METRIORHYNCHOID CROCODYLOMORPHS

**R. Carr, J. Lindgren, M. Schweitzer, H. Woodward, J. Scannella** SOFT TISSUE PRESERVATION AND PALEOECOLOGY OF A NEW GIANT PLIOPLATECARPINE MOSASAUR FROM THE BEARPAW SHALE OF MONTANA (U.S.A.)

**J. Chai, D. Jiang, Z. Sun** NEW SPECIMENS FOUND IN XINGYI FAUNA PROVIDE EVOLUTION INFORMATION OF THALATTOSAURIFORMES

**T. Cowgill, M.T. Young, J.A. Schwab, S. Walsh, L. Witmer, Y. Herrera, S. Brusatte** PARANASAL SINUS SYSTEM EVOLUTION IN METRIORHYNCHOID CROCODYLOMORPHS

**M.M. Johnson, D. Foffa, M.T. Young, S. Brusatte** THE ECOLOGICAL DIVERSIFICATION AND EVOLUTION OF TELEOSAUROIDEA (CROCODYLOMORPHA, THALATTOSUCHIA), WITH INSIGHTS INTO THEIR MANDIBULAR BIOMECHANICS

**T. Konishi, M. Ohara, A. Misaki, H. Matsuoka, H.P. Street** A NEW MOSASAURINE (SQUAMATA: MOSASAURIDAE) FROM WESTERN JAPAN WITH UNEXPECTED POSTCRANIAL MORPHOLOGY

**W. Lin, D. Jiang, O. Rieppel, R. Motani, A. Tintori, Z. Sun, M. Zhou** PHYLOGENY OF THE EOSAUROPTERYGIA (DIAPSIDA: SAUROPTERYGIA) INCORPORATING RECENT DISCOVERIES FROM SOUTH CHINA

**J.R. Lively** DISPARITY OF MOSASAURS IN THE WESTERN INTERIOR SEAWAY AND THE IMPORTANCE OF VARIABILITY TO THE DIVERSIFICATION OF MOSASAURINAE

**S.R. Mohr, A.R. LeBlanc, M. Caldwell** A NEW, NEARLY COMPLETE SPECIMEN OF PROGNATHODON OVERTONI (SQUAMATA: MOSASAURIDAE) FROM THE CAMPANIAN BEARPAW FORMATION OF ALBERTA, CANADA

**P. Sander, L. Schmitz, T. Wintrich, N. Klein** TERRESTRIAL VS. MARINE ORIGIN OF VIVIPARITY IN MARINE REPTILES: EVIDENCE FROM A NEW *CYMBOSPONDYLUS* SKELETON

**A.S. Wolniewicz** A NEW ICHTHYOSAURID (REPTILIA: ICHTHYOSAURIA) FROM THE BLUE LIAS FORMATION (HETTANGIAN–SINEMURIAN, LOWER JURASSIC) OF WARWICKSHIRE, UNITED KINGDOM, WITH IMPLICATIONS FOR THE TAXONOMY AND PHYLOGENY OF ICHTHYOSAURIDAE

**M.T. Young, J.A. Schwab, D. Dufeau, K. Dollman, L. Witmer, Y. Herrera, S. Walsh, L.E. Zanno, X. Xu, S. Brusatte** BRAINS, VEINS AND SINUSES: ENDOCRANIAL ADAPTATIONS OF THE LAND-TO-SEA TRANSITION IN THALATTOSUCHIAN CROCODYLOMORPHS

**A.R. Zietlow** HOW TO MAKE MONSTERS: CLADISTIC ANALYSIS OF ONTOGENY IN FOUR MOSASAUR TAXA RECOVERED ANCESTRAL PATTERNS OF MOSASAURID SKULL GROWTH

**THURSDAY, OCTOBER 15, 2020, 3:30PM EDT-4:30PM EDT  
MESOZOIC HERPETOLOGY & CENOZOIC HERPETOLOGY NETWORKING SESSION**

**MESOZOIC HERPETOLOGY**

**POSTERS**

**T.L. Adams, S.K. Drumheller, H.M. Maddox, C.R. Noto, C.D. Sumrall** INCREASED SAMPLING OF *DELTASUCHUS MOTHERALI*, A NEOSUCHIAN FROM THE CENOMANIAN OF TEXAS, AND SUPPORT FOR ENDEMISM IN APPALACHIAN CRETACEOUS CROCODYLIFORMES

**A. Brum, T. Simões, A. Piacentini, R. Figueiredo, J. Sayão, A.W. Kellner** GREATER DIVERSITY OF ELASMOSAURID PLESIOSAURS FROM ANTARCTICA REVEALED BY NEW FOSSILS FROM THE CAMPANIAN OF THE SNOW HILL ISLAND FORMATION, JAMES ROSS BASIN, ANTARCTICA

**H. Chen, S. Jiang, A.W. Kellner, X. Cheng, Z. Xinjun, R. Qiu, Y. Li, X. Wang** NEW ANATOMICAL INFORMATION ON *DSUNGARIPTERUS WEII* WITH A FOCUS ON THE PALATAL REGION

**M. Connely, J. Cavigelli** ‘WALKING IN THE RAIN’: A NEW PTEROSAUR TRACKSITE SHOWING SUBAERIAL PERAMBULATIONS.

**B. Fallon, R. Boessenecker** MULTISPECIES LEATHERBACK ASSEMBLAGE FROM THE CHANDLER BRIDGE AND ASHLEY FORMATIONS (OLIGOCENE) OF SOUTH CAROLINA, U.S.A.

**J.A. Frederickson, B. Davis, R. Cifelli** A NEW ASSOCIATED SKELETON OF THE RARE SPHENODONTIAN *EILENODON ROBUSTUS* FROM THE UPPER JURASSIC MORRISON FORMATION OF UTAH

**R. Hirayama** FOSSIL TURTLES FROM THE LATE CRETACEOUS (TURONIAN) OF KUJI, IWATE PREFECTURE, NORTHERN JAPAN

**B.P. Holbach** AN ASSESSMENT OF CLIMATE AND ENVIRONMENTAL CHANGES OF THE HELL CREEK FORMATION USING THE BIOSTRATIGRAPHY OF SIX TURTLE TAXA

**S.E. Jasinski, A.B. Heckert, A.J. Lichtig, C. Sailer, P. Dodson** A RARE PLASTOMENID TURTLE (TESTUDINES: PLASTOMENIDAE) FROM THE END OF THE CRETACEOUS IN NORTH DAKOTA AND SURVIVORSHIP OF PLASTOMENIDS ACROSS THE CRETACEOUS-PALEOGENE BOUNDARY

**P. Jiménez-Huidobro, O.A. López-Conde, M.L. Chavarría-Arellano, H. Porras-Múzquiz** THE OLDEST OCCURRENCE OF A YAGUARASAUROIDE MOSASAUROID FROM THE LATE CENOMANIAN-EARLY TURONIAN OF COAHUILA, NORTHERN MEXICO

**N.P. Kelley, L. Johnson, B. Gibson** A PROBABLE *TORETOCNEMUS* (REPTILIA: ICHTHYOSAURIA) PARTIAL SKULL FROM THE LATE TRIASSIC ANTIMONIO FORMATION OF SONORA, MEXICO

**A.H. Lee, C.R. Noto** HISTOLOGICAL ANALYSIS OF THE ARLINGTON ARCHOSAUR SITE FOSSILS SUPPORTS NICHE PARTITIONING AND ENVIRONMENTAL STABILITY AS DRIVERS OF BIODIVERSITY IN THE WOODBINE GROUP

**A.J. Lichtig, S.G. Lucas** A TESTUDINOID TURTLE FROM THE UPPER CRETACEOUS OF NEW MEXICO

**H.M. Maddox, S.K. Drumheller, T.L. Adams, C.R. Noto** ONTOGENY OF *DELTASUCHUS MOTHERALI* (NEOSUCHIA, CROCODYLIFORMES): IMPLICATIONS FOR PALEOECOLOGY AND NICHE PARTITIONING

**W. McCuen** NEW MARINE REPTILES FROM THE LATE CRETACEOUS OF SOUTH CAROLINA, INCLUDING FIRST OCCURRENCES OF ELASMOSAURIDAE, *CLIDASTES*, *MOSASAURUS*, AND "*LIODON*"

**A. Mohebn, R. Hirayama, M. AbdelGawad, A. Sileem, M. Aly** NEW RECORD OF TESTUDINES AND AVES FOSSILS FROM BAHARIYA FORMATION (CENOMANIAN), BAHARIYA DEPRESSION, EGYPT

**T. Rodrigues, M. Melotti, M. Dantas, D. Riff, T. Marinho, E. Pereira** FURTHER EVIDENCE OF NICHE PARTITION BETWEEN BAURUSUCHID CROCODYLIFORMS AND ABELISAURID DINOSAURS IN THE UPPER CRETACEOUS BAURU GROUP (BRAZIL)

**S. Saber, J. Sertich, G. Abu El-Kheir, K. Ouda, S. El-Sayed, P.M. O'Connor, E. Seiffert, H. Sallam** THE OLDEST GAVIALOID CROCODYLIFORM ('THORACOSAUR') FROM THE CAMPANIAN QUSEIR FORMATION OF BARIS OASIS, WESTERN DESERT, EGYPT

**M. Sprague, M. McLain** A RHAMPHORHYNCHINE PTEROSAUR MANDIBLE FROM BONE CABIN QUARRY, MORRISON FORMATION, WYOMING

**J. Stiegler, R. Hernández-Rivera, J.M. Clark** TWO SMALL CROCODYLIFORMES FROM THE MIDDLE JURASSIC LA BOCA FORMATION OF TAMAULIPAS, MEXICO

**H.P. Street, E.L. Bamforth** SKELETALLY IMMATURE PLESIOSAURS FROM A MARINE REPTILE BONEBED FROM THE UPPER CRETACEOUS OF SASKATCHEWAN, CANADA

**T. Szczygielski, D. Surmik** A THOUGH TURTLE – HEALED DAMAGE ON A *MONGOLEMYS* SHELL FROM THE LATE CRETACEOUS OF MONGOLIA

**T. Wintrich, J. Vanhoefer** A SPECIALIZED RESPIRATORY SYSTEM IN PLESIOSAURS (SAUROPTERYIA): BREATHING WITH THE LONG NECK

**X. Wu, Q. Shang, C. Li** A NEW NOTHOSAUROID (SAUROPTERYGIA) FROM CHINA

**Y. Yin** CRANIAL MORPHOLOGY OF THE LOWER TRIASSIC ICHTHYOSAURIFORM *CHAOHUSAURUS BREVIFEMORALIS* (REPTILIA: ICHTHYOSAURIFORMES) BASED ON DIGITAL RECONSTRUCTIONS

### TALKS

**R. Belben** RESOLVING THE PTEROSAUR BAUPLAN USING A QUANTITATIVE TAPHONOMIC APPROACH

**A.G. Dhobale, D.M. Mohabey, B.T. Samant, D. Kumar** REPTILIAN TETRAPODS OF UPPER CRETACEOUS (MAASTRICHTIAN) VOLCANIC SEDIMENTS ASSOCIATED WITH OLDEST LAVA PILES OF NORTHEASTERN DECCAN TRAPS: RESPONSE TO DECCAN ERUPTIONS

**N. Jagielska, S. Brusatte, M. O'Sullivan, I. Butler, T. Challands, N. Clark, N. Fraser, A. Penny, D. Ross, M. Wilkinson** AN EXCEPTIONALLY WELL PRESERVED PTEROSAUR FROM THE MIDDLE JURASSIC OF SCOTLAND

**A.W. Kellner, L.C. Weinschütz, J. Sayão, R.A. Bantim, B. Holgado** NEW INFORMATION ON *KERESDRAGON VILSONI* (PTEROSAURIA, AZHDARCHOIDEA, TAPEJAROMORPHA) FROM A CRETACEOUS BONEBED IN BRAZIL

**B. Kligman, W. McClure, M. Korbitz, B. Schumacher** A NEW SPHENODONTIAN REPTILE WITH PECULIAR MANDIBULAR MORPHOLOGY FROM THE UPPER TRIASSIC OF THE PURGATOIRE RIVER VALLEY, SOUTHEASTERN COLORADO

**B.M. Rothschild** EVIDENCE FOR DETERMINATE GROWTH IN SYNAPSIDS, MARINE REPTILES, AND DINOSAURS: NON-DESTRUCTIVE DETERMINATION OF SKELETAL MATURITY

**T.R. Simoes, M. Caldwell, S.E. Pierce** SPHENODONTIAN PHYLOGENY AND THE IMPACT OF MODEL CHOICE ON DIVERGENCE TIMES AND EVOLUTIONARY RATES

**D.M. Unwin, D. Martill** IDENTITY, HOMOLOGY, AND COMPOSITION OF FIBER-LIKE STRUCTURES ASSOCIATED WITH THE PTEROSAUR INTEGUMENT

### CENOZOIC HERPETOLOGY

#### POSTERS

**A.P. Cossette** INTRASPECIFIC VARIABILITY IN AN ONTOGENETIC SEQUENCE OF THE BASAL CROCODYLIAN *BOREALOSUCHUS FORMIDABILIS* AND ITS IMPLICATIONS FOR THE RECOGNITION OF FOSSIL SPECIES

**A. Erb** BRAINCASE ANATOMY OF THE PALEOCENE CROCODYLIFORM *RHABDOGNATHUS*.

**A.K. Hastings, B. Schubert, J. Bourque** OLDEST RECORD OF *ALLIGATOR* IN THE SOUTHEASTERN UNITED STATES HAD SMALL BODY SIZE IN SUBTROPICAL ENVIRONMENT

**J. Head** NORTH BY NORTH-WEST: A NEW ANILIID SNAKE TAXON FROM THE MIDDLE EOCENE OF WYOMING AND A REAPPRAISAL OF THE FOSSIL RECORD OF 'ANILIID' SNAKES

**P.A. Kloess** CREATING A 3D MORPHOSPACE OF TURTLE SKULL VARIATION TO FACILITATE THE IDENTIFICATION OF FOSSILS **COLBERT PRIZE ENTRY**

**S.G. Lucas, A.J. Lichtig** *CARDICHELYON* SP., A NEW TESTUDINOID MORPHOTYPE FROM THE PALEOCENE (PUERCAN-TORREJONIAN) OF NEW MEXICO

**M.S. Riegler, L.W. Vinola, M.C. Vallejo-Pareja, A.R. Campins, J.I. Bloch** QUATERNARY CAVE DEPOSITS OF JAMAICA: REGIONAL SQUAMATE EXTIRPATION AND FIRST RECORD OF ANURAN EXTINCTION IN THE GREATER ANTILLES

**M.A. El-Hares, H. Sallam, H. Zaher, D. EL-Mekkawy, S. El-Sayed, E. Seiffert, M.S. Antar** NEW RECORDS OF LEGLESS SQUAMATES FROM THE EARLIEST UPPER EOCENE DEPOSITS OF THE FAYUM DEPRESSION, EGYPT

**L.W. Vinola** ANALYSIS OF TERRESTRIAL VERTEBRATE BIOGEOGRAPHICAL HISTORY OF THE GREATER ANTILLES **COLBERT PRIZE ENTRY**

**E. Whiting, D.L. Fox** LIZARD BYTES: THREE-DIMENSIONAL DENTAL TOPOGRAPHY ANALYSIS OF EXTANT PLEURODONT SQUAMATES, WITH IMPLICATIONS FOR RECONSTRUCTING THE DIETS OF EXTINCT FOSSIL SQUAMATES **COLBERT PRIZE ENTRY**

### TALKS

**D. Meyer, B.S. Bhullar, J.A. Gauthier** THE FIRST COMPLETE SPECIMEN OF THE OLIGOCENE ANGUID *PAROPHISAURUS PAWNEENSIS* WITH IMPLICATIONS FOR THE PHYLOGENY OF ANGUIDAE

**H. Petermann, J.A. Gauthier** INTRASPECIFIC VARIABILITY IN AN EXTANT SQUAMATE AND ITS IMPLICATIONS FOR USE OF SKELETOCHRONOLOGY IN EXTINCT VERTEBRATES

### THURSDAY, OCTOBER 15, 2020, 8:00PM EDT 9:00PM EDT HOLOCENE AND PLEISTOCENE MAMMALIAN MACROECOLOGY AND FAUNAL STUDIES NETWORKING SESSION

### POSTERS

**T.J. Anderson** BISON FROM THE SNAKE RIVER FOSSIL SITE, MINNESOTA

**J. Baker, J. Meachen, L. DeSantis** DIETARY BEHAVIOR OF WOLVERINES FROM NATURAL TRAP CAVE (WYOMING) AS INFERRED FROM DENTAL MICROWEAR TEXTURE ANALYSIS

**D. Balassa, D.R. Prothero, V.J. Syverson** HOW DID COUGARS AND BOBCATS RESPOND TO THE CHANGES AT THE END OF THE PLEISTOCENE?

**N. Brand, C. Widga, B. Schubert** MUSK OX MEASUREMENTS: DIFFERENTIATING THE TEETH AND CRANIA OF THE FOSSIL WOODLAND MUSK OX *BOOTHERIUM* FROM THE TUNDRA MUSK OX *OVIBOS*

**K. Brooks** DETERMINING PROBABLE CAUSE OF DEATH AND CHANCE OF BONE DISEASE IN A MAMMOTH FROM SOUTHEASTERN IDAHO

**M. Davis, K. Szymanski, J. Fuster, J. Cohen, L. DeSantis, E. Lindsey, J. Meachen, F.R. O'Keefe, J. Southon, W.J. Binder** ASSESSING MIGRATION IN PLEISTOCENE HERBIVORES AT RANCHO LA BREA – YEA OR NEIGH? **COLBERT PRIZE ENTRY**

**J. Erdman** A MAMMOTH HYBRID FROM IDAHO: TAXONOMIC COMPARISONS AND RADIOCARBON DATING

**L. Finkelman, E.B. Davis, B. Boyd, A. Hart, C. Johnson** ANTHROPOGENIC AND NON-ANTHROPOGENIC CONTRIBUTIONS TO END-PLEISTOCENE MEGAFUNAL EXTINCTIONS IN THE AMERICAN WEST

**D. Flores, W. Godwin, C.J. Bell, P.J. Lewis** IDENTIFICATION OF THE PLEISTOCENE FAUNA FROM MCFADDEN BEACH, TX

**C.J. Hohman, E. Scott, A.C. Dooley** SHIFTING FAUNAS AND CHANGING CLIMATE: NEW REMAINS OF MIDDLE TO LATE PLEISTOCENE EQUUS FROM SOUTHWESTERN RIVERSIDE COUNTY, CALIFORNIA

**M.P. Jovanovic, K. Bogićević, J. Agusti, H. Blain** PALEOCLIMATIC RECONSTRUCTION OF THE LATE PLEISTOCENE FROM SERBIA BASED ON RODENT ASSEMBLAGES

**P.J. Lewis, J. Moretti, M.D. Flores, W. Godwin, C.J. Bell, E. Dickinson, A. Hartstone-Rose** THE FIRST RECORD OF *HOMOTHERIUM* FROM MCFADDEN BEACH, TEXAS

**H. Machado** TOOTH MORPHOMETRIC ANALYSIS CONFIRMS STASIS IN LATE PLEISTOCENE HORSES FROM RANCHO LA BREA

**M.A. Macias, R.K. McAfee** *LESTODON* DOESN'T WANT YOUR AVOCADO TOAST: DEBUNKING THE DIETARY MYTHS OF THE LATE PLEISTOCENE SLOTHS (MAMMALIA, PILOSA)

**A. Petherick, J. Reuther, S. Anderson, S. Shirar, L. DeSantis** DIETARY BEHAVIOR OF ALASKAN POLAR BEARS (*URSUS MARITIMUS*) IN RESPONSE TO ARCTIC WARMING, AS INFERRED FROM PAST (~1 KA) AND PRESENT SPECIMENS VIA DENTAL MICROWEAR TEXTURES

**O. Potapova, I.S. Pavlov, V.V. Plotnikov, E. Maschenko, M. Dehasque, B. Shapiro, L. Dalen, N. Suzuki, J.F. Hoffecker, A. Protopopov** A NEW WOOLLY MAMMOTH (*MAMMUTHUS PRIMIGENIUS* BLUMENBACH, 1799) FROM KOTELNY ISLAND, NOVOSIBIRSK ARCHIPELAGO, RUSSIA

**A.R. Reynolds, T. Lowi-Merri, A.L. Brannick, D. Evans** DIRE WOLF IDENTIFIED FROM THE LATE PLEISTOCENE OF ALBERTA USING GEOMETRIC MORPHOMETRICS

**I. Sanchez-Uribe, R. Guzmán-Gutierrez, H.E. Rivera-Sylva, V.G. Lopez-Diaz de Leon, C.A. Lopez-Palma** NEW PLEISTOCENE LOCALITY FROM CHIHUAHUA, MEXICO

**N.S. Usachenko** METHODS OF DETERMINING THE GENDER, SIZE, AND AGE OF 'COLA', A PLEISTOCENE MAMMOTH DISCOVERED IN SOUTHEASTERN IDAHO

## **TALKS**

**N.L. Ackermans, D.E. Winkler, M. Clauss, D. Codron, J. Hatt** CORRELATION OF DIETARY PROXIES IN A LONG-TERM EXPERIMENT ON SHEEP (*OVIS ARIES*)

**M.D. Biernat, W. Khumalo, S. Mavuso, A. McGrosky** REGIONAL DIFFERENCES OF EARLY *HOMO* PALEOECOLOGY

**W.J. Binder, J. Cohen, J. Meachen, F.R. O'Keefe, E. Lindsey, L. DeSantis, J. Southon** RANCHO LA BREA 'TOUGH TIMES' FROM THE BOTTOM UP: CLIMATE CHANGE AFFECTS MORPHOLOGY, ECOLOGY, AND TAPHONOMY

**R.W. Burroughs** GLACIAL CYCLES DRIVE QUATERNARY POPULATION DYNAMICS IN THE SAGEBRUSH VOLE, *LEMMISCUS CURTATUS* (RODENTIA, ARVICOLINAE)

**N. Freymueller, C. Myers, M.I. Pardi, F.A. Smith** MINIMAL MESO-CARNIVORE RELEASE WITHIN THE FELID GUILD FOLLOWING THE PLEISTOCENE MEGAFUNAL EXTINCTION

**C. Hedberg, F.A. Smith, S.K. Lyons** THE LEGACY OF MEGAFUNAL EXTINCTION: A FINE-SCALE EXAMINATION OF FUNCTIONAL DIVERSITY OVER THE LATE QUATERNARY

**J.S. Keller, S.K. Lyons, S. Newsome, F.A. Smith** GRASSHOPPER MICE OF UNUSUAL SIZE: CLIMATE- AND EXTINCTION-DRIVEN ECOLOGICAL SHIFTS IN *ONYCHOMYS* OVER 22,000 YEARS AT HALL'S CAVE

**A.A. Kelly, J.H. Miller, L. DeSantis, M.J. Wooller, C. Seaton, P.S. Druckenmiller** WHEN GRAZERS DIDN'T JUST EAT GRASS: DIETARY PREFERENCES OF BISON AND HORSE IN NORTHERN ALASKA

**N. Loughlin, D.L. Fox** COMPARING THE FUNCTIONAL ECOLOGY AND TAPHONOMIC DIFFERENCES BETWEEN HOLOCENE AND MODERN NORTH AMERICAN MAMMALIAN COMMUNITIES ACROSS THE TRANSITION BETWEEN FOREST AND PRAIRIE BIOMES

**R.K. McAfee, S.M. Beery, S. Cooke, R. Rimoli, J. Almonte, P. Lehman** A NEW SPECIES OF THE GROUND SLOTH *PAROCNUS* (MAMMALIA, PILOSA, MEGALONYCHOIDEA) FROM THE LATE PLEISTOCENE-EARLY HOLOCENE OF THE DOMINICAN REPUBLIC

**J. Meachen, M.J. Wooller, B.D. Barst, J. Funck, C. Crann, M. Cassatt-Johnstone, B. Shapiro, E. Hall, S. Hewitson, G. Zazula** FROZEN IN TIME: THE TALE OF A PLEISTOCENE WOLF PUP FROM THE YUKON TERRITORY

**K.M. Meltesen, E. Whiting, D.L. Fox** THE LATITUDINAL DIVERSITY GRADIENT OF MODERN NORTH AMERICAN MAMMALS MASKS MULTIPLE ORDINAL LEVEL PATTERNS: IMPLICATIONS FOR THE ORIGIN OF THE MAMMALIAN DIVERSITY GRADIENT IN THE LATE CENOZOIC FOSSIL RECORD

**R.S. Mohammed** RECONSTRUCTING TRINIDAD'S LATE PLEISTOCENE VERTEBRATE COMMUNITY: NEW INSIGHTS FROM HISTORIC AND ONGOING EXCAVATIONS

**A.M. Mychajliw, T.C. Rick, N.D. Dagtas, J.M. Erlandson, B.J. Culleton, D.J. Kennett, M. Buckley, C. Hofman** ECOLOGY AND BIOGEOGRAPHY OF AN UNEXPECTED SHORT-FACED BEAR (*ARCTODUS SIMUS*) FROM THE CALIFORNIA CHANNEL ISLANDS

**K. O'Brien, C.A. Tryon, N. Blegen, B. Kimeu, J. Faith, J. Rowan** FIRST APPEARANCE OF GRÉVY'S ZEBRA (*EQUUS GREVYI*), KAPTHURIN FORMATION, KENYA

**F.R. O'Keefe** A HIGH-RESOLUTION RECORD OF MEGAFUNAL EXTINCTION FROM RANCHO LA BREA: TEMPO, MODE, AND CAUSALITY

**S. Pineda-Munoz, Y. Wang, A.B. Tóth, S.K. Lyons, J.L. McGuire** HUMANS HAVE SHAPED THE CLIMATIC DISTRIBUTIONS OF MODERN NORTH AMERICAN MAMMALS

**E. Scott, S.M. Gust** DEMOGRAPHY OF LATE PLEISTOCENE *EQUUS OCCIDENTALIS* FROM RANCHO LA BREA, CALIFORNIA, BASED UPON DENTAL AND PELVIC DATA

**F.A. Smith, A. Villasenor, E.A. Elliott Smith, C. Tomé, S.K. Lyons, S. Newsome** THE MISSING PIECE: LATE PLEISTOCENE CHANGES IN THE ECOLOGICAL FUNCTION OF A MAMMAL COMMUNITY IN NORTH AMERICA

**N.S. Vitek, J.C. Hoeflich, I. Magallanes, S.M. Moran, R.E. Narducci, S.B. Ocon, V.J. Perez, J. Pirlo, M.S. Riegler, M. Rodgers, M.C. Selba, M.C. Vallejo-Pareja, M.L. Ziegler, M.C. Granatosky, J.I. Bloch** PHYLOGENY OF FOSSIL AND EXTANT NEW WORLD PORCUPINES: RE-EVALUATION OF AN EARLY PLEISTOCENE PORCUPINE SKELETON FROM FLORIDA WITH TROPICAL, ARBOREAL MORPHOLOGY

**U.P. Wibowo, G. van den Bergh, S. Hayes** ATTRIBUTION OF GENERA ACCORDING TO THE  
INDONESIAN PROBOSCIDEAN MORPHOLOGY OF THE HIND LIMB

**T. Yang, T. Chi, Y. Gan, C. Chang** THE FIRST LEOPARD FOSSILS FROM TAIWAN INFERRED BY THE  
INTEGRATION OF MORPHOLOGICAL AND GEOMORPHOMETRIC ANALYSES

**FRIDAY, OCTOBER 16, 2020, 10:00AM EDT 11:00AM EDT**  
**BIOMECHANICS & FUNCTIONAL MORPHOLOGY NETWORKING SESSION**

**POSTERS**

**R.J. Brocklehurst, P. Fahn-Lai, S. Regnault, K. Angielczyk, S.E. Pierce** SHOULDER JOINT RANGE OF  
MOTION IN FOSSIL SYNAPSIDS AND THE ORIGINS OF MAMMALIAN LOCOMOTOR DIVERSITY

**P. Fahn-Lai, S. Regnault, A. Biewener, S.E. Pierce** COMPARING 3D SHOULDER MOBILITY AND  
MUSCLE MOMENT ARMS IN SPRAWLING AND UPRIGHT AMNIOTES

**M.A. Green, K. Fischenich, J.J. Eberle, T.R. Lyson** APPLYING 2D AND 3D IMAGING TECHNIQUES TO  
EVALUATE BITE FORCE IN MODERN AND EARLY PALEOCENE MAMMALS **COLBERT PRIZE ENTRY**

**B. Hart** MANUS BIOMECHANICS OF A GIANT MASTODON FROM THE GRAY FOSSIL SITE  
SUGGESTS THE ABILITY TO TRAVERSE UNEVEN TERRAIN IN A KARSTIC AND MOUNTAINOUS  
REFUGIUM **COLBERT PRIZE ENTRY**

**D. Nakai, S. Fujiwara** MORPHOLOGICAL INDICES FOR DIGGING ABILITY AND STRATEGIES USING  
FORELIMBS IN EXTINCT MAMMALS **COLBERT PRIZE ENTRY**

**C. Ormsby, S. Wallace, J. Samuels** INFERRED LOCOMOTION OF SELECT FELIFORMS: IMPLICATIONS  
FOR *BARBOUROFELIS LOVEORUM* (BARBOUROFELIDAE) AND *NIMRAVIDES GALLIANI* (FELIDAE,  
MACHAIRODONTINAE) FROM THE LATE MIOCENE (LATEST CLARENDONIAN) OF FLORIDA  
**COLBERT PRIZE ENTRY**

**Z. Tseng, S. Garcia Lara** A CONSTRUCTIONAL CONSTRAINT HYPOTHESIS FOR VERTEBRATE JAW  
EVOLUTION

**M. Walsh, K. Shimada** TORSO MORPHOLOGY IN EXTANT QUADRUPED AMNIOTES TO INFER THE  
BODY MORPHOLOGY OF FOSSIL TAXA

**K.E. Widrig, J. Watanabe, B.S. Bhullar, D.J. Field** THREE-DIMENSIONAL ATLAS OF PECTORAL  
MUSCULOSKELETAL ANATOMY IN THE EXTANT TINAMOU *NOTHOPROCTA*  
*PENTLANDII* (PALAEOGNATHAE: TINAMIDAE) **COLBERT PRIZE ENTRY**

**R. Wilhite** A DETAILED ANATOMICAL STUDY OF THE M. CAUDOFEMORALIS LONGUS  
IN *ALLIGATOR MISSISSIPPIENSIS* WITH IMPLICATIONS FOR RECONSTRUCTIONS OF TAIL  
MUSCULATURE IN EXTINCT ARCHOSAURS

**TALKS**

**S.H. Ascari, P.D. Polly** FINITE ELEMENT ANALYSES OF THE FUNCTION OF THE PEDAL CLAWS  
OF *DEINONYCHUS ANTIRRHOPUS*

**A.R. Beyl, A. Moore, R. Sookias, R.B. Benson** CAN AGNOSTIC ORNSTEIN-UHLENECK MODELING OF  
STYLOPOD CIRCUMFERENCES IDENTIFY LOCOMOTORY REGIME SHIFTS IN DINOSAURIA?

**P.A. van Bijlert, A. van Soest, A.S. Schulp** INTRODUCING THE NATURAL FREQUENCY METHOD: TAIL BIOMECHANICS PREDICT ENERGETICALLY OPTIMAL WALKING SPEED OF *TYRANNOSAURUS REX*

**D.J. Button, L.B. Porro, P.M. Barrett** FINITE-ELEMENT MODELING OF FOSSIL TAXA: HOW CLOSE IS CLOSE ENOUGH? SENSITIVITY ANALYSES ON THE SKULL OF *MEGAPNOSAURUS KAYENTAKATAE*

**H. Chase, B.W. Tobalske** BIRD TO THE BONE: MECHANICAL ADAPTATION IN THE AVIAN WING

**D.C. D'Amore, L. St.Marie** BREVIROSTRY AS A MAJOR CAUSE OF TOOTH MODIFICATION, REDUCTION, AND LOSS IN NUMEROUS SAUROPSID LINEAGES

**O.E. Demuth, P. Bishop, J.R. Hutchinson** 3D VOLUMETRIC MUSCULOSKELETAL MODELING OF LOCOMOTORY BIOMECHANICS IN *EUPARKERIA CAPENSIS*

**K.K. Formoso** TERRESTRIAL POSTURE AND ITS CONTROLS ON SECONDARILY AQUATIC AMNIOTE EVOLUTION: FORELIMB CHANGES IN LAND-TO-SEA LINEAGES

**J.D. Fortner, A. Wilken, I. Cost, K. Sellers, K. Middleton, C. Holliday** THE ROLE OF SYMPHYSEAL TISSUES AND SUTURES ON MANDIBLE FUNCTION IN ARCHOSAURS

**M.B. Habib, M. Pittman, T.G. Kaye** PTEROSAUR SOFT TISSUES REVEALED BY LASER-STIMULATED FLUORESCENCE ENABLE IN-DEPTH ANALYSIS OF WATER LAUNCH PERFORMANCE

**C. Holliday, A. Wilken, S. Sullivan, C. Verhulst, K. Sellers, E. Lessner, J.D. Fortner, K. Middleton** MYOLOGY OF THE REPTILIA: 3D MODELING OF JAW MUSCLES AND ITS UTILITY IN PALEOBIOLOGY

**J.R. Hutchinson, A.R. Cuff, P. Bishop, K.B. Michel, A. Wiseman, R. Gagnet** ESTIMATION OF HINDLIMB LIMB MUSCLE AREAS FROM SKELETONS IN EXTANT AND EXTINCT ARCHOSAURS

**K.E. Jones, B.V. Dickson, K. Angielczyk, S.E. Pierce** EVOLVING ON THEIR OWN LANDSCAPE: UNRAVELLING FUNCTIONAL TRADE-OFFS IN SYNAPSID AXIAL EVOLUTION

**S. Klein, H. Chase, B.W. Tobalske** WAIER DID FLIGHT COME FROM: ONTOGENIC TRANSITIONS IN BIRDS USING WING-ASSISTED INCLINE RUNNING CAN SHED LIGHT ON THE FLIGHT CAPABILITIES OF EXTINCT SPECIES

**W. Ma, S. Lautenschlager, M. Pittman, R.J. Butler** MANDIBULAR ADAPTATIONS IN THE DIETARY DIVERSIFICATION OF THEROPOD DINOSAURS

**A.R. Manafzadeh, S.M. Gatesy** FROM BONES TO MOBILITY TO LOCOMOTION: RECONSTRUCTING HIND LIMB POSES IN EXTANT ARCHOSAURS

**S.L. Olroyd, C.A. Sidor** A 3D COMPARATIVE ANALYSIS OF THE REFLECTED LAMINA OF THERAPSIDS PROVIDES CLUES TO ITS FUNCTION BEFORE THE EVOLUTION OF THE MAMMALIAN EAR

**J. Peterson, Z. Tseng, S. Brink** BITE FORCE ESTIMATES IN JUVENILE *TYRANNOSAURUS REX* BASED ON SIMULATED PUNCTURE MARKS

**R. Pintore, A. Houssaye, S.J. Nesbitt, J.R. Hutchinson** LIMB BONE ADAPTATIONS TO POSTURAL CHANGES IN EARLY ARCHOSAURS: QUANTIFICATION OF FEMORAL SHAPE VARIATION BETWEEN QUADRUPEDS AND BIPEDS.

**D. Rhoda, M. Segall** THE KINETIC FORAGING SYSTEM OF SNAKES IS HIGHLY INTEGRATED

**D. Smith, D. Gillette** RECONSTRUCTED HINDLIMB MUSCULATURE AND FUNCTION IN THE THERIZINOSAUR *NOTHRONYCHUS* WITH IMPLICATIONS FOR THE OPISTHOPUBIC PELVIS IN MANIRAPTORAN THEROPODS

**H.P. Tsai, C. Griffin** THE CARTILAGINOUS HIPS OF DIPLODOCOIDEA: FUNCTIONAL IMPLICATIONS FOR HIGHLY SPECIALIZED LOCOMOTOR BEHAVIORS AMONG SAUROPODS

**M.L. Turner, S.M. Gatesy** INTERMETATARSAL MOBILITY AND GRADES OF FOOT CONTACT IN THE AMERICAN ALLIGATOR: BUILDING A NEW PERSPECTIVE ON ARCHOSAURIAN FOOT EVOLUTION

**A. Wilken, K. Sellers, I. Cost, R. Rozin, K. Middleton, C. Holliday** COMPARATIVE BIOMECHANICS OF THE OTIC JOINT AND SUSPENSORIUM IN SAUROPSIDS

**FRIDAY, OCTOBER 16, 2020, 1:00PM EDT 1:45PM EDT  
TAPHONOMY AND STRATIGRAPHY NETWORKING SESSION**

**POSTERS**

**M. Armour-Chelu** TAPHONOMY OF STELLER'S SEA COW FROM BERING ISLAND, NORTH WEST PACIFIC

**E.L. Bamforth** LOG JAMS AND JUVENILES: UNUSUAL DEPOSITS AT THE K-PG BOUNDARY (66 MA) IN SOUTHERN SASKATCHEWAN, CANADA

**A.K. Behrensmeyer** NUTRIENT RECYCLING AND TAPHONOMIC BIAS IN THE VERTEBRATE FOSSIL RECORD

**R.W. Blob, I.Z. Espinoza** HYDRODYNAMIC DISPERSAL OF ALLIGATOR BONES: IMPLICATIONS FOR TAPHONOMIC INTERPRETATIONS OF FOSSIL DEPOSITS OF CROCODYLIANS AND MORPHOLOGICALLY SIMILAR TAXA

**J. Cohen, N. Noriega, E. Pitcher, E. Lindsey, L. DeSantis, J. Meachen, F.R. O'Keefe, J. Southon, W.J. Binder** TAPHONOMIC VARIATION AMONG PITS AT RANCHO LA BREA INDICATE LITTLE CHANGE IN DEPOSITIONAL ENVIRONMENT THROUGH THE END OF THE PLEISTOCENE

**M. Gaetano, J.H. Miller, E.J. Wald, P.S. Druckenmiller** CHEW ON THIS: EXPANDING DIAGNOSTIC CRITERIA OF UNGULATE-GNAWED BONES

**T.J. Haupt, C.J. Flis, R.T. Bakker, D.T. Temple** DIMETRODON'S DISASSEMBLING PREY: MULTIPLE TAPHONOMIC SIGNATURES AT CRADDOCK BONE BED, SEYMOUR, TX,

**A.A. Kilmury, K. Brink** STRATIGRAPHIC DISTRIBUTION OF VERTEBRATES FROM THE LATE CRETACEOUS WESTERN INTERIOR SEAWAY IN MANITOBA, CANADA

**C.R. Noto, J. Peterson** HYDRODYNAMIC TRANSPORT POTENTIAL OF MODELLED TURTLE SHELL IN A CONTROLLED FLUVIAL SETTING: A CASE STUDY IN EXPERIMENTAL TAPHONOMY

**K. Pontieri, B. Pobiner, R. Potts** PATTERNS OF CHEWING DAMAGE TO MODERN BONES FROM A STRIPED HYENA DEN IN SOUTHERN KENYA

**J. de Rooij** BITE MARKS ON *TRICERATOPS* RIBS ATTRIBUTED TO CROCODYLIAN SCAVENGING

**I. Sanchez, A.B. Heckert, N.A. Brand, J.R. Foster, R.K. Hunt-Foster, J.J. Eberle** TAPHONOMY OF VERTEBRATE MICROSITES IN THE UPPER CRETACEOUS (LATE CAMPANIAN-EARLY MAASTRICHTIAN) WILLIAMS FORK FORMATION OF NORTHWESTERN COLORADO

**S.H. Scott, M.J. Ryan, D. Evans** A TAPHONOMIC ANALYSIS OF A MONODOMINANT *WENDICERATOPS PINHORNENSIS* BONEBED FROM THE OLDMAN FORMATION (CAMPANIAN) OF ALBERTA REPRESENTING THE OLDEST EVIDENCE OF HERDING BEHAVIOR IN CERATOPSIDS

**Y. Shi, V. Gu, A.A. Farke** TAPHONOMIC BIAS IN HORSE PHALANGES FROM THE BARSTOW FORMATION (MIOCENE) AND LA BREA TAR PITS (PLEISTOCENE) OF CALIFORNIA, U.S.A.

**B.C. Siviero, E. Rega, M. McLain, L. Brand, A. Chadwick, D. Nelson** IDENTIFICATION OF TOOTH TRACES FROM AN *EDMONTOSAURUS ANNECTENS* BONEBED WITHIN THE LANCE FORMATION (MAASTRICHTIAN), WYOMING

**L.N. Weaver, T.S. Tobin, J.R. Claytor, W.A. Clemens, G.P. Wilson** REVISED STRATIGRAPHIC RELATIONSHIPS OF THE MIDDLE PART OF THE TULLOCK MEMBER OF THE FORT UNION FORMATION (GARFIELD COUNTY, MONTANA, U.S.A.) ELUCIDATES POST K-PG MAMMALIAN RECOVERY DYNAMICS **COLBERT PRIZE ENTRY**

**K. Wiersma-Weyand, S. Läbe, P. Sander** ORGANIC PHASE PRESERVATION IN FOSSIL DINOSAUR AND OTHER TETRAPOD BONE FROM DEEP TIME: OSTEOCYTE-LIKE STRUCTURES LIBERATED FROM TETRAPOD BONES FROM THE LOWER PERMIAN OF TEXAS

**R.D. Wilkinson, T.D. Cullen, D. Evans** PALEONTOLOGY AND SEDIMENTOLOGY OF A MULTI-TAXIC BONEBED IN THE HELL CREEK FORMATION OF MONTANA, U.S.A.

## **TALKS**

**S. Chakravorti** PUTATIVE ERYTHROCYTE STRUCTURES REVEAL FOR THE FIRST TIME THE EFFECT OF PYRITIZATION ON PROTEIN PRESERVATION IN A 250 MILLION YEARS OLD FOSSIL AMPHIBIANS FROM THE PANCHET FORMATION, EASTERN INDIA

**S.K. Drumheller, C.A. Boyd, B. Barnes, M. Householder** BIOSTRATINOMIC ALTERATIONS OF A HADROSAUR 'MUMMY' SUGGEST AN UNEXPECTED PATHWAY FOR SOFT TISSUE PRESERVATION

**W.J. Freimuth, D. Varricchio, A.L. Brannick, L.N. Weaver, G.P. Wilson** MAMMAL-BEARING REGURGITALITES POTENTIALLY ATTRIBUTABLE TO *TROODON FORMOSUS* AT THE EGG MOUNTAIN LOCALITY, UPPER CRETACEOUS TWO MEDICINE FORMATION, MONTANA, U.S.A.

**J. Gallucci** SOFT TISSUE AND CELLULAR PRESERVATION IN PALEOGENE VERTEBRATE FOSSILS OF THE NEBRASKA AND SOUTH DAKOTA BADLANDS

**S.M. Gatesy, M.L. Turner** DINOSAURS IN DISGUISE: SUBSTRATE FLOW ACCOUNTS FOR UNUSUAL EARLY JURASSIC TRACKS

**S. Kim, Y. Lee, I. Hwang, Y. Gihm, N. Kim, S. Choi** A TAPHONOMIC STUDY OF THE COLONIAL DINOSAUR NESTING GROUND FOUND IN THE UPPER CRETACEOUS NATURAL LEVEE DEPOSITS (WIDO VOLCANICS), WI ISLAND, SOUTH KOREA

**R. Laker, P.D. Gingerich, S. Kidwell** STRONG VARIATION IN DIAGENESIS OF BONES AS A FUNCTION OF SEQUENCE-STRATIGRAPHIC CONTEXT: EOCENE VALLEY OF THE WHALES, EGYPT

**J. McHugh, S.K. Drumheller, A. Riedel, M. Kane** INVERTEBRATE-MODIFIED DINOSAUR FOSSILS FROM THE MYGATT-MOORE QUARRY IN WESTERN COLORADO REVEAL NEW INSIGHTS INTO DECAY AND DECOMPOSITION IN THE LATE JURASSIC PERIOD.

**J.H. Miller, J. Goff** PREDATORS RULE THE ROOST: SMALL MAMMAL TAPHONOMY AT LANDSCAPE-SCALES

**A. Roy, M. Pittman, C. Colleary, T.G. Kaye, E.T. Saitta** SEDIMENT-ENCASED THERMAL MATURATION EXPERIMENTS CHEMICALLY SIMULATE NATURAL FOSSILIZATION

**H.E. Smith, M. Morley, J. Bevitt, U. Garbe, Y. Rizal, J. Zaim, M. Rizki Puspaningrum, Aswan, A. Trihascaryo, G. Price, J. Louys** A TAPHONOMIC ANALYSIS OF VERTEBRATE-BEARING CAVE BRECCIA IN SOUTHEAST ASIA

**FRIDAY, OCTOBER 16, 2020, 1:45PM EDT 2:30PM EDT**  
**QUANTITATIVE METHODS**

### **POSTERS**

**A. Bailleul, J. Lu, Z. LI** IODINE-BASED CONTRAST-ENHANCED COMPUTED TOMOGRAPHY APPLIED TO FOSSILIZED TISSUES: A CASE STUDY IN A FOSSIL BIRD PROVIDES POSITIVE RESULTS

**P. Brady, M.S. Springer** PSEUDOEXTINCTION ANALYSES AND ANCESTRAL STATE RECONSTRUCTION: EVALUATING FOSSIL PLACEMENT ACCURACY IN MAMMALIAN PHYLOGENETICS **COLBERT PRIZE ENTRY**

**E. Ehon** INFLUENCE OF DIFFERENT ACID TREATMENTS ON THE RADIOCARBON CONTENT SPECTRUM OF BONE MATERIAL AS DETERMINED BY RPO/ACCELERATOR MASS SPECTROMETRY

**T.J. Halliday, R. Garwood** THE EFFECT OF REGIONAL PATCHINESS ON THE EVOLUTION OF SIMULATED PHYLOGENIES

**M. Kane** IDENTIFYING JURASSIC THEROPOD GENERA USING GIS MAPS OF TOOTH SERRATIONS

**H. Lee, B. Esteve-Altava, A. Abzhanov** PHYLOGENETIC AND ONTOGENETIC CHANGES OF THE ANATOMICAL ORGANIZATION AND MODULARITY IN THE SKULL OF ARCHOSAURS

**S. Mills** PALEOENVIRONMENTAL INFERENCE USING A MODIFIED SØRENSEN'S INDEX **COLBERT PRIZE ENTRY**

**B. Neale, J.H. Miller, E.J. Wald, P.S. Druckenmiller** OWL PELLETS OF THE ARCTIC NATIONAL WILDLIFE REFUGE REVEAL SPATIAL GRADIENT IN SMALL MAMMAL COMMUNITIES **COLBERT PRIZE ENTRY**

**A.E. Nelson, D.A. Croft** CALCULATING BODY MASS FOR NOTOUNGULATES USING HEAD-BODY LENGTH BASED ON A WIDE RANGE OF MODERN MAMMALS BEYOND UNGULATES

**T.R. Pansani** PALEOMETRY: THE DEVELOPMENT AND IMPROVEMENT OF TECHNIQUES APPLIED TO THE STUDY OF FOSSIL VERTEBRATES

**J. S. Silviria** RECONSTRUCTING MAMMALIAN PHYLOGENY USING MORPHOMETRIC DATA: INSIGHTS FROM A PRELIMINARY CLADISTIC ANALYSIS OF HORSES (PERISSODACTYLA, EQUIDAE, EQUINI, *EQUUS*)

**E.M. Simpson, B. Crowley, D. Sturmer** TESTING A NON-DESTRUCTIVE METHOD FOR ANALYZING PRESERVATION OF VERTEBRATE REMAINS

**B. Thomas, S. Taylor, J. Solliday** CROSS-POLARIZATION AND SECOND HARMONIC GENERATION IMAGING REVEAL BONE COLLAGEN DECAY PATTERNS IN FOUR FOSSILS

**O. Wilson, R.J. Asher** USING COMBINED METHODS TO REASSESS THE PHYLOGENETIC AFFINITIES OF THE SOUTH AMERICAN NATIVE UNGULATES

**A. Wiseman, A.R. Cuff, P. Bishop, K.B. Michel, O.E. Demuth, J.R. Hutchinson** A WORKFLOW FOR PRODUCING AND ANALYSING SUBJECT-SPECIFIC MUSCULOSKELETAL MODELS AND SIMULATIONS IN COMPARATIVE BIOMECHANICS

**M.R. Wyatt, S.S. Hopkins, E.B. Davis** USING 2D DENTAL GEOMETRIC MORPHOMETRICS TO IDENTIFY MODERN *PEROGNATHUS* AND *CHAETODIPUS* SPECIMENS (RODENTIA, HETEROMYIDAE)

**J.S. Zijlstra** THE *HESPEROMYS* PROJECT: A NEW DATABASE OF TETRAPOD NOMENCLATURE

## TALKS

**A.D. Apgar, H. Henson, Z. Seaman, K. Seaman, A. Henson** INTEGRATING GROUND-PENETRATING RADAR, GEOCHEMICAL, AND PETROGRAPHICAL RESULTS TO INVESTIGATE A TRACKWAY AND BONEBEDS WITHIN THE MORRISON FORMATION

**R.J. Asher, R.M. Beck, D.J. Field, R.B. Benson** FOSSILS AND THE TREE OF LIFE: MAKING GENOMIC DATA INFORMATIVE FOR EXTINCT VERTEBRATES WITHOUT DIRECT ACCESS TO MOLECULES

**P.Z. Barrett, S.S. Hopkins** FIRST TOTAL-EVIDENCE PHYLOGENY OF THE HYAENIDAE AND ENIGMATIC FOSSIL VIVERROIDS REVEALS NOVEL RELATIONSHIPS

**A. Canoville, W. Zheng, L.E. Zanno, M. Schweitzer** CAN KERATAN SULFATE BE USED TO DISCRIMINATE MEDULLARY BONE IN NON-AVIAN DINOSAURS?

**A. Du, E. Friedlander, J. Rowan, Z. Alemseged** PLACING PROBABILITIES ON WHETHER A FOSSIL TAXON WAS TRULY ABSENT FROM A SITE OR HAS NOT BEEN FOUND YET

**D.L. Fox, J.S. Keller, D. Birlenbach, K.P. McNulty** TESTING RODENT DENTAL ECOMETRICS AS PREDICTORS OF CLIMATE AND BIOME

**S.S. Groh, P. Upchurch, J. Day, P.M. Barrett** THE DOS AND DON'TS OF DATING: COMPARING DIFFERENT TIP-DATING METHODS TO ESTIMATE NEOSUCHIAN DIVERGENCE TIMES

**S. Hoffmann, M. D'Emic, K. Skonieczny, D. Mayback** UTILITY OF MICROCT IN CEMENTUM-BASED AGE ESTIMATION OF PALEOGENE *CORYPHODON*

**J.J. Jacisin, A.M. Lawing** THE CAPACITY OF QUANTITATIVE SHAPE ANALYSIS WITH GEOMETRIC MORPHOMETRIC METHODS FOR TAXONOMIC DELIMITATION USING MID-TRUNK SNAKE VERTEBRAE

**F.A. Perini, D.D. Casali, J.J. Flynn** MACROEVOLUTIONARY TRENDS IN NOTOUNGULATA, AN ENDEMIC RADIATION OF EXTINCT SOUTH AMERICAN HERBIVOROUS MAMMALS

**A.H. Rankin, R.J. Asher** TOTAL-EVIDENCE APPROACH TOWARDS GLIRES PHYLOGENY: TOPOLOGICAL AND BIOGEOGRAPHIC DIFFERENCES WHEN INCLUDING ULTRACONSERVED ELEMENTS (UCES)

**S. Roy, A. Roy, M. Pittman** IMPROVING PALEOCOLOR RECONSTRUCTION WITH MACHINE LEARNING

**S. Scarpetta** ULTRACONSERVED ELEMENTS OVERWHELM MORPHOLOGICAL SIGNAL IN COMBINED-EVIDENCE ANALYSES

**D. Surmik, B.M. Rothschild, T. Szczygielski, M. Zubko, M. Dulski, M. Wojtyniak, P. Duda** PALEO-PATHOPHYSIOLOGY: A MULTIDISCIPLINARY-BASED DIG DEEP INTO FOSSIL BONE

**T.J. Thomson** A NEW METHODOLOGICAL FRAMEWORK FOR ACCURATELY INFERRING AMNIOTE CLAW FUNCTION USING MULTIPLE MORPHOLOGICAL METRICS AND FUNCTIONALLY BASED CATEGORIES

**S. Wright, L.A. Vietti, M. Clementz** FROM MICROFOSSILS TO MOLARS: TESTING THE APPLICATION OF THE SOFTWARE PACKAGE AUTOMORPH TO FOSSIL MAMMAL TEETH

**B. Wynd, J. Uyeda, S.J. Nesbitt** INCLUDING DISTORTED SPECIMENS IN ALLOMETRIC ANALYSES: USING GENERALIZED LINEAR MIXED MODELS TO ACCOUNT FOR SAMPLE DEFORMATION

**C. Yu, Q. Jiangzuo, E. Tschopp, H. Wang, M. Norell** MORPHOLOGICAL INFORMATION CHALLENGES CHARACTER EQUAL WEIGHTING AND INDEPENDENCE

**FRIDAY, OCTOBER 16, 2020, 3:00PM EDT 4:00PM EDT  
DINOSAUR SYSTEMATICS, DIVERSITY AND ECOLOGY NETWORKING SESSION**

**POSTERS**

**I. Aguilar-Pedrayes** FACIAL KERATIN AND TOOTH PRESENCE: COEVOLUTION FOR TRAITS IN DINOSAURS

**H.M. Avrahami, P.J. Makovicky, L.E. Zanno** THE CRANIAL ANATOMY OF A NEW ORODROMINE FROM THE CENOMANIAN-AGED MUSSENTUCHIT MEMBER OF THE CEDAR MOUNTAIN FORMATION, UTAH

**J.S. Cabrera Hernández, M.A. Montellano-Ballesteros, R. Hernández-Rivera** PERINATAL HADROSAURS FROM THE EL GALLO FORMATION (LATE CRETACEOUS), EL ROSARIO, BAJA CALIFORNIA, MEXICO

**J.A. Case, M.C. Lamanna** DOES THE LATE CAMPANIAN–EARLY MAASTRICHTIAN HERBIVOROUS DINOSAUR FAUNA OF THE ANTARCTIC PENINSULA REPRESENT THE SOUTHERN END OF A LATITUDINAL CLINE FROM SOUTH AMERICA?

**K. Chiba, M.J. Ryan, M. Saneyoshi, S. Konishi, Y. Yamamoto, B. Mainbayar, K. Tsogtbaatar** TAXONOMIC RE-EVALUATION OF *PROTOCERATOPS* (DINOSAURIA: CERATOPSIA) SPECIMENS FROM UDYN SAYR, MONGOLIA

**J.E. D'Angelo** A NEW PHYLOGENETIC ANALYSIS OF SAUROPODS WITH INCREASED EMPHASIS ON NON-NEOSAUROPODS

**E.T. Drysdale, K. Chiba, F. Therrien, G.M. Erickson, D.K. Zelenitsky** HISTOLOGICAL ANALYSIS OF *PROSAUROLOPHUS MAXIMUS* (HADROSAURIDAE, SAUROLOPHINAE) FROM SOUTHERN ALBERTA, CANADA REVEALS EVIDENCE FOR AN EXTENDED JUVENILE GROWTH PERIOD, AND THE EVOLUTION OF GIGANTISM WITHIN A LATE CAMPANIAN (LATE CRETACEOUS) HADROSAURID LINEAGE

**D.R. Dunfee, R.C. Ridgely, M.C. Lamanna, L. Witmer** ONTOGENETIC ANALYSIS OF THE SKULL OF THE EARLY-DIVERGING IGUANODONTIAN *DRYOSAURUS ELDERAE* (DINOSAURIA: ORNITHOPODA) FROM THE UPPER JURASSIC MORRISON FORMATION OF UTAH: NEW INSIGHTS FROM MICROCOMPUTED TOMOGRAPHY **COLBERT PRIZE ENTRY**

**S. Ekhtiari, S. Popovic, R. Nagesan, F. Bertozzo, D. Tanke, M. Crowther, D. Evans** FIRST RECORD OF THE REPETITIVE STRAIN INJURY FIBULAR TENDINITIS IN A DUCKBILLED DINOSAUR

**S. Finch, J.A. Wilson Mantilla, B.B. Britt, M. D'Emic** PROLONGED TOOTH FORMATION TIME IN THE CRETACEOUS BRACHIOSAURID SAUROPOD DINOSAUR *ABYDOSAURUS MCINTOSHI*

**T.E. Gallagher, J. Poole, J. Schein** EVIDENCE OF SCALE DIVERSITY IN THE LATE JURASSIC SAUROPOD *DIPLODOCUS* SP. FROM THE MOTHER'S DAY QUARRY, MONTANA

**J.P. Garderes, P.A. Gallina, J.A. Whitlock, N. Toledo** DESCRIPTION AND FUNCTIONAL ANATOMY OF THE QUADRATE OF THE DICRAEOSAURID SAUROPOD *BAJADASAURUS PRONUSPINAX* FROM THE LOWERMOST CRETACEOUS OF PATAGONIA

**A.B. Heckert, M.T. Carrano, Z. Ore, L.S. Howell, K. Schneider** IMPLICATIONS OF THE DISTRIBUTION OF DISEASE AND INCIDENCE OF INJURIES IN NON-AVIAN MESOZOIC DINOSAURS

**B. Holland, N.E. Campione, P. Bell, F. Fanti, M.J. Vavrek, R. Sissons, Y. Wang, S. Hamilton, C. Sullivan** A JUVENILE LAMBEOSAURINE BONEBED FROM THE WAPITI FORMATION OF NORTHWESTERN ALBERTA, CANADA

**M.N. Hudgins, P. Bell, N.E. Campione, F. Fanti, R. Sissons, M.J. Vavrek, D.W. Larson, C. Sullivan** NEW THESCELOSAURID (DINOSAURIA: ORNITHISCHIA) MATERIAL FROM THE WAPITI FORMATION (CAMPANIAN) OF NORTHERN ALBERTA, CANADA

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**L. Rolleri, T.A. Gates, L.E. Zanno** A POSSIBLE LAMBEOSAURINE (HADROSAURIDAE: DINOSAURIA) HUMERUS FROM THE LATE MAASTRICHTIAN HELL CREEK FORMATION OF SOUTH DAKOTA

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**B.S. Salem, G. Abu El-Kheir, M.C. Lamanna, E. Gorscak, S. El-Sayed, H. Sallam** A NEW TITANOSAURIAN SAUROPOD DINOSAUR PARTIAL SKELETON FROM THE LATE CRETACEOUS (CAMPANIAN) OF THE KHARGA OASIS, WESTERN DESERT OF EGYPT

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**M. Son, Y. Lee, B. Zorigt, J. Park, S. Lee, S. Kim, K. Lee** A JUVENILE *YAMACERATOPS DORNGOBIENSIS* (ORNITHISCHIA, CERATOPSIA) FROM THE UPPER CRETACEOUS JAVKHLANT FORMATION OF MONGOLIA

**Y. Wang, C. Sullivan, A.R. LeBlanc** ANATOMICAL AND HISTOLOGICAL DATA INDICATE UNCINATE PROCESSES TO BE HOMOLOGOUS ACROSS ARCHOSAURIA **COLBERT PRIZE ENTRY**

**J.A. Whitlock, K. Smith, S. Winters** A JUVENILE DIPLODOCID SAUROPOD FROM THE MORRISON FORMATION (LATE JURASSIC) PRESERVING A SKIN IMPRESSION

**H. Yoon, Y. Lee, S. Jung, D. Kong, S. Kim, M. Son** A SMALL AND MEDIUM-SIZED ORNITHOPOD TRACKSITE FROM THE LOWER CRETACEOUS HAMAN FORMATION, SOUTH KOREA

**Q. Zhang, L. Jia, H. You** A PROBABLE LARGEST SAUROPODOMORPH DINOSAUR FROM THE EARLY JURASSIC OF YUNNAN PROVINCE, CHINA

**M. Zondo, J.N. Choiniere, P.M. Barrett** BIOSTRATIGRAPHIC CORRELATION OF UPPER KAROO-AGE FOSSILS FROM THE MPANDI FORMATION OF SENTINEL RANCH, TULI BASIN, ZIMBABWE

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**V. Arbour, L.E. Zanno, D. Evans** EVIDENCE FOR INTRASPECIFIC COMBAT, RATHER THAN ANTIPREDATOR DEFENSE, AS THE SELECTIVE PRESSURE UNDERLYING THE EVOLUTION OF ANKYLOSAURINE TAIL CLUBS

**E.R. Bender, T.A. Gates** QUANTIFYING THE INFLUENCE OF MULTIPLE SOCIO-SEXUAL SIGNALS IN THE EVOLUTION OF CERATOPSID DINOSAURS

**F. Bertozzo** A TAIL TALE: INJURIES IN CAUDAL NEURAL SPINES OF HADROSAURIDAE REVEALED BY AN EXTENSIVE PALEOPATHOLOGICAL REVISION OF ORNITHOPODA

**L. Czepinski** NEW PROTOCERATOPSID SPECIMENS IMPROVE THE AGE CORRELATION OF THE UPPER CRETACEOUS GOBI DESERT STRATA

**M. Fabbri, G. Navalón, D.S. Paredes, N.K. Mongiardino, M.E. Vergara, B.S. Bhullar** CRANIOFACIAL CONSTRAINT AND INNOVATION IN THE HEADS OF SAURISCHIA

**M.M. Gilbert, E. Snively, H. Woodward, D.M. Cooper, J. Scannella, T.T. Tokaryk** SYNCHROTRON MICROCT COMPARISON OF HUMERI IN *TRICERATOPS* AND EXTANT-MODEL *BISON* CONSISTENT WITH INFLATIONARY EARLY GROWTH IN CERATOPSID DINOSAURS

**E. Gorscak, M.C. Lamanna, V. Díez Díaz, D. Schwarz, B.S. Salem, G. Abu El-Kheir, H. Sallam** A TITANOSAURIAN SAUROPOD FROM THE CAMPANIAN QUSEIR FORMATION OF THE KHARGA OASIS, EGYPT, SUPPORTS AFRO-EURASIAN DINOSAUR FAUNAL CONNECTIVITY DURING THE LATE CRETACEOUS

**L. King, Q. Zhao, E. Rayfield, M.J. Benton** AVIAN-LIKE ENDOCRANIAL TRAITS OF A JUVENILE *PSITTACOSAURUS LUJIATUNENSIS* AND THE PAEDOMORPHIC NATURE OF THE BIRD BRAIN

**J.V. Leite, A. Goswami, P.M. Barrett** METACARPUS EVOLUTION IN NON-AVIAN DINOSAURS

**P.J. Makovicky, G. Darrough, T.M. Cullen, M. Fix, E. Gorscak, A. McDonald, E.T. Saitta, A. Shinya, R. Stinchcomb, J. Wiersma** NEW SPECIMENS OF THE BASAL HADROSAUROID, *PARROSAURUS MISSOURIENSIS*, FROM THE LATE CRETACEOUS OF MISSOURI, U.S.A.

**J.A. Reizner, H. Woodward, E. Freedman Fowler** HISTOLOGIC GROWTH DYNAMIC STUDY AND POPULATION BIOLOGY OF THE CERATOPSID DINOSAUR *EINIOSAURUS PROCURVICORNIS* FROM A DEATH ASSEMBLAGE OF THE UPPER CRETACEOUS TWO MEDICINE FORMATION OF NORTHWESTERN MONTANA

**C. Woodruff, E. Wolff, M.J. Wedel, L. Witmer** SAURO-THROAT: THE FIRST OCCURRENCE OF A RESPIRATORY INFECTION IN A NON-AVIAN DINOSAUR

**M. Wosik, K. Chiba, F. Therrien, D. Evans** TESTING SIZE-FREQUENCY DISTRIBUTIONS AS A METHOD OF ONTOGENETIC AGING: A LIFE HISTORY ASSESSMENT OF HADROSAURID DINOSAURS FROM THE DINOSAUR PARK FORMATION OF ALBERTA, CANADA, WITH IMPLICATIONS FOR HADROSAURID PALEOECOLOGY AND ONTOGENETIC SEGREGATION

**FRIDAY, OCTOBER 16, 2020, 4:00PM EDT 4:45PM EDT  
EDUCATION AND OUTREACH & COLLECTIONS NETWORKING SESSION**

### **EDUCATION AND OUTREACH**

#### **POSTERS**

**H. Chase** DECOLONIZING THROUGH INTERDISCIPLINARITY: A ROOTS-BASED INTEGRATION APPROACH

**C. Cortes, K. Smith, N. Czaplewski, R. Whitten, J. Hargrave** EXPLOREMOS: SUPPORTING THE ADVANCEMENT OF MINORITIES IN STEM

**D. DeSantis, L. DeSantis** IMPROVING SCIENTIFIC LITERACY THROUGH THE EXPLORATION AND MANIPULATION OF DATA FROM EXTANT AND EXTINCT MAMMALS

**A.C. Dooley, D. Radford, M.J. Wedel, J.E. Atterholt, T. Nalley** 'BROADER IMPACTS', AN EXHIBIT PROGRAM FOCUSING ON BASIC RESEARCH

**C. Griffin, M.R. Stocker** "HOW DO YOU KNOW WHERE TO DIG?": USING A STUDENT-DRIVEN EXPERIENTIAL LEARNING ACTIVITY TO TEACH HYPOTHESIS-BASED FIELDWORK IN A LARGE GENERAL EDUCATION UNIVERSITY COURSE

**A.K. Hastings, K. Ollanketo, S. Glick** INTERACTIVE DINOSAUR LESSONS FOR ALL AGES THAT EXPLAIN COMPLEX ANATOMY AND BODY SIZE TO HELP DISPEL COMMON MISCONCEPTIONS

**C. Holliday, A. Wilken, S. Sullivan, E. Lessner, K. Sellers, K. Middleton, C. Ward** PALEONTOLOGY  
ENGAGEMENT IN RURAL PUBLIC SCIENCE EXPOS

**T. Kerr, L.A. Vietti** AUGMENTING THE REALITY OF WYOMING'S RICH FOSSIL RESOURCES: DOES  
AUGMENTED REALITY ENHANCE MUSEUM VISITOR EXPERIENCE AND OUTREACH?

**T.J. Lepore, K. Lepore, L. Taylor, A. Scharnagl, C. Muskelly** ACTIVE LEARNING AND STEAM IN  
PALEONTOLOGY: CASE STUDIES WITH NEURODIVERSE ADULTS AND FEMALE-IDENTIFYING K-12  
STUDENTS

**K. Matsui, T. Karasawa** INTERACTING WITH THE UNTOUCHABLE: UTILIZING MULTIMEDIA-BASED  
VISUAL CONTENTS FOR THE JAPANESE NATIONAL MONUMENT, THE *TANIWHASAUROS*  
*MIKASAENSIS* (MOSASAURIDAE)

## COLLECTIONS

### POSTERS

**N. Volden, T. Mayfield-Meyer, H. Cantrell** NEW MEXICO MUSEUM OF NATURAL HISTORY AND  
SCIENCE PALEONTOLOGY COLLECTIONS DATA MADE PUBLICLY AVAILABLE THROUGH ARCTOS

## 2020 SVP Virtual Meeting Schedule

There are three key components to the meeting:

- **Pre-recorded talks and posters**, grouped into themes, available for viewing 24/7 Sunday 11 – Saturday 17 October.
- **Asynchronous moderated Q&A** associated with each presentation available Mon 12 – Fri 16 October. Leave a question and presenters will get back to you in their own time.
- **Live content**: workshops, live networking sessions linked to themes, diversity and student-postdoc events, Mon 12 – Fri 16 October.

## SVP 2020 format compared to previous meetings

Our virtual-only format necessitated changes to the structure of the SVP Program this year, but this has offered us opportunities to program content in novel ways. For example, the lack of a fixed talk and poster schedule allows you to engage with presentations in personally customized ways at the times most convenient to you, without the need to choose between competing presentations at fixed times. To exploit these changes and to offer members a different experience, we made an early decision to rely less on traditional taxon-based sessions and to explore other ways to bring members of the SVP community together. In addition to taxonomic sessions for some popular groups (e.g., dinosaurs, mammals), we also unified presentations by theme, which either reflect work in a particular sub-discipline (e.g., biomechanics) or a broader research topic (e.g., the application of novel quantitative methods to evolutionary questions). As a result, many sessions represent a mix of taxa and timescales: we hope you like this new approach. These live networking sessions map to the main session themes in the Program, but a few themed sessions share the same live session. We have allocated time based on the number of presentations allotted to each theme. In doing this, we have also tried to ensure that the members of the many small sub-communities that make up SVP each get a dedicated time in which to interact in real time with each other and to pose questions to the presenters. Other elements of the Program will be familiar, with sessions dedicated to Symposium, Romer Prize, Preparator's, and Education & Outreach presentations. Colbert Poster Prize presentations have been allocated to the most relevant themed sessions and their status as a prize nominee is noted in the Program & Abstracts volume.

## SVP Session Themes

Anatomical & Developmental Explorations of the Mammalian Skull  
Biomechanics & Functional Morphology  
Bird Biology & Evolution  
Cenozoic Herpetology  
Collections  
Dinosaur Systematics, Diversity & Ecology  
Education & Outreach  
Evolution & Biology of Non-Avian Theropods  
Fishes & Chondrichthyans: Evolution & Distribution  
Holocene & Pleistocene Mammalian Macroecology and Faunal Studies  
Late Cenozoic Mammalian Macroecology & Macroevolution  
Macroecology & Macroevolution  
Mammalian Skeletal Morphology  
Marine Mammals  
Marine Reptile Diversity & Biology  
Mesozoic & Early Cenozoic Mammalian Evolution  
Mesozoic Herpetology  
Paleozoic Tetrapods & Lissamphibians  
Permo-Triassic Tetrapods  
Preparators  
Quantitative Methods  
Romer Prize  
Symposium: Paleoneurology  
Symposium: Dietary Reconstruction  
Taphonomy & Stratigraphy

All session themes are allocated their own live networking session, except for the following themes which have been combined into the following networking sessions: Mammalian Skeletal Morphology and Marine Mammals; Mesozoic Herpetology and Cenozoic Herpetology; Education & Outreach and Collections.

[Click here for the schedule](#), so that you may view when the live content is scheduled.

## Marine Mammals

### A NEW DISCOVERY OF SIRENIA FROM THE LATE EOCENE IN BENI SUEF DISTRICT, NORTH EASTERN DESERT, EGYPT

Abdel Gawad, Mohamed<sup>1</sup>, Hassan, Safiya<sup>2</sup>, Abd El-Gaied, Ibrahim<sup>2</sup>, Salama, Yasser<sup>2</sup>, Abdel Gawad, Gouda<sup>2</sup>

<sup>1</sup>Geology, Cairo University, Giza, Egypt, <sup>2</sup>Geology, Beni-Suef University, Beni-Suef, Egypt

Well preserved Sirenia postcranial remains (vertebrae, ribs, and fragmentary limb bones) from the late Eocene succession exposed in the Beni Suef district, located in the north Eastern Desert, are recorded for the first time. The late Eocene succession of the Beni Suef Formation is divided into the Qurn and Tarbul members. Qurn Member consists of silty shale, gypsiferous shale, and marl, and is rich in benthic and planktonic foraminiferal species. We recorded the vertebrate remains from the Tarbul member, which consists of marly limestone, marl with thin beds of hard burrowed limestone, shale, and chalky limestone. The depositional environment of the Tarbul member was already revealed from the benthic foraminiferal assemblages ranging from inner to middle ramp with a high oxygen level condition. The specimens are preserved at the Vertebrate Paleontology Laboratory (VPL) of the Geology Department, Faculty of Science, Cairo University. A taxonomic and detailed morphologic description of Sirenia materials will be achieved. Sirenia are well known from the Eocene–Oligocene deposits of Egypt, especially in the Fayum area. In addition to the Fayum area, Sirenia are also known from other localities in Egypt, such as the middle Eocene of Gebel Mokattam near Cairo, Ain Musa near Cairo, and the Isthmus of Suez. There are two lineages of Sirenia recorded in Egypt: Protosirenidae and Dugongidae. In Africa, Sirenia have previously been recorded in the Eocene of Libya, Somalia, Togo and Madagascar. This discovery provides a new locality for the Sirenia in the Eocene deposits of Egypt.

#### Symposium: Dietary Reconstruction

### CORRELATION OF DIETARY PROXIES IN A LONG-TERM EXPERIMENT ON SHEEP (*OVIS ARIES*)

Ackermans, Nicole L.<sup>1</sup>, Winkler, Daniela E.<sup>1</sup>, Clauss, Marcus<sup>1</sup>, Codron, Daryl<sup>2</sup>, Hatt, Jean-Michel<sup>1</sup>

<sup>1</sup>Vetsuisse Faculty, University of Zurich, Zurich, Switzerland, <sup>2</sup>University of the Free State, Bloemfontein, South Africa

Dietary reconstruction often relies on dental wear-based proxies. Depending on the chosen method, these proxies

may reflect different temporal resolutions: macrowear (absolute tissue loss) represents a cumulative life-time signal, mesowear represents a long-term signal maintained by the abrasion-attrition wear equilibrium, and dental microwear texture analysis (DMTA) is thought to reflect the last few meals (days to weeks), thus most sensitive to recent dietary changes. Even though widely applied, the exact processes mesowear and DMTA actually represent remain unclear and we question whether these proxies also reflect absolute tissue loss on a millimeter to micrometer scale. Additionally, current analytical methods of DMTA include a large number of parameters that make data processing and interpretation cumbersome.

In order to gain a better understanding of the relationship between wear proxies and tooth wear processes, we tested how they correlate in a long term feeding experiment performed on sheep (*Ovis aries*, n = 38) fed diets of varying abrasiveness. Volumetric crown tissue loss and mesowear change were recorded over the course of 17 months. 3D microwear texture analysis (DMTA) was conducted at the end of the experiment on the same teeth to compare the effects of diet at the macroscopic and microscopic scales over time. We hereby correlate: (1) DMTA parameters with each other, for the maxillary molars (M1, M2, M3), and the second mandibular molar (m2); (2) Mesowear to DMTA in M1, M2, M3, and m2; (3) and volumetric crown tissue loss to mesowear and DMTA in M2.

Many DMTA measures correlated highly with each other, suggesting that they provide similar information and could possibly be reduced in number in future studies. However, few DMTA parameters correlated with mesowear, mesowear change, or volumetric tissue change. These findings caution against interpreting DMTA patterns in terms of actual tissue removal until these dental wear processes can be better understood at the microscopic and macroscopic levels.

**Funding Sources** This study was part of project 31003A\_163300/1 funded by the Swiss National Science Foundation.

#### Paleozoic Tetrapods & Lissamphibians

### AN UPDATED DESCRIPTION OF *CALLIGENETHLON WATSONI* BASED ON COMPUTED TOMOGRAPHY AND THE RESULTING IMPLICATIONS FOR THE TAXONOMY OF THE GENUS *CALLIGENETHLON*

Adams, Gabrielle R., Maddin, Hillary C.  
Earth Science, Carleton University, Ottawa, Ontario, Canada

The Joggins Fossil Cliffs in Nova Scotia, Canada, are known for their exceptional preservation of Pennsylvanian-aged tetrapod communities. One enigmatic but major constituent in these paleoenvironments are embolomeres, which were moderately-sized aquatic predators.

*Calligenethlon watsoni*, first described by Steen in 1934, was identified from a skull roof and scattered postcrania preserved in an upright lycopsid tree stump. Several specimens have since been attributed to this genus, all of which are similarly disarticulated and found within fossilized tree stumps. However, the most recently reported embolomere material, specimen NSM 994GF1.1, is an articulated anterior skeleton found as beach float. It was described by Holmes and Carroll and tentatively attributed to *Calligenethlon*, making it the best-preserved and most complete specimen for the genus. Few diagnostic characteristics are known for *Calligenethlon* and attributions to this genus frequently rely on a distinctively gracile ilium and a small body size although the latter has been challenged as truly diagnostic. However, as *Calligenethlon* is the only embolomere known from Joggins, any small but otherwise indeterminate embolomere material has been tentatively assigned to this taxon.

Here we provide an updated analysis of the genus *Calligenethlon* based on the first-ever anatomical description of NSM 994GF1.1 using micro-computed tomography. The specimen uniquely provides postcrania unequivocally associated with a skull and therefore permits a new assessment of other specimens currently attributed to *Calligenethlon*. Preliminary results reveal that the skull of NSM 994GF1.1 is consistent with that of the type specimen, as well as those referred to *Calligenethlon* by Carroll. These all show a similarly narrow skull roof with parallel lateral margins, rather than concave ones seen in *Archeria* and other embolomeres. All the skulls attributed to *Calligenethlon* bear elongate tabular horns that extend posteriorly parallel to each other and to the skull roof lateral margins. This morphology seems to be unique to this genus. Assessment is ongoing but other features uniting NSM 994GF1.1 and other *Calligenethlon* material are a strongly developed olecranon process and progressive ossification of the intercentra. Further examination will hopefully address questions of variation and reveal new features to replace size as the main diagnosis of this important early embolomere genus.

## Mesozoic Herpetology

### INCREASED SAMPLING OF *DELTASUCHUS MOTHERALI*, A NEOSUCHIAN FROM THE CENOMANIAN OF TEXAS, AND SUPPORT FOR ENDEMISM IN APPALACHIAN CRETACEOUS CROCODYLIFORMES

Adams, Thomas L.<sup>1</sup>, Drumheller, Stephanie K.<sup>2</sup>, Maddox, Hannah M.<sup>2</sup>, Noto, Christopher R.<sup>3</sup>, Sumrall, Colin D.<sup>2</sup>

<sup>1</sup>Curatorial, Witte Museum, San Antonio, Texas, U.S.A.,

<sup>2</sup>Department of Earth and Planetary Sciences, University of Tennessee, Knoxville, Tennessee, U.S.A., <sup>3</sup>Department

of Biological Sciences, University of Wisconsin–Parkside, Kenosha, Wisconsin, U.S.A.

New material attributable to multiple individuals of *Deltasuchus motherali*, a neosuchian from the Cenomanian of Texas, reveals numerous features that were not present in the fragmentary holotype. These new elements provide additional characters upon which to base more robust phylogenetic analyses. Previous analyses have recovered *D. motherali* forming a monophyletic clade with *Paluxysuchus newmani*, basal to Goniopholididae and other neosuchians. In order to test the evolutionary relationships of *D. motherali* and *P. newmani* within Neosuchia, a set of phylogenetic analyses were conducted using revised character codings for *D. motherali* that include new information derived from those elements that do not demonstrate any ontogenetic variability. In addition, a recently described crocodyliform (TMM 42536-2) from the Upper Cretaceous (early Campanian) Aguja Formation of Brewster County, Texas also was added to the analyses. The resulting phylogenetic analyses recovered all three Texas taxa within a clade of crocodyliforms, separate and diagnosable from goniopholidids and pholidosaurs. Characteristics of this new clade include: naris completely enclosed by premaxilla; long posterior ramus of prefrontal reaching the median region of the orbits; lateroventral border of the orbit composed by lacrimal and jugal; anterior and posterior rami of jugal comparable in depth; the posterior ramus of the jugal beneath the infratemporal fenestra is rod-shaped; jugal does not exceed the anterior margin of orbit; median process of the frontal extends anterior to the tip of the prefrontal; postorbital with anterolateral process present; surangular extends to the posterior region of the retroarticular process. The close connection between *P. newmani*, *D. motherali*, and TMM 42536-2 provides further support of an endemic group of Cretaceous neosuchians, currently best known from the subcontinent of Appalachia. This newly identified clade represents an Early Cretaceous radiation of crocodyliforms that coincided with the opening of the Western Interior Seaway. Taken all together, the analyses strengthen the argument that during the transition from the Early to Late Cretaceous of Texas the major vertebrate clades responded differentially, with non-eusuchian neosuchian crocodyliforms evolving gradually, whereas that for dinosaurs indicates rapid faunal change.

**Funding Sources** This research was funded by NSF DUE IUSE GEOPATHS-IMPACT grant #1600376, and the National Geographic Society, grant #C325-16.

## Fishes & Chondrichthyans: Evolution & Distribution

### ON THE HISTOLOGY OF TREMATASPIDIFORMES (AGNATHA) AND DISCORDICHTHYIFORMES

## (GNATHOSTOMATA), LOWER VERTEBRATES FROM THE PALEOZOIC OF RUSSIA

Afanassieva, Olga<sup>1</sup>, Bakaev, Alexandr<sup>1</sup>, Kogan, Ilja<sup>2</sup>  
<sup>1</sup>Paleoichthyological Laboratory, Borissiak Paleontological Institute of Russian Academy of Sciences, Moscow, Russian Federation, <sup>2</sup>Department of Palaeontology and Stratigraphy, Geological Institute, TU Bergakademie, Freiberg, Germany

New histological data on the exoskeleton and dental structures of different groups of early vertebrates allow to clarify how hard tissues developed in their onto- and phylogenesis. The fine structure of the shield of *Timanaspis kossovoii* (Timanaspidae, Tremataspidae, Osteostraci) was investigated based on new well-preserved material (Late Silurian, North Timan). The exoskeleton of *Timanaspis* is characterized by the presence of all three layers typical of osteostracans: mesodentin superficial layer and bony middle and basal layers. Like in other jawless vertebrates, hard covers of osteostracans lack enamel. In *Timanaspis*, enameloid tissue is present in the apical part of large tubercles of the dorsal side of shield and the uppermost part of smooth ventral shield. Study of thin-sections revealed the laminated structure of tissue in the tubercles, which provides the first evidence of superposition growth in timanaspids. Discordichthyiformes are an enigmatic group of fishes known from the middle-late Permian of European Russia. Originally described as actinopterygians based on similarities in skull and squamation, they exhibit pectoral and two dorsal fin spines, but apparently no ossified fin rays. Histological studies of *Mamulichthys ignotus* have revealed the absence of hypermineralized tissues (enamel homologues or enameloid) in scales, spines and dermal bones, while marginal teeth possess acrodin caps and collar enamel covering the shafts. This stands in contrast to the distribution of hypermineralized tissues in the phylogeny of Osteichthyes, enamel being absent in the basalmost osteichthyan *Lophosteus* (Late Silurian to Early Devonian, Northern Hemisphere), appearing on the scales of *Andreolepis* (Late Silurian, Sweden), covering dermal bones in *Psarolepis* (Late Silurian to Early Devonian, China), and being present on the teeth of more advanced osteichthyans. Bones, scales and spines of discordichthyiforms are ornamented with bony tubercles (odontodes), mushroom-shaped with a medially narrow base. The absence of buried odontodes in the bones and the presence of traces of breakage and resorption let us suppose that growth of skeletal elements was accompanied by basal resorption and shedding of odontodes, a process similar to tooth replacement in other osteichthyans. Thus, shedding of odontodes, which emerged on the oral margins, probably spread over the whole dermal skeleton of discordichthyiforms.

**Funding Sources** This research was funded by RFBR according to the research project 19-34-90040.

## Dinosaur Systematics, Diversity & Ecology

### FACIAL KERATIN AND TOOTH PRESENCE: COEVOLUTION FOR TRAITS IN DINOSAURS

Aguilar-Pedrayes, Isaura  
Earth Sciences, Montana State University, Bozeman, Montana, U.S.A.

Research on birds and reptiles, whose diversity is over triple that of mammals, indicates that beaks and teeth occur in a mutually exclusive manner. The macroevolution of these associations has only recently been explored, and these studies focus on the clade Aves and non-avian Coelurosauria. Currently, many hypotheses state an adaptive advantage for this trade-off but haven't been tested on a macroevolutionary scale. Examples in other types of dinosaurs and non-adaptive alternatives have yet to be explored thoroughly – for example, trait evolution correlation and phylogenetic history. Here I test if keratin specialization coevolved with tooth distribution across dinosaurs. My central hypothesis is that tooth distribution is negatively correlated with keratin ridges, representing beak-like keratin sheath, which leads to the eventual loss of teeth across dinosaurs. My approach is to use recently developed variable-rate phylogenetic comparative methods to a dataset of the tooth and cranial traits from specimens in Saurischia and Ornithischia. The diagnostic bone surface used as a proxy for the presence of keratin ridge in fossils is simple smooth grooved textures with foramina at the distal jaw end. Here I test for independence between these traits using Bayes Factor while accounting for shared ancestry. These methods will also be used for the reconstruction of ancestral values, and to quantify how the rate in evolution in these traits change over time. Preliminary results show rear and forward jaw tooth loss and jaw tip expansion of facial keratin ridge in theropods; retention of back teeth with a small toothless keratin sheath at the tip of the jaws in ornithischians, and sauropods lose the back teeth, and in some cases, the toothed jaw area coexists with the keratin ridge. There is support for a negative correlation of tooth position with keratin presence in the upper jaw with a strong phylogenetic signal (BF = 8.25;  $\lambda = 0.7$ ). This research suggests ancestry could have a significant role in determining both traits and could thus constrain a lineage animal's future feeding behavior and ecological function. On the other hand, the sauropod case contradicts the notion that teeth can't coexist with beak-like keratin. This case could either be evidence that the proxy for keratin ridge is inadequate or sauropods weren't using this structure in the same way as other animals.

## Late Cenozoic Mammalian Macroecology & Macroevolution

### RHINOCEROTIDS AS THE ECOLOGICALLY MOST SUCCESSFUL SIWALIK UNGULATES: ENAMEL HYPOPLASIA BASED IMPLICATION

Ahmad, Rana Manzoor<sup>1</sup>, Khan, Abdul Majid<sup>2</sup>, Waseem, Muhammad Tahir<sup>2</sup>, Ameen, Muhammad<sup>2</sup>, Roohi, Ghazala<sup>3</sup>  
<sup>1</sup>Department of Zoology, University of Okara, Okara, Pakistan, <sup>2</sup>Department of Zoology, University of the Punjab, Lahore, Pakistan, <sup>3</sup>Pakistan Museum of Natural History, Islamabad, Pakistan

Enamel hypoplasia (a dental defect characterized by thinning of tooth enamel) has been used by many researchers as a strong and reliable stress marker in various extinct as well as living mammalian taxa. The different types of enamel hypoplasia have different etiologies. Among these, linear enamel hypoplasia is the most common type and is usually associated with nutritional and/or environmental stresses faced by the animals during their life histories; so, it can be a good source for tracing out the ecological preferences of the prehistoric mammalian fauna. Even then, negligible comparative data is available on enamel hypoplasia based paleoecological implications of the extinct ungulates especially from the Siwalik region. In an effort to fill this gap, a comparative analysis of linear enamel hypoplasia in early Miocene–early Pleistocene ungulates from the Siwaliks of Pakistan was performed to compare the resilience of ungulate families against prehistoric paleoecological stresses. The chronological age of the material analyzed is 18.3–0.6 Ma. According to the current results, 41% of the total analyzed giraffid dental remains have an occurrence of linear enamel hypoplasia, followed by 35% of tragulid, 34% of hippopotamid, 30% of cervid, 26% of equid, 24% of bovid, 19% of suid, and 10% of rhinocerotid dental remains. The relative lack of linear enamel hypoplasia within the rhinocerotid remains suggests that they were the most ecologically successful Siwalik ungulates. Although this study could not explain the exact ecological precursor for this success, it does clearly indicate the ecological success of rhinocerotids compared to other ungulates.

### Anatomical & Developmental Explorations of the Mammalian Skull

#### FIRST COMPLETE ENDOCAST OF AN OXYAENID (*DIPSALIDICTIS KRAUSEI*)

Ahrens, Heather E., Passero, Marita  
Biology, High Point University, High Point, North Carolina, U.S.A.

Endocasts, which serve as indirect evidence of brain morphology and brain size, are necessary for the documentation and evaluation of patterns of brain evolution and encephalization. In particular, some authors have suggested that carnivoramorphans had a higher degree of encephalization, along with additional neuroanatomical adaptations, that may have contributed to their success over creodont taxa during the dramatic turnover of carnivore clades during the Paleogene of North America. However, the majority of analyses have focused on the more diverse carnivoramorphans and hyaenodont clades. Here we present the first complete endocast of an oxyaenid based on the exceptionally-preserved, late Paleocene taxon *Dipsalidictis krausei*. The digital endocast was compared to previously described endocasts of several Paleogene carnivores, including *Protictis schaffi*, *Proviverra typica*, *Thinocyon velox*, *Tritemnodon agilis*, and *Vulpavus palustris*. The endocast of *Dipsalidictis krausei* is dorsoventrally flattened and similar in overall proportions to that of *Tritemnodon agilis*. In addition, several features indicate minimal neocortical expansion in *Dipsalidictis krausei*, including large piriform lobes, as indicated by a high rhinal fissure, a singular neocortical sulcus, and dorsal exposure of the midbrain. The short, slightly arched lateral sulcus comprises the lone neocortical sulcus. Posteriorly, the cerebellar vermis is distinct, projecting more caudally than in comparative taxa. On the ventral surface, casts of the exits for all cranial nerves can be identified. Many of these features indicate that expansion of the neocortex had not reached the same extent as observed in modern carnivorans. However, the relative size was similar to that of the later Eocene creodonts, *Thinocyon velox* and *Tritemnodon agilis*, as well as the Paleocene carnivoramorphans *Protictis schaffi*. This first complete endocast of Oxyaenidae demonstrates that oxyaenid neuroanatomy was similar to other early Paleogene carnivores and will be crucial for determining patterns of convergent evolution in neocortical expansion in carnivorous mammal clades.

### Mesozoic & Early Cenozoic Mammalian Evolution

#### A NEARLY COMPLETE CRANIUM OF 'PTERODON' SYRTOS AND THE EVOLUTION OF AFRO-ARABIAN 'PTERODON' (HYAENODONTA, HYAINAILOURINAE)

Al-Ashqar, Shorouq F.<sup>3</sup>, Borths, Matthew R.<sup>1</sup>, Seiffert, Erik<sup>2</sup>, El-Sayed, Sanaa<sup>3</sup>, Antar, Mohamed S.<sup>4</sup>, Sallam, Hesham<sup>5</sup>

<sup>1</sup>Division of Fossil Primates, Duke Lemur Center, Duke University, Durham, North Carolina, U.S.A., <sup>2</sup>Department of Integrative Anatomical Sciences, University of Southern California, Los Angeles, California, U.S.A., <sup>3</sup>Department of Geology, Mansoura University, Mansoura, Egypt, <sup>4</sup>Geology and Paleontology Department, Egyptian

Environmental Affairs Agency, Maadi, Egypt, <sup>5</sup>School of Sciences and Engineering, American University in Cairo, New Cairo, Egypt

During the Paleogene in Afro-Arabia, most terrestrial mammalian carnivores belonged to Hyaenodonta, an extinct lineage primarily distinguished from Carnivora by the presence of a carnassial pair between each set of molars. Afro-Arabian hyaenodonts were ecologically diverse, ranging from small-bodied mesocarnivores to gigantic hypercarnivores. The Fayum Depression of Egypt preserves multiple lineages of hyaenodonts that cross the Eocene–Oligocene boundary. Successive quarries in the Jebel Qatrani Formation document changing hyaenodont diversity, primarily represented by dental remains. Here, we report one of the most complete hyaenodont cranium ever recovered from the upper sequence of the Jebel Qatrani Formation. Some partial hyaenodont crania have been recovered from the upper sequence of the Jebel Qatrani Fm., but most are referred to *Apterodon*, a medium-sized mesocarnivore. The new, hyena-sized cranium from Quarry I preserves the complete upper tooth row. The long, shearing metastyle and reduced and mesially shifted protocones indicate a hypercarnivorous diet. Based on dental comparisons, we tentatively refer the cranium to '*Pterodon*' *syrtos*, a hyainailourine hyaenodont previously known from the roughly contemporaneous Quarry M. The complete cranium reveals that '*P.*' *syrtos* has three premolars and two molars, a reduced dental formula compared to other Fayum hyainailourines such as *Akhmatenavus* and European hyainailourines such as *Pterodon*. The cranium preserves the clover-shaped lambdoidal crest and long pharyngeal tube that unites Hyainailouroidea. The zygomatic arches are deep and robust and the external nares are wide and flaring. As in other recent phylogenetic analyses, our Bayesian clock analysis indicates that the genus *Pterodon* is paraphyletic. Originally constructed around Eocene European cranial specimens, the new Fayum cranium allows us to reevaluate Afro-Arabian '*Pterodon*' and explore characters that distinguish Afro-Arabian from Eurasian hyainailourines. This effort will better inform the biogeographic history of this group of hypercarnivores that apparently dispersed across the Tethys Seaway multiple times, and persisted well into the Neogene.

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#### **Fishes & Chondrichthyans: Evolution & Distribution**

#### **CASTING A FISHNET INTO THE LATE CRETACEOUS WESTERN INTERIOR SEAWAY – MARINE VERTEBRATES IN A UNIQUE BONEBED**

#### **FROM THE NIOBRARA CHALK OF WESTERN KANSAS, U.S.A.**

Allen, Jonathan G., Shimada, Kenshu  
Department of Biological Sciences, DePaul University,  
Chicago, Illinois, U.S.A.

The Niobrara Chalk in western Kansas, U.S.A., is a rock formation formed in the Late Cretaceous Western Interior Seaway of North America and is well known for diverse fossil marine vertebrates. However, vertebrate remains in the rock unit are generally sparse and commonly represented by larger taxa. FHSM VP-644 is a calcareous rock specimen collected from the Niobrara Chalk in Gove County, Kansas, and housed in the Sternberg Museum of Natural History in Hays, Kansas. Its exact stratigraphic horizon within the formation is uncertain, but its occurrence in Gove County suggests that it must be of late Coniacian or early-middle Santonian in age. It is a unique specimen because it is packed with numerous, small, disarticulated bones and teeth of fossil marine vertebrates with very little matrix that can be characterized as a bonebed. A portion of the rock matrix was dissolved in acetic acid to extract skeletal and dental elements. Our preliminary analysis shows that the paleofauna is found to be taxonomically diverse, consisting of at least 16 fish taxa. They include chondrichthyan taxa such as *Cretoxyrhina mantelli*, *Squalicorax* cf. *S. falcatus*, *Nanocorax microserraton*, *Telodontaspis*(?) sp., and *Rhinobatos* sp., as well as osteichthyan fishes like *Palaeobalistum* sp., *Lepisosteus* sp., *Ichthyodectes ctenodon*, Plethodidae indet., Albulidae indet., *Pachyrhizodus minimus*, *Cimolichthys nepaholica*, *Stratodus apicalus*, *E. gladiolus*, *E. petrosus*, and at least one more species of *Enchodus*. In addition, several mosasaur teeth have been discovered. The bonebed has a rather poor stratigraphic constraint, likely represents a time-averaged unit possibly due to a temporal sea level fluctuation, contains only incomplete, mostly microscopic, skeletal remains, and is dominated by remains of *Enchodus* spp. However, it is significant given that it has already yielded about one-quarter of the total number of fish taxa reported from the Niobrara Chalk to date. More remarkably, the recovered fossils include remains of several taxa known from only one or two previous examples, or even recorded for the first time, in the Niobrara fossil record. Thus, collecting fossils from the bonebed is like casting a fishnet into the Western Interior Seaway where the diversity and relative abundance of taxa in the bonebed possibly represent a more accurate picture of vertebrate composition within the Seaway than the previously known fossil record of the Niobrara Chalk based on surface-collected samples.

#### **Mesozoic & Early Cenozoic Mammalian Evolution**

## RECENTLY DISCOVERED SPECIMENS OF *ACRITOPARAMYS* AND *FRANIMYS* HIGHLIGHT THE DIFFERENCES BETWEEN THESE TWO GENERA, KNOWN FROM THE EARLY EOCENE OF THE BIGHORN BASIN, WYOMING

Anderson, Deborah K.  
Biology, St. Norbert College, De Pere, Wisconsin, U.S.A.

Species of *Acritoparamys* and *Franimys*, two genera of early Eocene ischyromyids, are of long-time interest because they are considered to represent the most 'primitive' and oldest known rodents. Studying the features of the oldest known rodents is key to establishing character polarity, the basis for phylogenetic investigations. The main challenge faced by previous researchers is that *Acritoparamys* and *Franimys* are very similar in size and morphology, and have been recovered from common biochronologic zones in the same geographic region, making it difficult to differentiate among species of these two genera. To address this issue, I completed a critical review of the alpha taxonomy of *Acritoparamys* and *Franimys* starting with new specimens recovered from the Willwood Formation, Bighorn Basin, Wyoming and comparing them to specimens from other geographic regions. Results include descriptions of previously unpublished specimens of known taxa and discovery of a new species of each genus. The new species have a mix of ancestral and advanced features, many of which are useful for differentiating between the two genera; for example, isolation of the hypoconulid from the entoconid, a defined p4 protoconid, P4 with an incipient hypocone and a well-developed anterior cingulum, and upper molars with hypocone close to protocone diagnose *Acritoparamys* relative to *Franimys*. In *Franimys*, the hypoconulid is not well defined and it is connected to the entoconid via the posterolophid; the p4 protoconid is significantly reduced, closer to the size of a cuspule; P4 lacks a hypocone and the anterior cingulum is weakly developed; and the upper molar hypocones are distinctive and set apart from the protocone. Among these characters, the well-defined hypoconulid and incipient P4 hypocone of *Acritoparamys* suggest that members of this genus are more derived than those of *Franimys*, although the fossil record of *Acritoparamys* is older. Results of this study can be used to further investigate the evolutionary relationships between these two 'primitive' genera and eventually to establish character polarity for future phylogenetic studies of early Eocene rodents.

### Mesozoic & Early Cenozoic Mammalian Evolution

## THE OSTEOLOGY OF *GONIACODON*: SHEDDING LIGHT ON THE ENIGMATIC 'TRIIISODONTIDAE'

Anderson, Sophia C.<sup>1</sup>, Shelley, Sarah L.<sup>2</sup>, Bertrand, Ornella C.<sup>1</sup>, Williamson, Thomas E.<sup>3</sup>, Brusatte, Stephen<sup>1</sup>  
<sup>1</sup>School of Geosciences, University of Edinburgh, Edinburgh, U.K., <sup>2</sup>Section of Mammals, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A., <sup>3</sup>New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, U.S.A.

After the end-Cretaceous extinction, mammals increased in taxonomic diversity, body size, and ecological specialization during the Paleocene. The 'Triisodontidae' are an enigmatic group of small to medium sized ungulate-like mammals well known from their dentition, which shows specializations towards carnivory. While 'triisodontids' are well-described from dental material, their postcrania remain largely unknown. Here we describe the postcrania of *Goniacodon*, the most completely represented 'triisodontid' to date, from previously undocumented and historic specimens from the Nacimiento Formation in the San Juan Basin, New Mexico. Phylogenetic analysis places 'triisodontids' as a basal member of Euungulata within Laurasiatheria. 'Triisodontidae' forms a paraphyletic stem to Mesonychia with *Goniacodon* as sister to a clade comprising *Eoconodon*, *Triisodon*, *Oxyclaenus*, and Mesonychia.

Anatomical comparisons show that the limb bones of *Goniacodon* are robust relative to its size, though less so than the other 'triisodontids'. Attachment sites on the lower limbs indicate well-developed muscles associated with powerful flexion and extension of the manus and pes. The forelimb morphology indicates moderate pronation and supination comparable to that of extant scansorial mammals. *Goniacodon* appears to have had fine control over its mobile lower limbs, and was capable of varied locomotion. Based on the posterior semicircular canal of the inner ear, which was visualized by high-resolution computed tomography scanning, the agility score of *Goniacodon* is 2.8, which is comparable to the American badger with similar body size.

Additionally, the high trigonid, prominent protoconid, and mesiodistally aligned hypoconulid crest on the molars of *Goniacodon* and other 'triisodontids' aid in effective shearing. This, coupled with large posterior premolars and well-developed premolar shearing blades particularly in *Triisodon* and *Oxyclaenus*, indicate a transition towards carnivory. Bite force estimates indicate that 'triisodontids' possessed high bite forces, with *Eoconodon coryphaeus* having a bite force of 7363 Newtons, 1.65 times that of the spotted hyena. This is likely to compensate for their dentition being, as yet, not as specialized as extant carnivores.

The osteology of *Goniacodon* provides insight into a group of ungulate-like mammals that show anatomical shifts to exploit carnivore niches, exemplifying the adaptability of mammals to thrive in ever-changing environments.

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## **Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

### **BISON FROM THE SNAKE RIVER FOSSIL SITE, MINNESOTA**

Anderson, Tasha J.  
Research, The Mammoth Site, Hot Springs, South Dakota, U.S.A.

In May 2019, The Mammoth Site crew began excavation of a buried bison locality at the active bison ranch at the Snake River Farms in east-central Minnesota. The area today is an active fen (like a bog but with greater water exchange from small streams and groundwater). Due to the nutrient-rich environment, all the bones are stained black. Preliminary excavations in 2019 illustrated that the area containing the bison remains is approximately 30 by 20 m. One area of concentration contains two complete bison skeletons, one which is articulated. Measurements were taken from the skull, femur, tibia, calcaneus, astragalus, and metatarsal from the articulated specimen. Osteometric comparisons with metrics in literature indicate the size is within the range of *Bison antiquus occidentalis* but as expected is also within the upper range of *B. b. bison* and the lower range of *B. a. antiquus*. Radiocarbon analysis from a bison molar 20 m from the articulated specimen dates to 3,527±36 cal BP (3,300±27 14C BP: middle-late Holocene). The 14C analysis seems at odds with the taxonomic determination of a species presumed to be late Pleistocene to early Holocene. A direct radiocarbon analysis of the articulated bison is being processed. Little is known about bison in this region of the upper Great Plains. It seems to have been the northernmost edge of where bison inhabited during the late glacial and Holocene, and would have been one of the first areas they would have vacated as the climate changed.

### **Fishes & Chondrichthyans: Evolution & Distribution**

### **THREE-DIMENSIONAL MORPHOMETRY OF OTOLITHS AS A TOOL FOR QUANTIFYING HABITAT AND LOCOMOTOR DIVERSITY IN MODERN AND FOSSIL TELEOSTS**

Andrews, James, Friedman, Matt  
Department of Earth and Environmental Sciences,  
University of Michigan, Ann Arbor, Michigan, U.S.A.

Otoliths ('ear stones') of teleost fishes are mineralized bodies contained within the inner ear, and are implicated in aspects of proprioception and potentially hearing. This role

in detecting movement and orientation suggests that the morphology of isolated otoliths might yield information about the ecology of the fish to which they belong. This is supported by anecdotal convergence in otolith morphologies between distant lineages with similar locomotor ecologies (e.g., pelagic taxa), and limited quantitative evidence that otolith morphology covaries with body shape. Otoliths are commonly found as isolated fossils, and have a rich record in the Cenozoic and latest Mesozoic. Although isolated otoliths can rarely be linked to fossil species based on skeletal remains, possible links between form and function in these elements might provide a powerful tool for assessing patterns of ecological, most specifically locomotor, diversity in the fish fossil record. Here we assess the relationship between habitat, rates of morphological change in otoliths, and trends in the evolution of otolith shape in order to assess the possible utility of fossil otoliths for addressing these same questions in deep time. Previous studies of otoliths have relied on two-dimensional landmarking schemes, potentially excluding important variation in otolith shape. We generated three-dimensional models of the left sagittal otolith of 70 extant and five fossil teleost fishes through  $\mu$ CT scanning. Landmarks were generated on the model surfaces and aligned using a generalized Procrustes analysis. These were then examined in a comparative framework utilizing a time-calibrated molecular phylogeny, with fossil taxa being placed as tips using fossil priors. A tanglegram generated between the time-calibrated phylogeny and a nearest-neighbor joined topology of Procrustes distances shows poor agreement between phylogeny and shape, suggesting a non-Brownian model of evolution. Morphological disparity and rates of phenotypic evolution were estimated within five habitat classes: reef, demersal, benthopelagic, bathypelagic, and bathydemersal. These analyses indicate that otolith shape is labile at broad phylogenetic scales, and that care should be taken when assessing taxonomic placement of ex-situ otoliths within the fossil record. Furthermore, broad trends in extant otolith shape across habitat may provide a promising new avenue for understanding ecological dynamics in the geological past.

**Funding Sources** University of Michigan Rackham Merit Fellowship.

### **Anatomical & Developmental Explorations of the Mammalian Skull**

### **A NEW TILLODONT SKULL WITH EXCEPTIONAL PRESERVATION FROM THE GREAT DIVIDE BASIN, WYOMING**

Anemone, Robert L.<sup>1</sup>, Ahrens, Heather E.<sup>5</sup>, Crowell, Jordan W.<sup>2</sup>, Lundeen, Ingrid K.<sup>3</sup>, Morse, Paul E.<sup>4</sup>, Yokley, Todd R.<sup>4</sup>

<sup>1</sup>Anthropology, The University of North Carolina at Greensboro, Greensboro, North Carolina, U.S.A., <sup>2</sup>Anthropology, The Graduate Center, City University of New York, New York, New York, U.S.A., <sup>3</sup>Anthropology, The University of Texas at Austin, Austin, Texas, U.S.A., <sup>4</sup>Sociology and Anthropology, Metropolitan State University of Denver, Denver, Colorado, U.S.A., <sup>5</sup>Biology, High Point University, High Point, North Carolina, U.S.A.

The early Eocene Smiley Draw fauna derives almost entirely from a uniquely rich sandstone locality (Tim's Confession, Carnegie Museum Locality 4026) in the Great Divide Basin (GDB) of southwestern Wyoming that has yielded nearly five thousand mammalian fossils from the Wasatchian North American Land Mammal Age (NALMA). Twenty-eight taxa representing ten mammalian orders comprise the Smiley Draw fauna, including the Stage 2 transitional morphotype of the omomyid *Tetonius matthewi*, which has been used to biostratigraphically date the fauna to Wasatchian biozone Wa4. The Order Tillodontia first appears in North America during the late Paleocene Clarkforkian NALMA as part of an intercontinental dispersal event from Asia. Subsequent evolution of the genus *Esthonyx* through the Wasatchian has been characterized as a single evolving lineage: *E. spatularius* (Wa2-4), *E. bisulcatus* (Wa5-7), *E. acutidens* (Wa7). Here we describe a nearly complete cranium of *Esthonyx*, CM 95508, with minimal 3D distortion collected from CM Locality 4026 and draw ecological and behavioral inferences from its morphology based on high-resolution computed tomography. The upper dental formula is 2-1-3-3, with closed roots on all teeth, including the large and procumbent I2, and a lack of the hypsodonty characteristic of Bridgerian tillodonts. The P2 is double-rooted, as observed in *E. spatularius* and unlike the single-rooted condition of *E. acutidens*. While the size and proportions of M1-2 agree well with those of *E. spatularius*, the enlarged P3-4 and M3 and greater ratio of P3 width to length more closely resemble those of *E. bisulcatus*. On the basis of dental morphology, we tentatively ascribe CM 95508 to *E. spatularius*, although it may represent a morphological intermediate between *E. spatularius* and *E. bisulcatus*, consistent with its Wa4 age. Semicircular canal curvature suggests that *E. spatularius* was terrestrial in its habits and capable of locomotion at slow to medium speeds. This evidence is consistent with the robust postcranial elements known from Bridgerian tillodonts, which are suggestive of semi-fossorial positional behaviors. Based on dimensions of the fenestrum vestibuli, the hearing range of *E. spatularius* would have resembled that of the domesticated dog (*Canis*) or flying fox (*Pteropus*). CM 95508 preserves the first known record of turbinates in a tillodont, revealing double-scrolled turbinates similar to those seen in extant artiodactyls.

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## Macroecology & Macroevolution

### THE CHANGING ROLES OF INSECT AND TETRAPOD HERBIVORES IN PROMOTING TERRESTRIAL ECOSYSTEM STABILITY FROM THE PENNSYLVANIAN TO THE TRIASSIC

Angielczyk, Ken<sup>1</sup>, Roopnarine, Peter<sup>2</sup>, Olroyd, Savannah<sup>3</sup>, Kammerer, Christian F.<sup>4</sup>, Pardo, Jason<sup>5</sup>

<sup>1</sup>Field Museum of Natural History, Chicago, Illinois, U.S.A., <sup>2</sup>California Academy of Sciences, San Francisco, California, U.S.A., <sup>3</sup>University of Washington, Seattle, Washington, U.S.A., <sup>4</sup>North Carolina Museum of Natural Sciences, Raleigh, North Carolina, U.S.A., <sup>5</sup>University of Calgary, Calgary, Alberta, Canada

The diversification of amniote herbivores from the Pennsylvanian through the Permian was a key event in vertebrate evolution. Not only did it greatly increase tetrapod morphological and functional disparity, it also resulted in a major restructuring of terrestrial communities. Diverse, abundant amniote herbivores became a central link between primary producers and tetrapod secondary consumers, allowing large carnivores to feed at lower trophic levels. The replacement of amniote herbivore-depauperate communities by communities with diverse herbivores raises the possibility that herbivore-rich communities were more stable or better able to resist disturbances that could cause species extirpation or extinction. However, previous experiments with the Cascading Extinctions on Graphs model suggest that insects played a more important role than amniote herbivores in increasing community perturbation resistance in the Pennsylvanian and Cisuralian (early Permian). Here we applied a new model to a series of communities spanning the Pennsylvanian to the Middle Triassic. The model quantifies the number of species that can stably co-exist in a community given a specified food web topology and a range of positive and negative species interactions. Experiments varying insect richness in North American Pennsylvanian-Cisuralian communities demonstrate the key role of insects in facilitating stable co-existence. By contrast, tetrapod herbivore richnesses in these communities are generally too low to have a comparable effect. The situation appears to have changed by the Lopingian (late Permian), as demonstrated by the natural experiment of the Permo-Triassic mass extinction in the Karoo Basin of South Africa. There, a latest Permian tetrapod assemblage with numerous amniote herbivore species distributed across several guilds is replaced by an Induan (Early Triassic) assemblage with greatly reduced herbivore diversity and a much lower capacity for stable species co-existence. Stability returns to the Karoo system in the Middle Triassic as tetrapod herbivores re-diversify.

Stability can also be experimentally induced by manipulating insect richness. Together, these results suggest that amniote herbivores did impact the stability of Pennsylvanian–Triassic terrestrial ecosystems, but the magnitude of that impact was strongly linked to their diversity. Furthermore, the importance of amniote herbivores in maintaining stability may be secondary to insects across the time interval.

## Quantitative Methods

### INTEGRATING GROUND-PENETRATING RADAR, GEOCHEMICAL, AND PETROGRAPHICAL RESULTS TO INVESTIGATE A TRACKWAY AND BONEBEDS WITHIN THE MORRISON FORMATION

Apgar, Alexandra D.<sup>1</sup>, Henson, Harvey<sup>1</sup>, Seaman, Zachariah<sup>1</sup>, Seaman, Kailey<sup>1</sup>, Henson, Angela<sup>2</sup>

<sup>1</sup>School of Earth Systems and Sustainability, Southern Illinois University Carbondale, Carbondale, Illinois, U.S.A., <sup>2</sup>STEM Education Research Center, Southern Illinois University Carbondale, Carbondale, Illinois, U.S.A.

Exposures of the Morrison Formation within the western U.S.A. are well-known for the preservation of prehistoric remains from the Jurassic Period. Outcrops near Thermopolis, Wyoming, contain Jurassic fauna such as *Camarasaurus*, *Diplodocus*, *Apatosaurus*, and *Allosaurus*, and include a large ichnofossil trackway. Previous studies concluded that these lime mud deposits were a result of seasonal wet/dry fluctuations forming shallow alkaline lakes. Non-invasive, high resolution ground-penetrating radar (GPR) data was collected from three field sites within this formation to extend site stratigraphy, identify subsurface bonebeds, and image dinosaur fossil remains. GPR is a geophysical technique that utilizes electromagnetic energy to create images of the near surface. An ultra-high frequency micro-GPR system was used to detect in situ bones to depths <1 meter, and a hyperstacking 350MHz system provided stratigraphic data down to 5 meters. Hand samples of Morrison Formation limestones and mudstones were also collected at each site for the purpose of performing geochemical analysis and petrographic examination. The combination of stratigraphic observations, geochemical and petrographic results, and interpreted GPR data have revealed new paleodepositional environment information for these sites. Furthermore, findings from this study suggest that the integration of GPR with geochemical and petrographic results could benefit future investigations and excavations of fossiliferous strata.

## Paleozoic Tetrapods & Lissamphibians

### NEW INSIGHTS ON THE TEMNOSPONDYL FAUNA FROM JOGGINS FOSSIL CLIFFS WITH DISCUSSION OF EARLY TEMNOSPONDYL RELATIONSHIPS

Arbez, Thomas, Mann, Arjan, Atkins, Jade B., Maddin, Hillary C.

Department of Earth Sciences, Carleton University, Ottawa, Ontario, Canada

The Joggins Fossil Cliffs, classified as a UNESCO World Heritage site, yields a long history of scientific research with more than 100 publications in over 150 years of research. For vertebrate paleontology, the significance of Joggins resides in the rich record of key tetrapod fossil groups preserved in the paleoenvironment they lived (*ecolagerstätte*) including many early or earliest occurrences of several diverse tetrapod clades, such as *Dendrerpeton* for Temnospondyli (only *Balanerpeton* occurs earlier), *Hylonomus* for Amniota, the oldest ‘Microsauria’ (e.g., *Leiocephalikon*, *Smilerpeton*) and *Asaphestera* and *Protoclepsydraps* for Synapsida. With the application of new tools to historical material and to the discovery of new material, new insights into tetrapod diversity at Joggins are now available.

A CT-scan and redescription of the most complete tetrapod specimen found at Joggins, the temnospondyl amphibian currently referred to *Dendrysekos*, allowed access to the internal anatomy revealing new anatomical structures for this specimen including the stapes, a sclerotic ring, and a partial braincase. The anatomical comparisons and phylogenetic analysis suggest that the genus *Dendrysekos* is a junior synonym of *Dendrerpeton*, as the diagnostic characters distinguishing the two genera are considered to be instead a combination of ontogenetic and preservational parameters. In addition, the phylogenetic analysis shows that early temnospondyl relationships are more uncertain than previously thought due to the low number of shared derived characters grouping the main early temnospondyl groups (Edopoidea, Dvinosauria, Eryopidae and Dissorophoidea).

Interestingly, a new skull, thought to belong to the same taxon as the articulated skeleton of *Dendrerpeton*, was recently discovered. The CT-scan of this skull shows that the specimen is clearly distinct from *Dendrerpeton* based on the shape of the skull and the location of orbits. The preliminary identification based on the 3D model suggests affinities with either Dissorophoidea or Dvinosauria. This would be the third temnospondyl genus known from Joggins (in addition to an undetermined cochleosaurid) and makes it the oldest representative of either Dissorophoidea or Dvinosauria. Together this work is allowing us to better understand the temnospondyl amphibian’s diversity in Joggins and address questions of early temnospondyl phylogenetic relationships.

**Funding Sources** NSERC RGPIN-06442.

### **Dinosaur Systematics, Diversity & Ecology**

#### **EVIDENCE FOR INTRASPECIFIC COMBAT, RATHER THAN ANTIPREDATOR DEFENSE, AS THE SELECTIVE PRESSURE UNDERLYING THE EVOLUTION OF ANKYLOSAURINE TAIL CLUBS**

Arbour, Victoria<sup>1</sup>, Zanno, Lindsay E.<sup>2</sup>, Evans, David<sup>3</sup>  
<sup>1</sup>Royal BC Museum, Victoria, British Columbia, Canada,  
<sup>2</sup>North Carolina Museum of Natural Sciences, Raleigh,  
North Carolina, U.S.A., <sup>3</sup>Royal Ontario Museum, Toronto,  
Ontario, Canada

Ankylosaurine tail clubs are a rare form of weaponry without close analogues among living taxa. In both popular media and the scientific literature, tail clubs are typically interpreted as antipredator defensive weapons that evolved through natural selection. However, in many extant animals with elaborate cranial weaponry, these weapons are used primarily for intraspecific combat and have evolved under sexual selection. Tail clubbing behaviors cannot be directly observed in ankylosaurs, so it is unclear if they were used primarily for antipredator defense or in intraspecific combat, and the role of natural vs. sexual selection in their evolution remains unclear.

Here we test two alternative hypotheses regarding the dominant selective pressures underlying the evolution of ankylosaur tail clubs: 1) they evolved primarily for antipredator defense, and 2) they evolved primarily for intraspecific combat. If tail clubs evolved in response to predation, then changes in tail morphology should be dependent upon some aspect of the predators in that ecosystem, such as maximum predator size, ecology, or overall biodiversity. If tail clubs evolved as weapons of intraspecific combat, then ankylosaur tail club morphology may follow allometric scaling and develop late in ontogeny; additionally, ankylosaur postcranial skeletons may also bear paleopathologies consistent with ritualized intraspecific combat, such as injuries to the ribs or flank armour. We tested the relationship between ankylosaur tail club knob size and apex predator body mass, and present new paleopathological data based on ROM 75860, the holotype of *Zuul crurivastator*.

We found no relationship between maximum tail club knob width and apex predator mass through time, suggesting that tail club morphology was not influenced by this aspect of predator biology. However, we did find tantalizing evidence for intraspecific combat in ankylosaurines: the postcranial skeleton of ROM 75860 has broken and healed osteoderms on both sides of the pelvis, but not elsewhere on the body. The localized nature of these injuries, the absence of theropod bite marks, and the observation that different osteoderms are at different stages of healing,

suggests that these were not inflicted by a predator; we interpret these injuries as having been inflicted by a conspecific. Taken together, these independent lines of evidence argue against antipredator defense as the primary function of ankylosaurine tail clubs.

### **Marine Reptile Diversity & Biology**

#### **REVISION OF THE GENUS *STYXOSAURUS* AND RELATIONSHIPS OF THE LATE CRETACEOUS ELASMOSAURIDS (PLESIOSAURIA, SAUROPTERYGIA) OF THE WESTERN INTERIOR SEAWAY**

Armour Smith, Elliott<sup>1</sup>, O'Keefe, Frank R.<sup>2</sup>  
<sup>1</sup>Department of Biology, University of Washington,  
Seattle, Washington, U.S.A., <sup>2</sup>Department of Biological  
Sciences, Marshall University, Huntington, West Virginia,  
U.S.A.

Growing evidence indicates that elasmosaurid plesiosaurs from the Late Cretaceous Western Interior Seaway are members of a single clade, Styxosaurinae. Postcranial characters are evolutionarily plastic in plesiosaurs, including neck length in elasmosaurs. Therefore, scrutiny of cranial osteology is pertinent to advancing understanding of Western Interior Seaway elasmosaurids. This study finds that an elasmosaurid specimen (UNSM 50132) from the Cenomanian of Nebraska is remarkably similar in cranial morphology to the Campanian *Styxosaurus snowii* (KUVP 1301). The phylogenetic affinity of UNSM 50132 was tested with a cladistic analysis with 94 Operational Taxonomic Units (OTU) and 270 anatomical characters, utilizing a previous character matrix with changes and additions. The analysis supports five unambiguous synapomorphies for the genus *Styxosaurus*: (1) dorsomedian ridge of premaxilla located posteriorly; (2) dorsal portion of squamosal reflected anteriorly in lateral view; (3) posteromedian ridge on the supraoccipital; (4) a sharp ridge or keel located adjacent to the mandibular symphysis; (5) a retroarticular process that is shorter in anteroposterior length than the glenoid. Four additional ambiguous synapomorphies that support the monophyly of *Styxosaurus* include: lateral expansion of the maxilla that supports caniniform teeth, anisodont dentition, anterior embayment of the squamosal arch, an elongate posteromedian process of the premaxilla, a rugose boss on the ectopterygoid, and elongate anterior to middle cervical centra. 67% of 100 bootstrap replicates support the monophyly of UNSM 50132 with three *Styxosaurus* OTUs. UNSM 50132 was previously referred to the genus *Thalassomedon*. The potential referral of UNSM 50132 to the genus *Styxosaurus* pushes back the earliest occurrence of Styxosaurinae in the Western Interior Seaway by over ten million years. Maximum parsimony analysis suggests

that all Western Interior Seaway elasmosaurids belong to a single clade, including the genera *Libonectes* and *Thalassomedon*. *Libonectes* and *Thalassomedon* have been previously recovered as outgroup taxa to a clade composed of the sister relationship of Styxosaurinae and Aristonectinae. This study highlights the need for greater taxon sampling of Early Cretaceous elasmosaurids to evaluate the timing of the divergence between Styxosaurinae and Aristonectinae divergence and the affinity of Late Cretaceous elasmosaurs found outside of the Western Interior Seaway.

## **Taphonomy & Stratigraphy**

### **TAPHONOMY OF STELLER'S SEA COW FROM BERING ISLAND, NORTH WEST PACIFIC**

Armour-Chelu, Miranda  
Anatomy, University of Uniformed Services, Boyds, Maryland, U.S.A.

The Steller's sea cow (*Hydrodamalis gigas*) inhabited the shallow reefs along the shoreline of Bering and Copper Island in the North West Pacific and was hunted to extinction by fur traders (promyshlenniki) during the latter half of the 18th century. Approximately one hundred years later its bones were avidly sought by natural history museums worldwide and an extensive collection was acquired for the Smithsonian Institution by Leonard Stejneger, then curator of birds.

A taphonomic study of this assemblage found that many bones had been recovered from a peat like substrate as shown by matted vegetation still contained within foramen and cranial sutures. This corroborates historical accounts of the recovery of sea cow skeletons and bones from terrestrial deposits a few hundred feet distant from the sea. The eastern shoreline of Bering Island comprises a series of capes and bays often associated with a well-developed berm, typically covered with a luxuriant vegetation. Partial skeletons of sea cow are occasionally found eroding from these banks indicating the deposition of carcasses above the tide line. Bering Island lies in the path of 50 to 60 cyclones per year that generate giant waves in excess of 30 feet, fully capable of transporting carcasses of marine mammals for burial in backshore deposits and potentially fossilization.

## **Biomechanics & Functional Morphology**

### **FINITE ELEMENT ANALYSES OF THE FUNCTION OF THE PEDAL CLAWS OF *DEINONYCHUS ANTIRRHOPUS***

Ascari, Silvia H., Polly, P. David

Earth and Atmospheric Sciences, Indiana University, Bloomington, Indiana, U.S.A.

The function of the hypertrophied pedal claws of deinonychosaurids has often been debated, because there are few modern analogs of terrestrial bipedal animals with singular enlarged claws on their pes. This study looks at the efficiency of the enlarged pedal claws of *Deinonychus antirrhopus* at performing the functions of digging, climbing, terrestrial locomotion, and pinning down prey, using Finite Element Methods and comparing them to the performance of claws of modern animals that are specialized for each of those functions. 3D scans of claws were collected from fossil *Deinonychus* and 22 living species of mammals and birds with specializations for these four functions. Finite element modeling was carried out in order to simulate scenarios for each function. To evaluate performance of terrestrial locomotion, forces were applied to simulate plantar collision of each claw with a flat surface and the stresses were compared between them, with lower stress measurements as indication of efficiency at that task. Similarly, performance at climbing was modeled by forces to the tips of the claws. Pinning and digging claws are modeled by translating the tips of the claw into a soft cube; material displacement is then measured as a change in the volume of the cube, with greater material displacement as indication for efficiency at digging, whereas less material displacement, and thus greater puncturing potential, is regarded as indication of efficiency at piercing and pinning down prey. Compared to modern claws, the hypertrophied pedal ungual of *Deinonychus* is found to best perform the function of pinning, to not perform well the function of digging, and has similar breaking points as modern pinning claws if used for terrestrial locomotion or climbing. A non-hypertrophied pedal ungual of *Deinonychus* performs as well as terrestrial claws, showing an adaptation for terrestrial locomotion, whereas the hypertrophied claw is clearly specialized for a different function, most likely pinning down prey.

**Funding Sources** Galloway, Perry, and Horowitz Fellowship from Indiana University.

## **Quantitative Methods**

### **FOSSILS AND THE TREE OF LIFE: MAKING GENOMIC DATA INFORMATIVE FOR EXTINCT VERTEBRATES WITHOUT DIRECT ACCESS TO MOLECULES**

Asher, Robert J.<sup>1</sup>, Beck, Robin M.<sup>4</sup>, Field, Daniel J.<sup>3</sup>, Benson, Roger B.<sup>2</sup>

<sup>1</sup>Zoology, University of Cambridge, Cambridge, U.K., <sup>2</sup>University of Oxford, Oxford, U.K., <sup>3</sup>Earth Sciences, University of Cambridge, Cambridge, U.K., <sup>4</sup>University of Salford, Salford, U.K.

Paleontology's fundamental contribution to science includes understanding how extinct species relate to the living. Major questions about antiquity and diversification all depend on accurately reconstructing fossils on the Tree of Life. However, fossils are poorly known compared to living species, having degraded with usually no traces of DNA or soft tissues. Molecular data are sometimes recovered from very recent fossils, but in general are exceedingly rare and will remain so for the foreseeable future. Here, we apply a method that incorporates genomic data from living species and, in turn, fundamentally reshapes the phylogenetic tree of living and fossil species alike. This method does not require direct access to fossil biomolecules, but can nonetheless change our understanding of the evolutionary affinities of long-extinct fossil groups. We incorporate genomic signal by using morphology reconstructed from predicted ancestors on well-corroborated trees of living species, and re-include such ancestors as terminal taxa in phylogenetic analyses of fossils. With examples from Mesozoic mammals and maniraptoran dinosaurs, we show that this method recovers a signal supported by genomic data for living taxa using only morphological data. Examples from mammals include monophyletic Laurasiatheria, Afrotheria, Xenarthra, and Euarchontoglires, as well as glirids and *Aplodontia* among sciuriform rodents. For fossils, our results indicate that at least some anatomically well-known North American 'condylarths' are more closely related to Laurasiatheria than Afrotheria. In addition, we demonstrate that morphological datasets applied to mammalian and maniraptoran phylogenetics vary in their ability to reconstruct well-corroborated clades. Some morphological datasets improve congruence of topologies derived from subsampled sequence alignments with the well-corroborated tree; others decrease congruence. We provide a set of criteria which we hope will be of use to the wider community in vetting the relative information content of morphological datasets relevant for paleontology, and hope to end at least some, seemingly intractable, debates about the phylogenetic affinities of long-extinct species lacking genomic data.

### Dinosaur Systematics, Diversity & Ecology

#### THE CRANIAL ANATOMY OF A NEW ORODROMINE FROM THE CENOMANIAN-AGED MUSSENTUCHIT MEMBER OF THE CEDAR MOUNTAIN FORMATION, UTAH

Avrahami, Haviv M.<sup>1</sup>, Makovicky, Peter J.<sup>2</sup>, Zanno, Lindsay E.<sup>3</sup>

<sup>1</sup>Biological Sciences, North Carolina State University, Raleigh, North Carolina, U.S.A., <sup>2</sup>Dept. of Earth and Environmental Sciences, University of Minnesota,

Minneapolis, Minnesota, U.S.A., <sup>3</sup>Paleontology, North Carolina Museum of Natural Sciences, Raleigh, North Carolina, U.S.A.

Orodromines are a clade of small-bodied neornithischian dinosaurs known predominantly from the Cretaceous (112–76 Ma) of North America. Although several species are known from relatively large assemblages of multiple, nearly complete individuals (e.g., *Oryctodromeus*, *Orodromeus*), the cranial anatomy of orodromines has not been comprehensively detailed, particularly in comparison to their sister group Thescelosaurinae. Here we describe select cranial elements of a new genus of orodromine from the Cenomanian-aged (98–96 Ma) Mussentuchit Member of the Cedar Mountain Formation, Utah. Described materials stem from several individuals of various ontogenetic stages and to date, include the braincase, dentary, frontal, lacrimal, palpebral, parietal, prefrontal, premaxilla, prootic, pterygoid, quadrate, squamosal, and surangular, allowing us to comment on individual and ontogenetic variation.

We estimate the skull length of a subadult individual of the Mussentuchit orodromine at 16.8 cm, suggesting this animal is similar in size to the largest orodromine, *Oryctodromeus* (skull length 18 cm). Additionally, some aspects of the skull morphology scale non-isometrically across ontogeny. For example, although both subadult and juvenile frontals have the same dorsoventral thickness, subadult frontals are 64% longer in rostrocaudal length, suggesting elongation, but not thickening, of the skull roof in ontogeny. Furthermore, an ontogenetic series of three surangulars varies in morphology and in the quantity, size, and location of foramina. The quadrate is well represented in *Orodromeus*, *Oryctodromeus*, *Zephyrosaurus*, and the Mussentuchit orodromine, and we document variation in this element within orodromines, including the degree of mediolateral curvature, prominence of the jugal and pterygoid wings, position of foramina, and size and placement of ventral condyles.

Finally, excellent preservation of cranial materials in our new taxon allows us to better characterize the distribution of taxonomically significant traits among thescelosaurids generally. In particular, we note that features previously considered autapomorphic for *Thescelosaurus*, such as a foramen located on the dorsal surface of the prefrontal near the dorsomedial margin of the supraorbital boss, and a dorsolaterally directed process on the lateral surface of the surangular, are present in the Mussentuchit orodromine, indicating they have a wider distribution among thescelosaurids than previously recognized.

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### Paleozoic Tetrapods & Lissamphibians

## **SIGNIFICANT NEW PIPIMORPH REMAINS (AMPHIBIA, ANURA) FROM THE CENOMANIAN CANDELEROS FORMATION OF NORTHWESTERN PATAGONIA, ARGENTINA**

Báez, Ana M.<sup>2</sup>, Muzzopappa, Paula<sup>1</sup>

<sup>1</sup>CONICET, Fundación Azara, Universidad Maimónides, Ciudad Autónoma de Buenos Aires, Argentina,

<sup>2</sup>CONICET, Universidad de Buenos Aires, Museo Argentino de Ciencias Naturales, Ciudad Autónoma de Buenos Aires, Argentina

In northwestern Patagonia, the Neuquen Group, which constitutes part of the sedimentary filling of the Neuquen Basin, has yielded diverse vertebrate fossils that shed light on their evolution throughout most of the Late Cretaceous. In particular, the lowermost unit of this group, the Candeleros Formation, has furnished a large assortment of vertebrate remains, including the holotype of the pipimorph anuran *Avitabatrachus uliana*. Here we describe anuran material recently collected near the town of El Chocón, from outcrops of the Candeleros Formation exposed on the western coast of the Ramos Mexia Reservoir, Neuquen province. This material (Museo Municipal Ernesto Bachmann, Villa El Chocón-PV 259) consists of several incomplete, partially articulated postcranial elements exposed in ventral view, which clearly belong to a post-metamorphic individual. Seven discrete opisthocoelous presacral vertebrae, a sacral vertebra, and the anterior portion of the urostyle comprise the preserved axial skeleton. The centrum of the anteriormost discernable vertebra is missing, but it bears short transverse processes. Long transverse processes that might include coalesced ribs are associated with the succeeding two vertebrae, suggesting that they are presacrals III and IV. Vertebra IX bears distally expanded diapophyses that reach the iliac shafts. Expanded webs of bone denoting the presence of postsacral vertebrae occur on the anterior portion of the urostyle; the most anterior of these webs (vertebra X) are directed forward to join the posterior margin of the diapophyses on the preceding vertebra (IX). Although the anterior end of the ossified hypochord reaches the hind part of vertebra IX, it is not completely fused to the latter nor to the coccygeal neural arches, indicating that this specimen might not be a fully grown individual. This evidence calls into question the previous interpretation of *Avitabatrachus uliana* as having a fused sacrum and urostyle. Instead, the partial transverse processes on the isolated urostyle of the holotype might belong to a postsacral vertebra, with the last presacral centrum and sacral vertebra probably missing. This evidence confirms that the sacrum in pipoids results from different ontogenetic pathways and that the monovertebral sacrum formed by vertebra IX probably is a plesiomorphic condition that among pipimorphs evolved into a more

complex structure incorporating either the last presacrals or postsacral vertebrae.

## **Quantitative Methods**

### **IODINE-BASED CONTRAST-ENHANCED COMPUTED TOMOGRAPHY APPLIED TO FOSSILIZED TISSUES: A CASE STUDY IN A FOSSIL BIRD PROVIDES POSITIVE RESULTS**

Bailleul, Alida, Lu, Jing, Li, Zhiheng

Key Laboratory of Vertebrate Evolution and Human Origins, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China

Iodine-based contrasting agents for computed tomography (CT) have been used for decades in human medicine. These agents, such as Lugol's iodine (I<sub>2</sub>KI), positively enhance the contrast between soft (non-mineralized) tissues and mineralized tissues (bone and calcified cartilage) in biological samples. A recent study on avian heads determined that iodine-ethanol (I<sub>2</sub>E) outperforms Lugol's iodine, providing higher contrast between different soft tissues, but also between mineralized and soft tissues. Because I<sub>2</sub>E is a successful contrast agent for extant avian bone, here, we tested if this agent could also enhance contrasts in fossilized bone using a partial ankle joint from an extinct bird (pheasant) from the late Miocene of the Linxia Basin in northwest China.

Prior to any staining, the CT scans showed no microstructural details of the sample. After being immersed into a solution of 1% I<sub>2</sub>E for 7 days and scanned a second time under the same settings, the contrasts were drastically enhanced between the bony trabeculae, articular calcified cartilage, sediments, and mineral infillings inside vascular spaces. The sample then underwent three other staining-scanning cycles in a 2%, 3%, and finally 6% I<sub>2</sub>E solution, and the best results were obtained in 6% I<sub>2</sub>E. Half of this sample was then transformed into a ground-section to analyze the histological integrities of the tissues and the staining pattern of iodine using Energy Dispersive Spectroscopy. The other half of the sample was destined in a solution of pure ethanol for 8 days, which almost entirely removed the brown staining due to iodine absorption and did not cause any damage to the specimen. This method not only effectively increased the contrasts of fossilized avian bone trabeculae and calcified cartilage, it was also non-destructive and reversible. To our knowledge, this study represents the first use of a CT contrasting agent on any fossil material, and even though this method still has limitations, these preliminary results indicate that it has the potential to be used widely in vertebrate paleontology to improve CT imaging of fossilized tissues, pending some protocol refinement to annihilate any risk of permanent staining or breakage. Our

study shows for the first time that X-ray contrasting agents that successfully work on extant tissues can also be used on fossilized tissues, most likely regardless of their geologic age or taxonomic affinities.

**Funding Sources** China National Science Foundation 41772013; Chinese Academy of Sciences-President's International Fellowship Initiative (CAS-PIFI).

### **Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

#### **DIETARY BEHAVIOR OF WOLVERINES FROM NATURAL TRAP CAVE (WYOMING) AS INFERRED FROM DENTAL MICROWEAR TEXTURE ANALYSIS**

Baker, James<sup>1</sup>, Meachen, Julie<sup>2</sup>, DeSantis, Larisa<sup>1</sup>

<sup>1</sup>Vanderbilt University, Nashville, Tennessee, U.S.A., <sup>2</sup>Des Moines University, Des Moines, Iowa, U.S.A.

The wolverine (*Gulo gulo*) is often characterized as being an opportunistic hypercarnivore, that is capable of acquiring prey and scavenging carcasses. Today, these mustelids have become highly restricted from both historic and Pleistocene ranges to predominantly higher latitudes – though fossil occurrences throughout North America are rare. Recently, a new species from the Pliocene of eastern Tennessee was described, *Gulo sudorus*, both demonstrating their presence in warm and wet localities and their co-occurrence with alligators, sloths, red pandas, and tapirs. Pleistocene wolverines (*Gulo* sp.) have also been described from Natural Trap Cave in Wyoming (U.S.A.). Here, we examine the dental microwear textures of wolverine teeth from specimens collected from Natural Trap Cave (in collections at Kansas University, n = 10) as compared to a baseline of extant wolverines (n = 105 from Alaska). The Alaskan specimens were collected from 1963–2012 (in collections at the University of Alaska Museum of the North). Anterior and posterior regions of carnassial teeth in wolverines are used for shearing and crushing, respectively. As the talonid basin of lower first molars (the crushing facets) were often too damaged to examine dental microwear in the fossils, we instead examined the shearing facet of wolverines through time. While shearing facets are more likely to document tough food consumption, and are less likely to indicate hard object feeding, we nevertheless see dramatic differences in DMTA variables of complexity and textural fill volume between *Gulo* sp. at Natural Trap Cave and extant wild-caught wolverines from Alaska. Specifically, complexity and textural fill volume are significantly higher at Natural Trap Cave (p <0.01 and p <0.0001, respectively) as compared to extant wolverines. This difference may demonstrate a latitudinal shift in diet and/or a temporal shift to less hard food consumption, today. More work is

needed on recently extirpated/historic specimens from lower latitudes and higher latitude Pleistocene species to differentiate between the effects of latitude and time. Robust craniodental features capable of durophagy may be an adaptation to past diets (either historic or prehistoric), with hard-food consumption occurring less frequently today.

**Funding Sources** This work was performed on equipment funded by the National Science Foundation (1053839).

### **Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

#### **HOW DID COUGARS AND BOBCATS RESPOND TO THE CHANGES AT THE END OF THE PLEISTOCENE?**

Balassa, Daniella<sup>1</sup>, Prothero, Donald R.<sup>3</sup>, Syverson, Valerie J.<sup>2</sup>

<sup>1</sup>College of Natural Science and Mathematics, Cal State Long Beach, Northridge, California, U.S.A., <sup>2</sup>Department of Geosciences, University of Wisconsin, Madison, Wisconsin, U.S.A., <sup>3</sup>Natural History Museum of Los Angeles, Los Angeles, California, U.S.A.

At the end of the Pleistocene, most of the large mammals vanished from North America, including the predators (such as saber-toothed cats, dire wolves, Ice Age lions, and short-faced bears). Previous studies have shown that the coyotes of the late Pleistocene were bigger and more robustly built to compete for larger prey and then grew smaller and more gracile in the Holocene when their predator competition and large prey both disappeared. How did the surviving large cats respond to this event? We compared cougars (*Puma concolor*) and bobcats (*Lynx rufus*) from the late Pleistocene Rancho La Brea asphalt deposits (35–9 ka) to their modern counterparts. The most commonly fossilized bones of these rarely fossilized cats – lower first molar in the jaw, the third metacarpal (MC3) in the front paw, and the third metatarsal (MT3) in the hind foot – were measured with digital calipers. Even though the size range of Pleistocene La Brea specimens were contained within the modern range in most variables, the Pleistocene cougars were significantly larger in the first molar and MC3, although they were significantly smaller in the MT3 (using Hotelling's T<sup>2</sup> test of bivariate significance). The bobcats, on the other hand, were not statistically different in their m1, but the Pleistocene bobcat paws and feet were significantly larger. We also compared the fossil specimens by age to see if climate change during the glacial-interglacial transition about 20,000 years ago might have made a difference; although most sample sizes were too small for robust statistical analysis, there were no evident changes through time. We conclude that Pleistocene cougars were like coyotes in competing with

larger competitors for larger prey during the Pleistocene, while bobcats have always specialized on smaller prey and therefore were not affected by the change in the competition or prey during the megafaunal extinction.

### Taphonomy & Stratigraphy

#### LOG JAMS AND JUVENILES: UNUSUAL DEPOSITS AT THE K-PG BOUNDARY (66 MA) IN SOUTHERN SASKATCHEWAN, CANADA

Bamforth, Emily L.

Research and Collections, Royal Saskatchewan Museum, Eastend, Saskatchewan, Canada

The latest Mesozoic and earliest Cenozoic rocks of southwest Saskatchewan, Canada contain some of the finest exposures of the Cretaceous-Paleogene (K-Pg) Boundary in North America. The Frenchman Formation (66 Ma) represents a northern extension of Montana's upper Hell Creek Formation, with the overlying Paleocene Ravenscrag Formation coeval with the Tullock Formation. One of the most notable K-Pg sites in the province comes from the 'Hwy 37 Locality', near the town of Shaunavon, SK. Here, the local 'Ferris No. 1' coal seam is approximately 150 cm thick. The distinct K-Pg tonstein ('boundary clay') is found in the middle of this coal deposit. The pure, pinkish clay of the K-Pg Boundary layer occurs 75 cm above the base of the coal and measures 1-2 cm in thickness. The coal above the K-Pg Boundary is characterized by blocky anthracite, overlain by 35-45 cm of finely laminated carbonaceous shale. Several significant fossils, including one of the earliest known Cenozoic mammals and a complete champsosaur skeleton, have been historically recovered from this terrestrial shale. This shale deposit is unique to the Hwy 37 Locality, being largely absent from other known K-Pg sites in the province. The coal below the K-Pg tonstein is also anthracitic, and contains recognizable tree fossils. These fossils are represented by laterally compressed segments of coalified logs and branches, raring in length from 15-40 cm, some with bark structures and growth rings still preserved. This type of fossil tree preservation is also found 3.5 m lower in section in an unusual 'log jam' deposit. This deposit, which extends laterally for at least 300 m, is characterized by laterally compressed segments of coalified trees, some with lengths exceeding 500 cm. The specimens are so well preserved that bark structure, burls and blisters of amber can be discerned. The plant fossils are more likely to represent angiosperm trees rather than *Metasequoia*, the dominant canopy-forming tree at the time. Vertebrate material recovered from this log jam deposit are mainly from juvenile animals, including fossils of a very young *Triceratops* and a hatchling *Troodon*. Ongoing study of these unusual deposits will help to elucidate

paleoecological and depositional events that took place just before, during, and immediately following the bolide impact and subsequent extinction in southwest Canada.

### Macroecology & Macroevolution

#### TURTLE PALEONICHE DYNAMICS PREDICT RANGE SHIFTS IN A WARMING WORLD

Barrett, Paul M.<sup>1</sup>, Waterson, Amy M.<sup>2</sup>, Schmidt, Daniela N.<sup>2</sup>, Valdes, Paul J.<sup>3</sup>, Yesson, Chris<sup>4</sup>, Holroyd, Patricia<sup>5</sup>, Collinson, Margaret E.<sup>6</sup>, Farnsworth, Alexander<sup>3</sup>, Nicholson, David B.<sup>1</sup>

<sup>1</sup>Earth Sciences, Natural History Museum, London, U.K., <sup>2</sup>Earth Sciences, University of Bristol, Bristol, U.K., <sup>3</sup>Geography, University of Bristol, Bristol, U.K., <sup>4</sup>Institute of Zoology, London, U.K., <sup>5</sup>University of California Museum of Paleontology, Berkeley, California, U.S.A., <sup>6</sup>Earth Sciences, Royal Holloway University of London, Egham, U.K.

Understanding past ecological response to global environmental change provides vital baseline data for estimating the potential resilience of extant taxa under future climate scenarios. Here, we assess the responses of terrestrial and freshwater testudines (tortoises, terrapins, and turtles) to the paleoclimatic transition from Cretaceous greenhouse to Oligocene icehouse conditions, using an ecological niche model (ENM) approach. We use the ENMs to reconstruct niches for past warm worlds and apply these to infer ecological responses to future climate scenarios that predict increased global temperatures and spreading arid biomes at mid-latitudes.

Modern and fossil testudine occurrence data were taken from the World Turtle Database and the Paleobiology Database, respectively. Current climate variables were derived from the U.K. Meteorological Office Unified Model HadCM3; paleoclimatic data were inferred from the related HadCM3BL-M2.1aD model; vegetation reconstructions were produced using BIOME4. The MaxEnt ENM was used to model testudine niches; it compares the climatic conditions at locations of occurrence records with randomly selected points from within the study region to create spatial predictions of habitat suitability. A five-fold cross validation procedure was used to create global models for the Maastrichtian and modern allowing the calculation of area under the curve statistics. MaxEnt percent variable contribution and permutation importance were used to estimate variable importance in ENMs. ENMs were calibrated for the Maastrichtian and projected to early Late Cretaceous and late Eocene time slices. Modern niches for testudine families and ecotypes were projected to a 2100 climate scenario to quantify the distribution of future suitable testudine environmental space.

Testudine niches are predicted to show poleward range expansion in the northern hemisphere, although their ability to track current, rapid environmental change remains unknown. Conversely, regional range contractions are projected to occur in southern Africa, central Asia and southern Europe due to decreased precipitation. These results demonstrate the utility and importance of deep time data in predicting future climatic impacts.

**Funding Sources** NERC Standard Grant (NE/J020389/1) awarded to PMB (PI), DNS (CI), PJV (CI) and MJC (CI).

### Quantitative Methods

### FIRST TOTAL-EVIDENCE PHYLOGENY OF THE HYAENIDAE AND ENIGMATIC FOSSIL VIVERROIDS REVEALS NOVEL RELATIONSHIPS

Barrett, Paul Z., Hopkins, Samantha S.  
Earth Sciences, University of Oregon, Eugene, Oregon, U.S.A.

The family Hyaenidae today is represented by only four living species, but this constitutes only a small fraction of known taxa from the fossil record. Relationships among living taxa have been thoroughly explored via molecular analyses, though much less work has been attempted on the diversity of extinct taxa. Furthermore, results from both molecular and morphological analyses have shown disagreement in relationships, while certain hypothesized stem hyaenids and viverroids have received little to no phylogenetic assessment. These taxa include the percrocotids (bone-crushing, hyena-like viverroids), lophocyonids (extremely hypocarnivorous feliforms), and additional well-preserved, yet unassessed Miocene viverroids. Thus, to combine all available datasets, we performed a total-evidence Bayesian phylogenetic analysis inclusive of a sample of stem-to-derived hyaenids, herpestids, viverrids and other unassessed viverroid taxa. The analyzed dataset includes stratigraphic occurrences, 257 morphological characters and mitochondrial genes of all living taxa in the analysis and ancient DNA from the cave hyena (*Crocota crocota spelaea*). The analysis, run in Beast2, returned *Dinocrocota* as a derived member of the Hyaenidae (94% posterior probability), to the exclusion of the ictitheres. Ictitheriinae was recovered as a monophyletic clade with 53 percent posterior probability, while the lophocyonids were recovered as sister to all living families, save the Nandiniidae (African palm civets). Finally, the African Miocene genera *Kanuites* and *Kichechia* were recovered as stem herpestids (71% posterior probability) compared to previously hypothesized viverrid relationships. These results suggest that the derived bone-crushing morphology and late Miocene occurrence of *Dinocrocota* represent an early

offshoot of this ecomorphology within hyaenids, and not a distant phylogenetic relationship as previously hypothesized, while broad ingroup inclusion for phylogenetic analyses, no matter the optimality criteria, avoids the pitfall of misleading evolutionary relationships when clade diagnosis is unclear due to incompleteness of fossil specimens.

### Permo-Triassic Tetrapods

### PHYTOSAURS (REPTILIA: ARCHOSAURIFORMES) FROM THE UPPER TRIASSIC STRATA OF THE DRY CIMARRON VALLEY, WESTERN OKLAHOMA AND NORTHEASTERN NEW MEXICO, U.S.A.

Barta, Daniel E.  
Anatomy and Cell Biology, Oklahoma State University  
College of Osteopathic Medicine at the Cherokee Nation,  
Tahlequah, Oklahoma, U.S.A.

Phytosaurs are common, semiaquatic Triassic archosauriform reptiles that serve as important index fossils for Triassic rocks in western North America. Despite their abundance and biostratigraphic utility, many aspects of phytosaur paleobiology, evolution, and systematics remain unknown or understudied. Therefore, description of new materials and restudy of historic specimens adds to knowledge of phytosaur biology and may clarify the relative ages of phytosaur-bearing rocks. The vertebrate fauna of the Upper Triassic strata in the Dry Cimarron Valley in western Oklahoma and northeastern New Mexico has received less attention than the more abundant vertebrates of the Dockum Group to the south. The Dry Cimarron Valley strata are locally subdivided into the (from oldest to youngest) Baldy Hill, Travesser, Sloan Canyon, and Sheep Pen Sandstone formations. To date, bony fish, metoposaurids, phytosaurs, and various reptile tracks have been reported from these exposures. Before faunal comparisons to other formations can be made, further description and phylogenetic analysis of the phytosaurs is needed to determine the number of taxa present. Two specimens are complete enough to warrant further description. Though they were previously assigned to various genera (*Machaeropsopus*, '*Pseudopalatus*,' '*Redondasaurus*,' and *Rutiodon*), they have not been assessed in light of recent revisions of phytosaur relationships and taxonomy. OMNH 2939 is a partial, possibly juvenile skull and postcrania from the Sloan Canyon Formation of Oklahoma, and OMNH 739 is a larger, more complete skull and some postcrania from the Sloan Canyon or Travesser Formation of New Mexico. To determine their phylogenetic affinities, I scored the specimens for 94 discrete characters in a recently published data matrix of 45 taxa/specimens. I

analyzed the matrix with TNT software, using a new technology search with extended implied weighting.

The specimens are recovered as sister OTUs. Their clade is part of the larger *Machaeroprotopus* complex, but they cannot be readily assigned to a known species within that genus, so both specimens are tentatively referred to *Machaeroprotopus* sp. This taxonomic assignment (1) concurs with the original pre-cladistic description of OMNH 739, (2) supports prior claims of a Norian age for the Dry Cimarron Valley strata based on the known stratigraphic range of *Machaeroprotopus*, and (3) suggests that a single phytosaur taxon is represented by the material recovered so far.

**Funding Sources** Oklahoma State University Center for Health Sciences.

## Symposium: Paleoneurology

### Mesozoic & Early Cenozoic Mammalian Evolution

#### A LUTETIAN OMOMYID PRIMATE FROM THE PONTIDE MICROCONTINENT, NORTH-CENTRAL ANATOLIA: IMPLICATIONS FOR SWEEPSTAKES DISPERSAL OF TERRESTRIAL MAMMALS DURING THE EOCENE

Beard, K. Christopher<sup>1</sup>, Métais, Grégoire<sup>2</sup>, Ocakoğlu, Faruk<sup>3</sup>, Licht, Alexis<sup>4</sup>

<sup>1</sup>University of Kansas, Lawrence, Kansas, U.S.A.,

<sup>2</sup>Muséum National d'Histoire Naturelle, Paris, France,

<sup>3</sup>Eskisehir Osmangazi University, Eskisehir, Turkey,

<sup>4</sup>University of Washington, Seattle, Washington, U.S.A.

A new genus and species of omomyid primate is reported from the middle Eocene (Lutetian) Lülük Member of the Uzunçarsidere Formation, Orhaniye Basin, north-central Anatolia. This is the first Eocene primate to be reported from the vast area between Switzerland and Pakistan. The new taxon is currently represented by a single dentary fragment, limiting the scope of morphological comparisons that can be made with related taxa. Nevertheless, its dentition differs fundamentally from that of contemporary European microchoerids. The new taxon most closely resembles North American middle Eocene omomyines such as *Mytonius hopsoni*, and it is therefore interpreted as a member of the Asian/North American omomyine radiation. Its occurrence on the Pontide microcontinent must have resulted from sweepstakes dispersal across the intervening Tethyan barrier that separated the Pontides from adjacent parts of Eurasia during the Lutetian. Sweepstakes dispersal by various terrestrial mammal clades, especially rodents and primates, was facilitated by Eocene greenhouse climatic conditions, which promoted extreme precipitation events and frequent flooding of major river drainages.

**Funding Sources** National Science Foundation (EAR-1543684) and the David B. Jones Foundation.

## Preparators

### WHEN *GLYPTOTHERIUM* FLIES: RELOCATION OF A MOUNTED SPECIMEN TO A NEW BASE

Behlke, Adam

Department of Paleobiology, Smithsonian Institution, Washington, District of Columbia, U.S.A.

The Smithsonian Institution National Museum of Natural History renovated the Fossil Hall and wanted to include the *Glyptotherium arizonae* specimen that was in the old hall on display. The specimen was mounted many years ago on a robust joist deck with mahogany trim. This deck was too large for the new space and did not match the new aesthetic. The base could not be trimmed down to fit in the smaller space because of the joist construction. The specimen has numerous bolts though the carapace and complete disassembly of the mount was deemed too risky for the health of the specimen. The mount consists of two pipes bolted to the base and a rainbow-shaped band of steel with supports on the inner side of the carapace. These two supports are independent, and we were concerned that torque on the pipes could damage the carapace. The selected option was to fabricate a new base and transfer the mounted carapace onto it.

To keep the pipes from moving during the transfer, 2x4 boards were bolted on either side of the pipes to create a clamp. Grooves for the pipes were cut into the boards to increase the clamping strength. Additional 2x4 boards were attached to the pipes below and perpendicular to the previous clamped boards to create stable lifting points outside of the carapace. The specimen was unbolted from the base and lifted into the air with two chain hoists and lifting straps. A spreader bar was used to prevent the straps from rubbing on the carapace. Once the pipes were lifted clear, the old base was wheeled away, and the new base pushed into place. The specimen was lowered on to the new base and secured in place.

Although, this is not to recommend that anyone rush out and lift mounted specimens, if done slowly, and all of the contact points with the base are locked in place, it should be possible to create a new base for any specimen.

## Taphonomy & Stratigraphy

### NUTRIENT RECYCLING AND TAPHONOMIC BIAS IN THE VERTEBRATE FOSSIL RECORD

Behrensmeyer, Anna K.

Paleobiology, Smithsonian Institution, Arlington, Virginia, U.S.A.

Paleontologists are keenly aware that the vertebrate fossil record is patchy in time and space: certain regions, strata, and geological formations are consistently rich in fossils, while others are not. Bone concentrations have been the focus of decades of taphonomic research, but explaining the vast areas of barren outcrops between productive patches has (not surprisingly) received little attention. Fluvial strata throughout the Phanerozoic record contain buried land surfaces marked by paleosols that once supported productive ecosystems, but most paleosols produce few fossils. Why? I propose that the scarcity of fossil remains in such contexts indicates efficient early post-mortem nutrient recycling in ancient ecosystems, and that this perspective contributes to understanding large-scale sampling biases in the fossil record. Rapid return of nutrients to an ecosystem plays a vital role in cycles of life, death and regeneration. Under normal equilibrium conditions, early post-mortem recycling processes operating both above and below ground should leave little for the fossil record. From this point of view, fossiliferous deposits represent ecological anomalies – failures of recycling processes to do their job – leaving nutrients withdrawn from the system to become fossils. Survival of organic remains could relate to local surfeits of nutrients contained in these remains (e.g., excess calcium), few recycling agents (e.g., macro-scavengers), and/or depositional processes that remove remains from the biologically active zone (e.g., deep burial). Taphonomic research in modern ecosystems shows that recycling of soft tissues usually occurs in days to months, with bones and teeth decomposing over years to centuries, depending on climate, soil conditions, and access for scavengers and decomposers. Examples from Permian to Miocene vertebrate-bearing formations highlight repeated patterns of fossil scarcity in floodplain paleosols contrasting with fossil concentrations in localized contexts such as abandoned channels, where a different balance of carcass input, recycling efficiency, and burial rates interfered with normal nutrient turnover. On a larger scale, this suggests that our samples of land vertebrate evolution and paleoecology are biased toward ecological settings subject to variable or unusual biological, physical, or chemical conditions that allowed remains to escape post-mortem recycling and be preserved as fossils.

**Funding Sources** Smithsonian Institution.

### **Mesozoic Herpetology**

#### **RESOLVING THE PTEROSAUR BAUPLAN USING A QUANTITATIVE TAPHONOMIC APPROACH**

Belben, Rachel  
Geology, University of Leicester, Leicester, U.K.

Despite more than 200 years of research, the pterosaur bauplan remains unresolved. A central issue concerns the relationship of the limbs via their inclusion in the flight apparatus and the extent of the wing membranes. As extant birds and bats show, differing constructions have profound consequences for the locomotor ability, ecology and evolutionary history of flying vertebrates. In pterosaur specimens with fossilised flight patagia the hind limbs appear to be connected to the forelimbs via a brachiopatagium and, in non-pterodactyls, to each other via a uropatagium. These interpretations are disputed, however, and their applicability to the vast majority of species, which lack any soft tissue evidence, is unknown. This study used quantitative taphonomic data to test these models and to establish, for the first time, their distribution across Pterosauria. Context is provided by bats and birds in which the construction, particularly the role of the hind limbs, is clear. Analysis of large samples, primarily from Messel (Eocene), show significant differences in hind limb posture. A symmetric, or near symmetric, 'splayed' posture is ubiquitous for bats, while in birds hind limbs adopt a wide range of postures, reflecting their functional and anatomical independence. The pterosaur data set consists of 300+ specimens representing almost the entire stratigraphic range of the clade and much of its anatomical, ecological and taxonomic diversity (18 out of 20 major clades). Plots of completeness versus articulation identified several taphonomic modes, the most important of which consists of skeletons that, while varying in terms of completeness, exhibit high values for articulation. A splayed 'bat-like' hind limb posture is typical for this taphonomic mode and present in a wide range of species, including non-pterodactyls and pterodactyls. Critically, the vast majority of soft tissue specimens that fall within this taphonomic mode also exhibit the splayed posture. Combined, the taphonomic data for skeletal and soft tissues provides strong support for a widespread, likely universal, occurrence of hind limb integration into the flight apparatus in pterosaurs. Taphonomic analysis also revealed a significant difference between correlations of the degree of articulation of the hind limbs for non-pterodactyls (relatively high) in which the hind limbs are connected to each other and pterodactyls (relatively low) where they are separate.

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### **Dinosaur Systematics, Diversity & Ecology**

#### **QUANTIFYING THE INFLUENCE OF MULTIPLE SOCIO-SEXUAL SIGNALS IN THE EVOLUTION OF CERATOPSID DINOSAURS**

Bender, Emerald R., Gates, Terry A.

North Carolina State University, Winston-Salem, North Carolina, U.S.A.

Bony cranial ornaments are among the best-recognized features of many dinosaurian groups, including Pachycephalosauria, Ceratopsia, and Hadrosauridae. These horns, frills, crests, and domes are predominantly purveyors of socio-sexual signaling information, though differently for each clade. The derived ceratopsian clades Chasmosaurinae and Centrosaurinae are unique among dinosaurs in having both a large frill and intricate frill crenellations and processes and, in many cases, large facial horns. This lineage presents an opportunity to examine the covariance in evolutionary trajectories between multiple sexually selective traits.

We quantified the evolutionary rate of ceratopsian frill size and complexity in relation to body size (through several measures). Body size and ornament morphology data were collected from the literature and include linear measurements and the quantification of frill complexity as the fractal dimension of the frill margin. The R package RRphylo (phylogenetic ridge regression) was used to detect evolutionary rate shifts and phenotypic trends in body size, frill complexity, and frill size across 40 time scaled trees of one topology. To examine the influence of horns on frill and body size among ceratopsians we used phylogenetic ANOVAs, differentiating postorbital horns and nasal horns as discrete characters.

Our analyses concur with other studies showing trends towards increasing body size, frill complexity, and relative frill size across the Ceratopsia. Basal Chasmosaurinae shows multiple rate shifts in ornamentation; specifically, rates increase in ornament complexity and decrease in frill size compared to centrosaurs. This difference is even more dramatic when the fractal dimension of the frills is considered. However, centrosaurs possessing only a nasal horn have longer and more complex frills relative to skull length compared to all other horned dinosaurs. These results suggest that the rapid evolution of size, complexity, and diversity of bony cranial ornaments in Late Cretaceous ceratopsians may be directly linked to the rapid acquisition of large body size (frill size evolves at about an equal evolutionary rate as femur length). Although no correlation was found between residual frill size and the acquisition of facial horns, the placement of a positive rate shift in complexity and a negative rate shift in frill size at the origination of Chasmosaurinae may imply a trade-off in the direction of investment in ornamental traits.

## Bird Biology & Evolution

### REINVESTIGATING THE ‘MAASTRICHT ICHTHYORNITHINE’ FROM THE LATEST CRETACEOUS OF BELGIUM

Benito, Juan<sup>1</sup>, Jagt, John W. M.<sup>2</sup>, Field, Daniel J.<sup>1</sup>

<sup>1</sup>Department of Earth Sciences, University of Cambridge, Cambridge, U.K., <sup>2</sup>Natuurhistorisch Museum Maastricht, Maastricht, Netherlands

Ichthyornithes, as flying stem birds close to the avian crown group, may be more representative of the ancestral condition of crown birds than any other Mesozoic avialans. As such, improving our knowledge of the diversity and morphological disparity of this group is critical for understanding the origin of crown birds. Though many fragmentary specimens have been identified as part of Ichthyornithes, only one well-studied taxon is currently recognized, *Ichthyornis dispar*. A partially described, unnamed specimen from the Maastricht Formation of Belgium (~66.7 Ma) has been previously suggested to show affinities with *Ichthyornis*, despite being ~20 million years younger than the best-known *Ichthyornis* material from the Niobrara Formation of Kansas. Previously identified material from the partially prepared ‘Maastricht ichthyornithine’ includes several elements encased in matrix, including limb bones, jaws, some vertebrae, and a tooth, although the material has not received further attention. Here, we investigate the specimen using high-resolution  $\mu$ CT, revealing the preservation of at least 13 cervical and thoracic vertebrae, as well as a well-preserved humerus, scapula, major manual phalanx and partial femur. We also illustrate that the elements previously identified as jaws are, in fact, ribs. The morphology of the Maastricht bird is remarkably similar to that of *Ichthyornis* in almost every regard, with the exception of the Maastricht specimen’s much larger size. The new specimen shows several diagnostic features of *Ichthyornis*, including the morphology of the cervical vertebrae and the presence of an internal index process, but it lacks a comparable scapular acromion process. Phylogenetic analyses of the new specimen using two alternative morphological matrices recover it in a well-supported clade with *Ichthyornis*, stemward of the clade uniting Hesperornithes and crown-group birds. The study of this and additional specimens of crownward Mesozoic ornithurines will allow a better understanding of the diversity and morphology of these Late Cretaceous taxa, which will have crucial implications for clarifying patterns of morphological evolution preceding the origin of modern birds.

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## Symposium: Paleoneurology

### EXPLAINING THE STRUCTURE OF SEMICIRCULAR CANALS IN ARCHOSAURS

Benson, Roger B.<sup>1</sup>, Bjarnason, Alex<sup>1</sup>, Bronzati, Mario<sup>10</sup>, Evers, Serjoscha<sup>8</sup>, Ezcurra, Martin<sup>9</sup>, Field, Daniel J.<sup>7</sup>, Giles, Sam<sup>6</sup>, Navalón, Guillermo<sup>1</sup>, Walsh, Stig<sup>5</sup>, Witmer, Lawrence<sup>4</sup>, Choiniere, Jonah N.<sup>3</sup>, Nesbitt, Sterling J.<sup>2</sup>

<sup>1</sup>Department of Earth Sciences, University of Oxford, Oxford, U.K., <sup>2</sup>Department of Geosciences, Virginia Tech, Blacksburg, Virginia, U.S.A., <sup>3</sup>Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa, <sup>4</sup>Ohio University, Athens, Ohio, U.S.A., <sup>5</sup>National Museums of Scotland, Edinburgh, U.K., <sup>6</sup>University of Birmingham, Birmingham, U.K., <sup>7</sup>University of Cambridge, Cambridge, U.K., <sup>8</sup>University of Fribourg, Fribourg, Switzerland, <sup>9</sup>Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina, <sup>10</sup>Universidade de Sao Paulo, Sao Paulo, Brazil

Semi-circular canals of the inner ear are subject to increasing study, particularly in light of their hypothesised relationship to agility and locomotor innovations such as flight and aquatic habits. However, many studies concern just single groups with little generality, and alternative explanations such as constraints imposed by braincase geometry have not generally been evaluated, leaving significant uncertainties.

We investigate living and extinct archosaurs spanning birds, crocodylians, and Triassic stem-group taxa with diverse locomotory traits, using 3D geometric morphometrics and explicitly phylogenetic comparative methods (N = 36 fossil species; N = 110 extant species). We use sliding semilandmarks to quantify the implied form of the membranous semicircular canals, comparing statistical explanations of shape variation using phylogenetic Procrustes ANOVA to untangle the roles of phylogeny, spatial constraint, allometry, and locomotor ecomorphology.

We find statistically significant general explanations of labyrinth shape across archosauriforms, which is remarkable given large differences in baseline labyrinth morphologies (e.g., in birds and crocodylians). Proportional enlargement of the labyrinth is significantly associated with increasing canal circularities. This implies functional selection for increased sensitivity causes size-increase and shape-optimisation. We also find evidence for spatial constraints in auditory specialists with enlarged cochleae, and in aquatic taxa with broad, flat skulls. Furthermore, posterodorsal rotation of the braincase in birds and pterosaurs is associated with posterodorsal rotation of the anterior canal.

Beyond the effects of braincase geometry, key locomotor traits show significant, independent effects, explaining ~20% of variation in labyrinth shape. Aquatic habits are associated with increases in endosseous canal diameter, bipedality is associated with increases in the height of the anterior canal, and flight is associated with increases in the length and roundedness of the anterior canal.

Triassic archosaurs show great variation in labyrinth morphology that is not represented today. Among these, labyrinths of early dinosauromorphs, some stem-archosaurs, and pterosaurs all have equal similarity to those of birds. This and other observations obstruct straightforward uses of labyrinth morphology to infer ecology in extinct species and urges caution in accepting ecological hypotheses of labyrinth shape variation.

## Fishes & Chondrichthyans: Evolution & Distribution

### THE OLDEST ASSOCIATED REMAINS OF THE CRETACEOUS SHARK *SCAPANORHYNCHUS*; A NEW ACQUISITION FROM THE LEBANON

Bernard, Emma L.<sup>1</sup>, Ward, David J.<sup>1</sup>, Underwood, Charles J.<sup>2</sup>

<sup>1</sup>Earth Sciences, Natural History Museum, London, U.K., <sup>2</sup>Earth and Planetary Science, Birkbeck College, London, U.K.

The Late Cretaceous Lebanese plattenkalk limestones have been known as a source of articulated fish remains since at least the 4th century AD and were first figured in 1698. The main source of fossils were small quarries in late Santonian limestones located north-east of Beirut near the Sahel Alma convent. It was from here that in 1887, Davis described the articulated remains of several genera of shark including a small long-snouted lamniform which he named *Rhinognathus lewisii*.

Two years later, in the BM(NH) Catalogue of Fossil Fishes, Woodward renamed Davis' new genus *Scapanorhynchus*; the original name being preoccupied by a beetle. He also described an additional species, *S. elongatus*, separated by its body proportions but having teeth like *S. lewisii*. This species was synonymised by Cappetta who, in 1980, monographed the Lebanese plattenkalk sharks from both Santonian and Cenomanian sites, recording no *Scapanorhynchus* specimens from the latter. He identified a larger specimen, referring it to *Scapanorhynchus* sp., suggesting it could be a separate taxon, similar to *S. raphiodon*, or an adult of *S. lewisii*.

Over the last century, quarrying has been largely within Cenomanian limestones which also contain rich faunas but apparently lacking deep water squaloid sharks seen in the Santonian. A combination of different water depth and an age separation of about 8 million years including the Cenomanian-Turonian anoxic event (OAE 2) could explain the difference in assemblages. No Santonian shark species have been found in the Cenomanian quarries.

One of the Cenomanian quarries at Hajoula, NE of Beirut, has just yielded a specimen of *Scapanorhynchus* which was recently acquired by the NHMUK. The specimen, (NHMUK PV P75110a, b) is part and counterpart exposing the head, less the snout tip and anterior part of the trunk. Most of the dentition and much of the cranial and branchial

skeleton is preserved. The teeth have been compared with a Santonian specimen of *S. lewisii* ([EB1] MNHN 1946-18-1620) and correspond in morphology but are almost double the size, similar to those of Cappetta's *Scapanorhynchus* sp. (MNHN 1946-18-1462).

Preliminary conclusions: The new NHMUK specimen is the first known example of an exceptionally preserved *Scapanorhynchus* outside the Lebanese Santonian. It confirms Cappetta's suggestion that either most of the Sahel Alma *Scapanorhynchus* specimens are juveniles or there is another dentally similar species present.

## Dinosaur Systematics, Diversity & Ecology

### A TAIL TALE: INJURIES IN CAUDAL NEURAL SPINES OF HADROSAURIDAE REVEALED BY AN EXTENSIVE PALEOPATHOLOGICAL REVISION OF ORNITHOPODA

Bertozzo, Filippo

School of Natural and Built Environment, Queen's University Belfast, Belfast, U.K.

Ornithopods show the highest frequency of paleopathological lesions in the dinosaurian fossil record. They were affected by a wide range of conditions, from injuries and infections to developmental disorders and even tumors. Until now a systematic overview of their distribution in the clade has not been undertaken. The current research addresses this issue and an extensive review of fossilized lesions is reported, ranging from Late Jurassic taxa, such as *Camptosaurus* and *Dryosaurus*, to Late Cretaceous hadrosaurids, with a wide range of conditions and patterns identified. The highest levels of pathological changes are detected in Hadrosauridae, localized in the trunk region, pedal elements and the tail. Basal taxa show a lower frequency due to the 'scaling effect' from basal, smaller forms to derived, larger taxa. Hadrosaurid material is also more abundant than non-hadrosaurid ornithopods, with a broader pool of individuals and therefore a higher likelihood of finding lesions. In particular, the tail of hadrosaurids displays a common pattern of injured neural spines in the proximal and middle caudals. Ten near-complete tails and approximately 300 isolated proximal and middle caudals of adult individuals from at least four different species show vertical or diagonal fractures and/or oblique bending of the neural spines. The location of the injuries also corresponds to the apical portion of the spine that lacks coverage of the interlaced lattice of ossified tendons. The injuries generally displayed bone resorption and proliferation indicative of healing, hence they did not affect the survival of the individuals. These conditions account for 32% of the pathologies recorded in the caudal regions, and 22% of the total pathologies identified in Hadrosauridae. It can be assumed that the occurrence of similar lesions at the same location in the tail, but in different taxa separated in time

and space, may result from a similar event, perhaps a similar behavior. Finite Element Analyses have been performed on a scanned caudal vertebra and on a modelled caudal series to determine the possible etiology of the trauma. The results show that the neural spine could have been bent and/or broken by a vertical, slightly oblique, heavy loading, presumably from another hadrosaur, on the proximo-middle region of the tail. It is tentatively suggested that these injuries could have resulted from mating, and that individuals with such pathologies were female.

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## Symposium: Paleoneurology

### BRAIN EVOLUTION OF EARLY PLACENTAL MAMMALS: THE IMPACT OF THE END-CRETACEOUS MASS EXTINCTION ON THE NEUROSENSORY SYSTEM OF OUR DISTANT RELATIVES

Bertrand, Ornella C.<sup>1</sup>, Brusatte, Stephen<sup>1</sup>, Shelley, Sarah L.<sup>2</sup>, Wible, John R.<sup>2</sup>, Williamson, Thomas E.<sup>3</sup>, Chester, Stephen G.<sup>4</sup>, Holbrook, Luke T.<sup>5</sup>, Lyson, Tyler R.<sup>6</sup>, Smith, Thierry<sup>7</sup>, Meng, Jin<sup>8</sup>

<sup>1</sup>School of Geosciences, University of Edinburgh, Edinburgh, U.K., <sup>2</sup>Section of Mammals, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A., <sup>3</sup>New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, U.S.A., <sup>4</sup>Department of Anthropology and Archaeology, Brooklyn College, City University of New York, Brooklyn, New York, U.S.A., <sup>5</sup>Department of Biological Sciences, Rowan University, Glassboro, New Jersey, U.S.A., <sup>6</sup>Denver Museum of Nature & Science, Denver, Colorado, U.S.A., <sup>7</sup>Directorate Earth and History of Life, Royal Belgian Institute of Natural Sciences, Brussels, Belgium, <sup>8</sup>Division of Paleontology, American Museum of Natural History, New York, New York, U.S.A.

The end-Cretaceous mass extinction, 66 million years ago, profoundly reshaped the biodiversity of our planet. After likely originating in the Cretaceous, placental mammals (species giving live birth to well-developed young) survived the extinction and quickly diversified in the ensuing Paleocene. Compared to Mesozoic species, extant placentals have advanced neurosensory abilities, enabled by a proportionally large brain with an expanded neocortex. This brain construction was acquired by the Eocene, but its origins, and how its evolution relates to extinction survivorship and recovery, are unclear, because little is known about the neurosensory systems of Paleocene species.

We used high-resolution computed tomography (CT) scanning to build digital brain models in 29 extinct placentals (including 23 from the Paleocene). We added these to data from the literature to construct a database of 98 taxa, from the Jurassic to the Eocene, which we assessed in a phylogenetic context.

We find that the Phylogenetic Encephalization Quotient (PEQ), a measure of relative brain size, increased in the Cretaceous along branches leading to Placentalia, but then decreased in Paleocene clades (taeniodonts, phenacodontids, pantodonts, periptychids, and arctocyonids). Later, during the Eocene, the PEQ increased independently in all crown groups (e.g., euarchontoglires and laurasiatherians). The Paleocene decline in PEQ was driven by body mass increasing much more rapidly after the extinction than brain volume. The neocortex remained small, relative to the rest of the brain, in Paleocene taxa and expanded independently in Eocene crown groups. The relative size of the olfactory bulbs, however, remained relatively stable over time, except for a major decrease in Euarchontoglires and some Eocene artiodactyls, while the petrosal lobules (associated with eye movement coordination) decreased in size in Laurasiatheria but increased in Euarchontoglires.

Our results indicate that an enlarged, modern-style brain was not instrumental to the survival of placental mammal ancestors at the end-Cretaceous, nor to their radiation in the Paleocene. Instead, opening of new ecological niches post-extinction promoted the diversification of larger body sizes, while brain and neocortex sizes lagged behind. The independent increase in PEQ in Eocene crown groups is related to the expansion of the neocortex, possibly a response to ecological specialization as environments changed, long after the extinction.

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### **Biomechanics & Functional Morphology**

#### **CAN AGNOSTIC ORNSTEIN-UHLENECK MODELING OF STYLOPOD CIRCUMFERENCES IDENTIFY LOCOMOTORY REGIME SHIFTS IN DINOSAURIA?**

Beyl, Alexander R.<sup>1</sup>, Moore, Andrew<sup>1</sup>, Sookias, Roland<sup>2</sup>, Benson, Roger B.<sup>2</sup>

<sup>1</sup>Anatomical Sciences, Stony Brook University, Poquott, New York, U.S.A., <sup>2</sup>Department of Earth Sciences, University of Oxford, Oxford, U.K.

It has long been recognized that several major lineages of dinosaurs evolved a quadrupedal locomotory mode from bipedal ancestors. However, pinpointing the transition

from bipedality to quadrupedality in the evolutionary history of these groups has proved challenging. Recent research drawing on data from extant and extinct tetrapods has demonstrated that the stylopod midshaft circumferences of bipeds and quadrupeds show distinctive scaling patterns. The humeri of quadrupeds are recruited to bear some of the mass of the body, and hence become relatively more robust than those of bipeds. This relationship may be used to identify shifts in locomotory mode across the evolutionary history of dinosaurs and related archosaurs. To discover such shifts, we applied recently developed Bayesian reversible-jump Markov chain Monte Carlo methods to a dataset of stylopod circumference measurements for 220 dinosauromorph taxa. This approach treats the slope and intercept of the stylopod scaling relationship as traits that evolve on a phylogeny under an Ornstein-Uhlenbeck (OU) process, and does not require a priori specification of locomotory mode. Our agnostic modeling approach produced seven major scaling regimes within Dinosauria. Collapsing nested clades found not to differ statistically in slope, intercept, or both through generalized least squares phylogenetic analysis of covariance reduced the number of regimes to four. These regimes included: a group comprising early-branching dinosaurs and dinosauromorphs, unambiguous bipeds, non-ceratopsid ceratopsians, and all iguanodontians; all of Sauropodomorpha; Scutellosaurus and later-branching thyreophorans; and Ceratopsidae. Of the four, Sauropodomorpha and the thyreophoran clade are not statistically different, suggesting convergence to a common regime. Surprisingly, we did not recover a shift between assumedly bipedal, basal sauropodomorphs and unambiguously graviportal sauropods. We also did not recover a shift within Iguanodontia, members of which have been considered quadrupedal based on trackway and osteological evidence. The regime shift within Ceratopsia is consistent with a switch to obligate quadrupedality. Our results provide evidence for clade-specific differences in the scaling relationship of stylopod circumferences, but so far cannot be explained strictly by inferred locomotory mode, indicating complexity in the effects of locomotion on the scaling relationships of limb shaft robustness in dinosaurs.

### **Anatomical & Developmental Explorations of the Mammalian Skull**

#### **MAMMALIAN CHEWING DEPENDS ON ROLLING OF THE JAW AND DEEP CONSERVATION OF TOOTH FORM AND FUNCTION**

Bhullar, Bhart-Anjan S.<sup>1</sup>, Manafzadeh, Armita R.<sup>2</sup>, Miyamae, Juri<sup>1</sup>, Hoffman, Eva A.<sup>3</sup>, Brainerd, Elizabeth<sup>2</sup>, Musinsky, Catherine<sup>4</sup>, Crompton, Alfred W.<sup>4</sup>

<sup>1</sup>Earth and Planetary Sciences, Yale University, New Haven, Connecticut, U.S.A., <sup>2</sup>Brown University, Providence, Rhode Island, U.S.A., <sup>3</sup>American Museum of Natural History, New York, New York, U.S.A., <sup>4</sup>Harvard University, Cambridge, Massachusetts, U.S.A.

We use a combination of 3D X-ray reconstruction of moving morphology (XROMM) in opossums (which, we show using discrete and quantitative characters, are little-modified from the therian ancestor) and an analysis of fossil and extant anatomy to argue that the unique mammalian food processing system originally required independent rolling of unfused hemimandibles. We posit that the original function of the therian tribosphenic molar was to process food in a reverse mortar-and-pestle arrangement by which the talonid 'mortar' moved transversely across the protocone 'pestle.' This transverse motion was enacted primarily by long-axis jaw rotation. We further synthesize experimental and comparative behavioral data and show that jaw roll is broadly conserved across extant mammals. Fusion of the jaw symphysis has occurred repeatedly in omnivorous and herbivorous therian clades and is associated with low-crowned teeth and grinding by transverse motion of the mandible. It is also associated with reduction of the angular process, which we argue serves to provide greater leverage for jaw-rolling musculature. The origin of the angular process appears to have lowered the insertions of the superficial masseter and medial pterygoid, which together enact jaw roll. Its appearance on the mammalian stem coincides with the outward tilting of the jaws at rest, requiring roll to bring them back into occlusion. Its reappearance at Cladotheria on the therian stem coincides with the appearance of the talonid. We suggest that the rotational processing stroke so evident in therians originated here, and that the tooth components involved have been fundamentally continuous since that origin, in spite of shifting cusp identities and a shift from shearing-dominated to grinding-dominated processing.

## **Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

### **REGIONAL DIFFERENCES OF EARLY *HOMO* PALEOECOLOGY**

Biernat, Maryse D.<sup>1</sup>, Khumalo, Wendy<sup>2</sup>, Mavuso, Silindokuhle<sup>3</sup>, McGrosky, Amanda<sup>1</sup>

<sup>1</sup>School of Human Evolution and Social Change, Arizona State University, Tempe, Arizona, U.S.A., <sup>2</sup>Geological Sciences, University of Cape Town, Cape Town, South Africa, <sup>3</sup>School of Geosciences, University of Witwatersrand, Witwatersrand, South Africa

The discovery of a partial hominin mandible (LD 350-1) from the Ledi-Geraru research area, Ethiopia pushed the fossil record of the genus *Homo* back 0.4 million years. Although LD 350-1 remains the earliest evidence of *Homo*, a set of hominin teeth with no taxonomic designation from the early Tulu Bor member of the Koobi Fora Formation (KNM-ER 5431) could represent a similar 'transitional form' from *Australopithecus* to *Homo*. This project explores the fauna associated with KNM-ER 5431 to reconstruct the site's paleoecology and compare it to that of LD 350-1. Additionally, we re-investigated the geology of the KNM-ER 5431 site to constrain the geological context of this specimen.

To compare the paleoecology of the two sites, we employed a correspondence analysis using the functional traits of the mammalian species found at each site. In addition, data from modern mammal communities and the other stratigraphic units were included from both the Koobi Fora Formation and the Ledi-Geraru research area. We found that the KNM-ER 5431 site clusters with modern sites dominated by fresh grass eating species and decreased precipitation. It falls away from the other fossil sites, which cluster together with modern sites dominated by grazing species and greater precipitation.

Stratigraphic investigation conducted around the KNM-ER 5431 site revealed that the site lies approximately 30 meters above a tuff, which will be chemically analyzed to help constrain the age of the site. Sedimentological analysis indicates that the area contains carbonate-rich lithologies indicative of water-logged deposition in a lacustrine setting and possibly an interspersed braided river system with mature floodplains. Well-punctuated, varves were also recorded, suggesting a seasonal water supply. Combined with the results of the correspondence analysis, it is highly likely that while there was less precipitation associated with the KNM-ER 5431 site, it had greater water availability, in the form of floodplains and braided river systems, than the LD 350-1 site and other fossil bearing members. However, it is important to note that the number of species associated with KNM-ER 5431 is drastically smaller than the other analytical units, which could potentially be driving the severe departure from the rest of the fossil assemblages.

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## **Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

### **RANCHO LA BREA 'TOUGH TIMES' FROM THE BOTTOM UP: CLIMATE CHANGE AFFECTS MORPHOLOGY, ECOLOGY AND TAPHONOMY**

Binder, Wendy J.<sup>1</sup>, Cohen, Joshua<sup>1</sup>, Meachen, Julie<sup>3</sup>, O'Keefe, Frank R.<sup>2</sup>, Lindsey, Emily<sup>4</sup>, DeSantis, Larisa<sup>5</sup>, Southon, John<sup>6</sup>

<sup>1</sup>Biology, Loyola Marymount University, Los Angeles, California, U.S.A., <sup>2</sup>Biological Sciences, Marshall University, Huntington, West Virginia, U.S.A., <sup>3</sup>Anatomy, Des Moines University, Des Moines, Iowa, U.S.A., <sup>4</sup>La Brea Tar Pits and Museum, Los Angeles, California, U.S.A., <sup>5</sup>Biological Sciences, Vanderbilt University, Nashville, Tennessee, U.S.A., <sup>6</sup>Earth System Science, University of California, Irvine, Irvine, California, U.S.A.

The Rancho La Brea (RLB) asphaltic deposits yielded a treasure trove of fossils from the late Pleistocene. Some of these deposits ('pits') represent distinct episodes. Pit 13 is a particularly good example due to the limited entrapment range, primarily between 15,500–17,000 RCYBP, which is a window into a time period from the end of the LGM to a few thousand years prior to the end-Pleistocene megafaunal extinction horizon. It has already been identified as the 'tough times pit' as dire wolves from this deposit have shown higher tooth breakage and wear which may relate to eating harder foods such as bone and/or potentially increased tooth damage interacting with prey or competitors. Another study indicated that dire wolf crania are smaller in this pit, suggesting nutrient deficiency. In order to investigate the potential impacts of climatic factors on the characteristics of megafauna in this deposit, we collected morphological, ecological, and taphonomic data on the five most common mammal species in Pit 13. Dire wolf limb bones were more likely to be smaller than those in the chronologically-bracketing deposits of Pit 91 and Pit 3, while sabertooth cats show stasis, and the opposite is seen in Pit 13 Pleistocene coyotes, which tended to be larger. Census data using relative pit minimum number of individuals (MNI) show that Pit 13 dire wolves had similar proportions among deposits, while sabertooth cat proportions decreased, and coyotes increased. Large herbivores also show relative changes in abundances across this time interval: bison were more abundant, while horses were less abundant. These patterns suggest unique conditions during Pit 13, in which carnivores show size-related changes and different ecological abundances. In addition, herbivore ratios were changing, which may have a bottom-up effect on large carnivores. Finally, taphonomic data show that Pit 13 fossils show significantly more abrasion suggesting increased fluvial conditions relative to other pits and the presence of water. Local climate records suggest that RLB didn't change as much as the surrounding areas, but there is a significant gap in the local insect/plant record, during which Lake Elsinore records show a cooler, wetter climate and a closed habitat. We propose these environmental conditions led to a change in herbivore composition, and a trophic cascade effect to carnivores during this time of deposition at RLB, which accounts for the 'tough times' in Pit 13.

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### Mammalian Skeletal Morphology

## DYNAMIC OPTIMIZATION AND SIMULATION OF JUMPING BIOMECHANICS AND PERFORMANCE IN EXTANT AND EXTINCT TERRESTRIAL VERTEBRATES

Bishop, Peter<sup>1</sup>, Falisse, Antoine<sup>2</sup>, De Groot, Freid<sup>2</sup>, Hutchinson, John R.<sup>1</sup>

<sup>1</sup>Comparative Biomedical Sciences, Royal Veterinary College, Hatfield, Hertfordshire, U.K., <sup>2</sup>Department of Movement Sciences, KU Leuven, Leuven, Belgium

Many animals jump during daily activity, to negotiate obstacles, escape predators or catch prey. A few clades of high-performance jumpers (e.g., anurans, prosimian primates) possess specialized bony or muscular anatomies for this behavior, but most tetrapods lack distinct, recognizable adaptations for jumping. In the absence of readily identifiable musculoskeletal adaptations, interpreting jumping behavior and its evolution across disparate clades in the fossil record has remained problematic. This is despite jumping potentially having played a role in the paleobiology of predatory taxa, such as felids and dromaeosaurs, as well as during the evolution of powered flight. Computational models of the musculoskeletal system provide an objective, quantitative avenue to understand and recreate jumping in extinct species. Using dynamic optimization, predictive simulations based on these models can be used to generate diverse behaviors *de novo*. Jumping in particular is an attractive behavior in this regard, as its performance criterion is relatively straightforward: get as high vertically (or as far forward) as possible in a single movement. Here, we use dynamic optimization to generate maximum vertical jumping simulations for a small bird, the elegant-crested tinamou (*Eudromia elegans*). Despite no encouragement or constraint to do so in the problem formulation, our 36-muscle (per leg), subject-specific model spontaneously performs a countermovement (crouch) before executing the jump. This is something that many animals (including birds) do, indicating that we can replicate key aspects of the jump on the basis of physics alone. Following an airborne phase, the model then successfully executes a landing manoeuvre, and the muscles function differently during this phase than during liftoff. The model is able to lift its centre of mass more than 30 cm above the ground, which is more than double its standing height, yet this is appreciably lower than the recorded jumping performance of other similarly-sized ground birds. We suspect that the apparent performance deficit is due to well-known power-generating limitations in the Hill-type model of muscle contraction, and perhaps

tendon compliance assumptions. Despite limitations, our preliminary results provide encouragement that we are closer to achieving a clearer, more detailed understanding of jumping behavior and its evolution in the vertebrate fossil record.

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## **Taphonomy & Stratigraphy**

### **HYDRODYNAMIC DISPERSAL OF ALLIGATOR BONES: IMPLICATIONS FOR TAPHONOMIC INTERPRETATIONS OF FOSSIL DEPOSITS OF CROCODYLIANS AND MORPHOLOGICALLY SIMILAR TAXA**

Blob, Richard W.<sup>1</sup>, Espinoza, Isabel Z.<sup>2</sup>

<sup>1</sup>Biological Sciences, Clemson University, Clemson, South Carolina, U.S.A., <sup>2</sup>R. C. Edwards Middle School, Central, South Carolina, U.S.A.

Understanding how fossils were deposited at a site is critical to interpreting the ecology of the organisms and communities from which they came. Flowing water can disperse or concentrate bones, particularly in animals that live near freshwater habitats like lakes and rivers. In this context, measurements of the tendency of flowing water to disperse skeletal elements have been collected for diverse taxa, including mammals, turtles, and birds. Knowledge of which bones disperse early or late can inform understanding of specific fossil concentrations. For example, a deposit comprised of mainly early-dispersing elements might have been transported to the location where it was concentrated, whereas a deposit with late-dispersing elements might reflect animals that were buried where they originally lived. Dispersal potential can be influenced by several factors, including the height of bones above the stream bed, bone density, and frontal area. Because these factors vary with bone morphology, taxon-specific dispersal data may be necessary to understand hydrodynamic impacts on the composition of fossil deposits from morphologically distinctive taxa. Crocodylians represent such a lineage. With a fossil record extending into the Mesozoic, many taxa lived near water and would have been subject to hydrodynamic influences after individuals died. However, the shapes of many of their bones, such as the skull and limb girdles, are considerably different from those of taxa tested previously. To provide a taphonomic context for concentrations of crocodylian fossils, we used a flow tank to measure the water speeds that would disperse bones from a subadult American alligator. Flow speeds were increased gradually until each element moved, and each element was tested four times to calculate its average dispersal speed. Also, the

skull was tested in four different orientations to test for effects on dispersal. Alligator bones sorted into three main dispersal groups: early (vertebrae, most girdle elements); intermediate (ribs, most limb bones); and late (mandible, pubis, and femur). Skull dispersal depended strongly on orientation, ranking intermediate with the snout upstream and palate up, but late with the snout upstream and palate down. Late dispersing elements were either dense or very flat. These results can refine interpretations of the taphonomic context of fossil crocodylians as well as other morphologically similar taxa, such as champsosaurs and phytosaurs.

## **Marine Mammals**

### **REAPPRAISAL OF THE ENIGMATIC EARLY ODONTOCETE *XENOROPHUS SLOANII*: FUNCTIONAL MORPHOLOGY, ONTOGENY, AND VARIATION REVEALED BY NEW FOSSILS FROM THE OLIGOCENE ASHLEY FORMATION OF SOUTH CAROLINA**

Boessenecker, Robert<sup>1</sup>, Geisler, Jonathan<sup>2</sup>

<sup>1</sup>Department of Geology and Environmental Geosciences, College of Charleston, North Charleston, South Carolina, U.S.A., <sup>2</sup>Department of Anatomy, New York Institute of Technology, Old Westbury, New York, U.S.A.

The early diverging, dolphin-sized, cetacean clade Xenorophidae are a short-lived radiation of toothed whales (Odontoceti) that independently evolved two features long thought to be odontocete synapomorphies: the morphology underlying echolocation and retrograde cranial telescoping (i.e., posterior migration of the viscerocranium). This clade was based on *Xenorophus sloanii*, which for the past century has been known only by a partial skull lacking a braincase and tympanoperiotics, collected around the year 1900 from the Ashley Formation (28–29 Ma, Rupelian) near Ladson, South Carolina. A large collection of new skulls and skeletons (ChM PV 5022, 5823, CCNHM 104, 168, 1077, and others) considerably expands the hypodigm for this species. As a result, *Xenorophus sloanii* will be by far, the best known of any Oligocene odontocete. This collection reveals that the holotype is a juvenile. *Xenorophus sloanii* is a relatively large odontocete (~75 cm CBL; BZW = 30–35 cm; est. body length 3.5–4 meters) with a moderately long rostrum (RPI = 2.5), marked heterodonty, limited polydonta (13–14 teeth), subtle cranial asymmetry, sagittal crest, intertemporal constriction, and drastically larger brain size than basilosaurid archaeocetes (EQ = 2.9). Postcanine teeth are strongly double-rooted with thick, rugose enamel, four to five accessory cusps, and thickened cementum in ontogenetically mature specimens. Two specimens are missing several teeth and possess alveoli infilled with

woven bone; tooth wear consists of mesial and distal wear facets on postcanines. Dental morphology, thickened cementum, a dorsoventrally robust rostrum and thick rugose enamel suggest raptorial feeding; oral pathology indicates traumatic tooth loss associated with mechanically risky predation attempts. Ontogenetic changes include elaboration of nuchal crests; fusion of the nasofrontal, occipito-parietal, and median frontal sutures; overhanging of the paranasal crest; greater excavation of the ant orbital fossa; lengthening of the nasals; and tighter squamosal-periotic articulation, providing critical insight into the ontogeny of early odontocetes. Phylogenetic analysis confirms xenorophid monophyly and its placement near the base of Odontoceti, and monophyly of a *Xenorophus* + *Albertocetus* clade sister to a *Cotylocara* + *Echovenator* + *Inermorostrum* clade.

**Funding Sources** National Science Foundation.

#### Preparators

#### SKELETONS IN THE CLOSET: A CURATORIAL CASE STUDY OF THE MACE BROWN MUSEUM OF NATURAL HISTORY, AND OTHER UNIVERSITY NATURAL HISTORY MUSEUMS

Boessenecker, Sarah

Geology, Mace Brown Museum of Natural History at the College of Charleston, North Charleston, South Carolina, U.S.A.

The Mace Brown Museum of Natural History (CCNHM) is a small paleontologically focused university museum in the Department of Geology and Environmental Geosciences at the College of Charleston. CCNHM is home to a unique and world-class collection of Oligocene age (30-million-year-old) cetacean (whale and dolphin) fossils, as well as home to the second largest collection of fossils from the Lee Creek Mine of North Carolina outside of the Smithsonian Institution. However, while the collection is unique in being one of the only institutions with such a large amount of these Oligocene cetacean fossils on display and in collections, it is not unique in some of the challenges it faces. University museums face many issues, such as poor or limited funding, unreliable climate control, limited security, and understaffing with high turnover, and many staff members have responsibilities split between museum work and academic work; while not all universities face all of these challenges, all face at least one of these problems. This curatorial case study of CCNHM compares other university museums to it and each other and analyzes these different areas where

there is overlap between institutions to see any patterns in similar issues faced by different institutions.

Curatorial quality was assessed for CCNHM collections through a thorough internal audit, and a Google survey was sent to other university natural history museums to assess their collections; while museums all reported differing methods of security, collections sizes, and budgets, no strong correlation was found between higher budgets and curatorial assessments; it may be that museums scoring higher in individual curatorial assessments have larger staff sizes, or staff members who do not split duties with teaching, and instead can focus solely on museum work.

#### Mesozoic & Early Cenozoic Mammalian Evolution

#### PERSISTENCE OF THE OLDEST HYAENODONT CLADE THROUGH THE EOCENE OF AFRICA

Borths, Matthew R.<sup>1</sup>, Heritage, Steven<sup>1</sup>, Gunnell, Gregg<sup>1</sup>, Friscia, Anthony<sup>2</sup>, Seiffert, Erik<sup>3</sup>

<sup>1</sup>Duke Lemur Center, Duke University, Durham, North Carolina, U.S.A., <sup>2</sup>Integrative Biology and Physiology, UCLA, Los Angeles, California, U.S.A., <sup>3</sup>Integrative Anatomical Sciences, University of Southern California, Los Angeles, California, U.S.A.

During the Paleogene, the most diverse and widely-spread group of carnivorous mammals was Hyaenodonta. The origin and early evolution of this group remain relatively obscure. Like primates, hyaenodonts appear suddenly in the fossil records of North America and Europe at the beginning of the Eocene. Most of these early Eocene hyaenodonts have four premolars and three molars that progressively increase in mesiodistal length. Only two hyaenodont taxa are known from the Paleocene: *Prolimnocyon chowi* from Asia and *Lahimia selloumi* from Afro-Arabia. Both have unexpectedly derived morphology for such ancient hyaenodonts. *Prolimnocyon chowi* has reduced m3s and *Lahimia* has three premolars. Previous analyses demonstrated *Prolimnocyon* is a limnocyonine, a clade that went extinct by the middle Eocene, and *Lahimia* is part of a clade that is thought to have gone extinct by the early Eocene. The disappearance of these early-occurring clades could be interpreted as evidence that the niches rapidly exploited by early, specialized hyaenodonts were not stable through the Eocene. Here, we report on a new, tiny hyaenodont from the latest Eocene of Egypt (Locality 41, Jebel Qatrani Formation). Like *Lahimia*, the new hyaenodont is a diminutive hypercarnivore with only three premolars. Also like *Lahimia*, it has relatively large trigonids and relatively reduced talonids. Bayesian phylogenetic analysis demonstrates the new L-41 hyaenodont is part of the *Lahimia* clade, and that that clade is nested deeply within Hyaenodonta. Using a newly developed locality-based method of Bayesian

biogeographic inference, the origin of Hyaenodonta is resolved in Eurasia, indicating a Paleocene dispersal of Hyaenodonta from Eurasia to Afro-Arabia, where the *Lahimia* clade apparently persisted throughout the Eocene. Extensive micro-fossil sampling in the early Oligocene quarries of the Fayum has not yet produced a *Lahimia*-like hyaenodont, suggesting the clade went extinct at the Eocene–Oligocene boundary. While there is little evidence of faunal change across the E–O boundary in Afro-Arabia on the scale of the faunal change in Eurasia and North America, the extinction of this long-lived early Paleogene lineage may offer insight into how the onset of the later Cenozoic climatic regime affected Afro-Arabian ecosystems.

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### Symposium: Dietary Reconstruction

#### ZN ISOTOPES AS A DIETARY AND TROPHIC PROXY IN FOSSIL TEETH: VARIABILITY IN LATE PLEISTOCENE SOUTHEAST ASIAN FOOD WEBS

Bourgon, Nicolas<sup>1</sup>, Jaouen, Klervia<sup>3</sup>, Bacon, Anne-Marie<sup>4</sup>, Dufour, Elise<sup>2</sup>, Demeter, Fabrice<sup>5</sup>, Shackelford, Laura L.<sup>6</sup>, Souksavatdy, Viengkeo<sup>7</sup>, Hublin, Jean-Jacques<sup>1</sup>, Tütken, Thomas<sup>8</sup>

<sup>1</sup>Department of Human Evolution, Max Plank Institute for Evolutionary Anthropology, Leipzig, Germany, <sup>2</sup>Archéozoologie, Archéobotanique: Sociétés, Pratiques, Environnements (AASPE), Muséum National d'Histoire Naturelle de Paris, Paris, France, <sup>3</sup>Géosciences Environnement Toulouse, Observatoire Midi Pyrénées, Toulouse, France, <sup>4</sup>Biologie, Anthropologie, Biométrie, Epigénétique, Lignées (BABEL), FRE 2029 CNRS, Université de Paris, Faculté de chirurgie dentaire, Montrouge, France, <sup>5</sup>UMR 7206 Eco-Anthropologie, Musée de L'Homme, Paris, France, <sup>6</sup>Department of Anthropology, University of Illinois at Urbana–Champaign, Urbana, Illinois, U.S.A., <sup>7</sup>Department of Heritage, Ministry of Information, Culture and Tourism, Vientiane, Lao People's Democratic Republic, <sup>8</sup>Arbeitsgruppe für Angewandte und Analytische Paläontologie, Institut für Geowissenschaften, Johannes Gutenberg-Universität Mainz, Mainz, Germany

While stable carbon and nitrogen isotope ratios of bone and dentin collagen represent established tools in archaeology for dietary reconstruction, their use is frequently hindered by protein preservation. In contrast, enamel can preserve pristine, diet-related isotope signatures in the bioapatite mineral phase. Recent developments in mass spectrometry

have facilitated the measurement of different non-traditional isotope systems of elements that also allow trophic level assessment. Among these, the stable isotope ratios of the trace element zinc (Zn) (including  $^{66}\text{Zn}/^{64}\text{Zn}$ , expressed as  $\delta^{66}\text{Zn}$ ) constitutes a promising dietary and trophic level indicator. Recently, its application to fossil enamel was validated and its long-term preservation potential, even in tropical settings with poor collagen preservation, was demonstrated. However, the underlying mechanisms which cause variability in  $\delta^{66}\text{Zn}$  values in food webs need to be further characterized.

Here, we present a Zn isotope dataset of tooth enamel of mammals ( $n = 63$ : herbivores = 36, omnivores = 24, carnivores = 4, including two hyenas) from two late Pleistocene fossil assemblages from Nam Lot (86 to 72 ka) and Tam Pà Ling caves (46 to 23 ka), in northeastern Laos. Notably, enamel  $\delta^{66}\text{Zn}$  values decrease systematically between different dietary categories ( $\delta^{66}\text{Zn}_{\text{herbivore}} > \delta^{66}\text{Zn}_{\text{omnivore}} > \delta^{66}\text{Zn}_{\text{carnivore}}$ , respectively  $0.68 \pm 0.18 \text{ ‰}$  [ $1\sigma$ ],  $0.40 \pm 0.23 \text{ ‰}$  [ $1\sigma$ ], and  $0.15 \pm 0.01 \text{ ‰}$  [ $1\sigma$ ]) in these two food webs. These results are in good agreement with expected feeding habits of modern populations of the species, and with those of the fossil assemblage of Tam Hay Marklot cave ( $n = 72$ ) from the same area. Thus, enamel  $\delta^{66}\text{Zn}$  values distinguish herbivores, omnivores, and carnivores. Interestingly, hyenas have elevated  $\delta^{66}\text{Zn}$  values ( $0.54 \pm 0.03 \text{ ‰}$  [ $1\sigma$ ]) compared to other sympatric carnivores, similar to the pattern observed in a modern African food web at Koobi Fora. Finally, the influence of multiple parameters on enamel  $\delta^{66}\text{Zn}$  variability was investigated. Using a Linear Mixed Model, we demonstrate that, besides diet, local geology can also affect enamel  $\delta^{66}\text{Zn}$  variability within a given food web. Although preservation of diet-related  $\delta^{66}\text{Zn}$  values in Pre-Quaternary teeth require further evaluation, our data indicate that Zinc isotopes are a promising new proxy to assess the trophic ecology of fossil vertebrates and reconstruct interactions within past terrestrial food webs.

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### Marine Reptile Diversity & Biology

#### EVOLUTION OF THE NEUROVASCULAR SYSTEM WITHIN THE SNOOTS OF METRIORHYNCHOID CROCODYLOMORPHS

Bowman, Charlotte I.<sup>1</sup>, Young, Mark T.<sup>1</sup>, Schwab, Julia A.<sup>1</sup>, Witmer, Lawrence<sup>3</sup>, Walsh, Stig<sup>2</sup>, Herrera, Yanina<sup>4</sup>, Brusatte, Stephen<sup>1</sup>

<sup>1</sup>School of Geosciences, University of Edinburgh, Edinburgh, Midlothian, U.K., <sup>2</sup>Department of Natural Sciences, National Museum of Scotland, Edinburgh, Lothian, U.K., <sup>3</sup>Department of Biomedical Sciences, Ohio

University, Athens, Ohio, U.S.A., <sup>4</sup>División Paleontología Vertebrados, Universidad Nacional de La Plata, La Plata, Buenos Aires Province, Argentina

During the Jurassic, metriorhynchoid crocodylomorphs underwent a major evolutionary transition, adapting to life in open marine environments. The osteological changes that occurred during this transition are well known (tail fin, flippers, loss of osteoderms) but the endocranial ones are not. In other secondarily marine tetrapods, such as cetaceans, the sensory and physiological demands of the underwater life necessitated a shift in internal rostral anatomy. In order to investigate if these changes are a common response to life in the sea, we digitally segmented the rostral neurovascular from CT scans of eight extant and extinct crocodylomorphs. Our sample includes metriorhynchids (*Cricosaurus araucanensis*, *C. schroederi*, *Metriorhynchus superciliosus*, and *Torvoneustes coryphaeus*), basal metriorhynchoids (*Pelagosaurus typus* and *Eoneustes gaudryi*), and a juvenile and adult example of two extant longirostrine species (*Tomistoma schlegelii* and *Gavialis gangeticus*). We found that metriorhynchoids have reduced antorbital sinuses positioned ventrally to the dorsal alveolar canals at the posterior of the snout, which is a condition shared with extant juvenile crocodiles but not with extant adults, which have large antorbital sinuses positioned dorsally, laterally and ventrally around the dorsal alveolar canals. This arrangement of smaller sinuses may have been beneficial in the high pressure environments the metriorhynchoids may have encountered when diving in the ocean. Trigeminal innervation is markedly different between the metriorhynchoids and extant taxa. Extant crocodylians have a complex network of nerve channels that are spaced to fully innervate all sides of the rostrum, whereas basal metriorhynchoids had fewer, larger channels, with a linear arrangement of openings on the skull. Furthermore, metriorhynchids had a greatly reduced trigeminal system, implying that facial somatosensation was no longer a principal sense; an intriguing possibility as during metriorhynchoid evolution, orbit size rapidly increased. Metriorhynchoids possess a pair of canals which connect the oral cavity to the nasal cavity through the palatine bones, and we hypothesise that these had a function in thermoregulation as these animals had large brains and large eyes and therefore may have used highly vascularised tissues on the roof of the mouth as a 'heat sink' to shed excess heat.

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#### **Colbert Poster Prize/Quantitative Methods**

#### **PSEUDOEXTINCTION ANALYSES AND ANCESTRAL STATE RECONSTRUCTION:**

#### **EVALUATING FOSSIL PLACEMENT ACCURACY IN MAMMALIAN PHYLOGENETICS**

Brady, Peggy, Springer, Mark S.

Evolution, Ecology and Organismal Biology, University of California, Riverside, Riverside, California, U.S.A.

The accuracy of fossil phylogenetics is difficult to assess because fossils are often incomplete and are usually represented only by morphological data, which is highly prone to convergence. Pseudoextinction analyses, which treat extant taxa as if they were extinct, are one way to address the accuracy of morphology within a phylogenetic framework. While previous pseudoextinction analyses have shown a general inability to accurately place fossils, recent work has suggested that the inclusion of hypothetical ancestors (based on ancestral state reconstructions) may increase the accuracy of taxon placement using morphological characters. However, these studies allowed for the inclusion of the direct hypothetical ancestor of each extant taxon that was included in the analysis. It remains to be determined if pseudoextinct taxa, which are a proxy for extinct taxa, can be accurately placed when their immediate hypothetical ancestor is unknown.

To investigate this problem, we employed molecular scaffolds for robustly supported molecular clades with the largest available mammalian morphological dataset from MorphoBank. This dataset is comprised of >4500 characters for 46 extant and 40 extinct species and includes at least one representative of every living placental order. These orders were sequentially treated as pseudoextinct in parsimony analyses by exempting them from the scaffold and recoding their soft morphological characters as missing. For each dataset with a pseudoextinct order, we performed a parsimony ancestral state reconstruction from a fully bifurcating tree that did not contain the pseudoextinct order to obtain hypothetical predicted ancestors. Each pseudoextinct order was then evaluated in six separate phylogenetic analyses using different combinations of fossil taxa, hypothetical predicted ancestors, and our molecular scaffold. We used Robinson-Foulds distances to evaluate the accuracy of phylogenetic analyses under these different treatments.

Our results suggest that morphological characters by themselves cannot be relied upon to accurately place placental orders. In treatments that included fossils, hypothetical predicted ancestors, and a molecular scaffold, only six of 19 pseudoextinct placental orders retained the same interordinal placement as on the molecular phylogeny. These results indicate that ancestral state reconstructions do not increase the accuracy of pseudoextinct taxon placement when the immediate hypothetical ancestor is unknown.

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## Holocene & Pleistocene Mammalian Macroecology & Faunal Studies

### MUSK OX MEASUREMENTS: DIFFERENTIATING THE TEETH AND CRANIA OF THE FOSSIL WOODLAND MUSK OX *BOOTHERIUM* FROM THE TUNDRA MUSK OX *OVIBOS*

Brand, Nickolas<sup>1</sup>, Widga, Chris<sup>2</sup>, Schubert, Blaine<sup>2</sup>

<sup>1</sup>Geosciences, East Tennessee State University, Johnson City, Tennessee, U.S.A., <sup>2</sup>East Tennessee Museum of Natural History, Johnson City, Tennessee, U.S.A.

The extinct woodland musk ox (*Bootherium bombifrons*) is a common faunal component in Pleistocene fossil sites in the southeastern and midwestern U.S.A. While closely related to the extant tundra musk ox (*Ovibos moschatus*), skeletal anatomy of *Bootherium* is poorly documented in the literature, and tentative identification of specimens to just the 'musk ox' level is a common occurrence in museum specimens, due in part to the lack of direct published comparisons of the anatomy of these musk oxen, as well as the frequently isolated nature of the fossils. Pleistocene fossil sites in Saltville, VA have previously yielded pollen samples that suggest a spruce and pine dominant boreal forest environment at low elevations in the late Pleistocene. Isolated and associated ovibovine fossils have been recovered from these sites, although identification has not been made to the genus level for many specimens. Most are isolated teeth, but no character aside from size has been shown to reliably differentiate teeth of extinct musk oxen from *Ovibos*. Eight modern *Ovibos* skulls with teeth were measured and compared to fossil specimens assigned to *Bootherium*, including eight partial crania and ten isolated teeth, with additional measured specimens coming from publications. Results suggest a consistent and significant proportional difference in the molars of *Bootherium* and *Ovibos*, wherein both the upper and lower molars of the former are proportionally wider than those of the latter. Cranial comparisons are made difficult by the fragmentary nature of fossil musk oxen skulls, but patterns were observed. Some standard skull measurements (including postorbital constriction breadth and foramen magnum breadth) overlapped considerably between the fossil and modern groups, while differences in the breadth across the occipital condyles, breadth across the orbits, and the length of the posterior portion of the skull were noted. This dataset suggests the first quantitative way to distinguish the crania and cheek teeth of *Ovibos* from those of extinct musk oxen. An isolated fossil tooth assigned to *Bootherium* from King Leo Pit Cave (Indiana) was the only adult fossil tooth to plot within the *Ovibos* cluster. If this tooth were assigned to *Ovibos*, it would become the southernmost record of the genus in North America. A deciduous fossil tooth from

Saltville also plotted within the *Ovibos* cluster, though it was the only deciduous tooth in the sample and may not be comparable.

**Funding Sources** East Tennessee State University Department of Geosciences.

### Permo-Triassic Tetrapods

### PHOTOGRAMMETRIC ICHNOLOGY OF A PERMIAN ICHNOLAGERSTÄTTE: PREHISTORIC TRACKWAYS NATIONAL MONUMENT, NEW MEXICO

Breithaupt, Brent H.<sup>1</sup>, Matthews, Neffra A.<sup>2</sup>, Gensler, Philip A.<sup>3</sup>, Dunn, Colin R.<sup>4</sup>, Lucas, Spencer G.<sup>5</sup>

<sup>1</sup>Wyoming State Office, BLM, Cheyenne, Wyoming, U.S.A., <sup>2</sup>National Operations Center, BLM, Denver, Colorado, U.S.A., <sup>3</sup>New Mexico State Office, BLM, Santa Fe, New Mexico, U.S.A., <sup>4</sup>Las Cruces District Office, BLM, Las Cruces, New Mexico, U.S.A., <sup>5</sup>New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, U.S.A.

The U.S.A.'s 100<sup>th</sup> national monument, Prehistoric Trackways National Monument (PTNM) was founded in 2009 to conserve, protect, and enhance the unique and nationally important paleontological, scientific, educational, scenic, and recreational resources found in the Robledo Mountains north of Las Cruces in Doña Ana County, New Mexico. The PTNM contains some of the most diverse and well-preserved Paleozoic tetrapod tracks in North America and some of the most scientifically significant early Permian tracksites known. In PTNM, fossilized traces are preserved in the lower Permian red beds of the Robledo Mountains Formation of the Hueco Group, deposited on the northwestern shore of a marine embayment, ~ 286 million years ago (Leonardian/Middle Artinskian). Due to the high occurrence, ichnotaxonomic diversity, and morphological preservational variants, the tracks at PTNM provide an unprecedented glimpse into the paleoecology of the early Permian. Indeed, these ichnites provide valuable information for the understanding of Paleozoic ichnotaxa worldwide, and have served as a 'Rosetta Stone' for rewriting global Permian tetrapod ichnotaxonomy. As such, this unique biotic assemblage presents an opportunity to use state-of-the-art, 3D digital documentation technology to conserve, protect, and visualize exceptionally preserved paleontological resources. Over the last decade, specimens selected from over 2,500 track-bearing slabs curated at the New Mexico Museum of Natural History and Science in Albuquerque were documented using close-range photogrammetric techniques. Representative examples of tracks and trackways of the ichnotaxa *Batrachichnus*, *Dimetropus*, *Dromopus* (preserving the activities of temnospondyl

amphibians, pelycosaurs, and early diapsids, respectively), and others were chosen for study. Three-dimensional image datasets from this documentation provide a permanent digital record of the tracks for in-depth evaluation and assessment. These studies also allow disassociated trackway blocks to be realigned, analyzed, and compared with neoichnologic information, providing a ‘snapshot’ of the activities and kinetics of movement of organisms as they traversed the ancient coastal plain of the Hueco seaway. In addition, the enhanced 3D visualization of novel ichnites (e.g., *Alacranichnus bradyi*, a scorpion resting trace) provide a unique look at some of the most scientifically significant ichnofossils known from a true trace-fossil Lagerstätte (Ichnolagerstätte).

### Symposium: Dietary Reconstruction

#### DEVELOPING CARIBOU ANTLERS AS ECOLOGICAL INDICATORS USING STABLE ISOTOPE ANALYSIS

Brenning, Matthew<sup>1</sup>, Longstaffe, Fred<sup>3</sup>, Fraser, Danielle<sup>2</sup>  
<sup>1</sup>Earth Science, Carleton University, Ottawa, Ontario, Canada, <sup>2</sup>Canadian Museum of Nature, Ottawa, Ontario, Canada, <sup>3</sup>University of Western Ontario, London, Ontario, Canada

*Rangifer tarandus* (caribou) have existed since the Pleistocene and, unlike many North American megafauna, survived through the Pleistocene–Holocene (~11,700 ybp) extinction event. Today, caribou are experiencing a dramatic shift in their arctic ecosystem. As a result, many major caribou populations in Canada are in steady decline. This study aims to determine whether *R. tarandus* antlers can be used as effective ecological indicators relative to other hard tissues such as bone and tooth enamel, using stable isotopes of oxygen, carbon, and nitrogen. Variation in the rate and timing of tissue development should result in different stable isotope profiles for each tissue. Antlers are unique in that they grow over a protracted period of time and, unlike bone and tooth enamel, regrow annually. Antlers should therefore reflect the isotopic composition of food and water taken in during the spring and summer of a single year, providing a high-resolution record of ecological conditions. Bones and teeth form and mineralize over a different time frame, therefore reflecting averages of diet and water intake over months to years. Fifteen males were selected from the Canadian Museum of Nature (CMN) archive based on geographic location, sex, maturity, and collection date. Approximately 30 samples were taken for each specimen from the mandible, third lower molar, and every 3 cm along the length of the antler, some of which neared 1 m in length. Samples were then processed using standard procedures for both collagen and carbonate extraction. Collagen carbon and nitrogen isotope ratios showed significant patterns of variation along the

length of antlers, demonstrating their potential as ecological indicators. Similarly, carbon isotope ratios from carbonate showed patterns different from that of the collagen, potentially providing another signal of ecological variation during growth. This study helps to provide a better understanding of the utility of stable isotope analysis of antler tissue. Antler tissue, which are commonly preserved in Pleistocene sediments and comprise a large portion of the CMN Pleistocene collections, can be used to address ecological changes among caribou during the Pleistocene–Holocene transition when 88% of North America megafauna became extinct. Moving forward, the stable isotope profiles of Pleistocene antlers will be measured and compared to their modern counterparts as a means of understanding their response to global change during the Holocene.

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### Evolution & Biology of Non-Avian Theropods

#### DESCRIPTION OF NEW TOOTH PATHOLOGIES IN *TYRANNOSAURUS REX*

Brink, Kirstin  
University of Manitoba, Winnipeg, Manitoba, Canada

Dental pathologies in theropod dinosaurs are relatively common. Most occurrences such as split, multiple, or dysmorphic carinae, where the overall shape of the tooth is normal but the carinae are abnormal, are thought to be caused by genetic factors. However, three teeth associated with the skull of the *Tyrannosaurus rex* SUE (Field Museum of Natural History PR2081) show abnormalities in overall tooth shape, including malformation and fusion. FMNH PR2081 was previously diagnosed with an oral infection common to birds, trichomonosis. Therefore, it is possible that the abnormalities in these teeth are not due to genetic factors during tooth development, but rather are caused by an infection in the soft tissue of the jaw that disrupted normal tooth development.

To determine if the pathologic teeth in FMNH PR2081 could have been caused by infection, the teeth were CT scanned to examine the defects in detail. All three teeth are short with thick dentine in the tips of the crowns and have large pulp cavities with incomplete roots basally, indicating they were still developing and unerupted when the animal died. The first tooth shows normal crown and denticle development, however is bent at a 45 degree angle and has broad, inconsistently spaced transverse undulations covering the entire crown. The other two teeth, one three times as large as the other, are fused together. The denticles on the carina of the small tooth are elongate and finger-like where they attach to the larger tooth. The larger

tooth has abnormal denticle development along the carinae, including miniature and double denticles, and also has a patch extra denticles on the lingual crown. The tip of the crown is bent and flattened.

An examination of published CT scans of FMNH PR2081 shows two empty alveoli at the back of the left maxilla, dorsal to the area of purported *Trichomonas* infection in the mandible. All other teeth associated with the skull are normal. Given the shape and origin of the pathologic teeth, it is possible that the infection spread to the upper jaw and disrupted the soft tissue around the dental follicles in a way that allowed tooth development to proceed, creating the pathologies. This study shows for the first time an example of tooth and denticle pathologies that were likely caused by infection instead of pre-determined genetic factors, and offers new information on the potential causes of dental defects in the fossil record.

## Permo-Triassic Tetrapods

### DREPANOSAURS: WEIRD TO THE BONE

Britt, Brooks B.<sup>1</sup>, Jackson, Alexa<sup>1</sup>, Horn, Audrey M.<sup>1</sup>, Theurer, Brandon C.<sup>1</sup>, Chure, Dan<sup>2</sup>, Engemann, George F.<sup>3</sup>, Scheetz, Rod D.<sup>1</sup>

<sup>1</sup>Museum of Paleontology / Geological Sciences, Brigham Young University, Provo, Utah, U.S.A., <sup>2</sup>Retired, Jensen, Utah, U.S.A., <sup>3</sup>Geology, University of Nebraska, Omaha, Omaha, Nebraska, U.S.A.

Derived drepanosaurids are enigmatic basal diapsids with bizarre adaptations that include a superficially bird-like skull, mole-like arms, and a tail that ends in a ‘claw’. With few exceptions, our knowledge is hindered by flattened specimens. Multiple 3D articulated skeletons from the Saints & Sinners Quarry imaged via segmentation of high-resolution micro CT scans provide significant insights into the highly derived dorsal vertebrae of this taxon from the latest Triassic-aged Nugget Sandstone of Utah.

Neural spines of the several anterior dorsal vertebrae are vertically elongated and the fused apices of two tallest spines (D2+D3?) form a notarium with a lateral cotyle that receives the distal end of the scapula. The laterally thickened apex of dorsal vertebra 2 is hollow and flares anteriorly with two prongs – possibly a cradle for the neural spine of dorsal vertebra 1, which precedes the notarium. The anterior dorsals have large/vertically elongate neural canals and minute, crescentic centra (wider than tall) that are transitional from minute cervical centra to the more posterior centra, which have deep (fish-like) ‘cotyles’ and deep, large lateral pneumatic fossae. There is a single, elongate, median prezygapophysis consisting of fused left and right zygapophyses except in the last couple of vertebrae where the prezygapophyses are paired. Pneumatic fossae are well-developed on the superior and

inferior sides of the transverse processes and the neural arch bears fine laminae as on pneumatic saurischian vertebrae. At mid-series, there is a vertical neural spine with those anterior to it strongly reclined and those posterior to it inclined anteriorly, overhanging the centrum. These specimens show that despite their small size, geologic age, and basal diapsid position, drepanosaurid vertebrae are highly derived in terms of the zygapophyses and extensive pneumatic features (laminae and fossae). These features indicate an extensive air-sac system like those of pterosaurs and derived saurischian dinosaurs. A synapomorphy of Diapsida is a unidirectional lung, which likely facilitated the pneumatic features in all these (aforementioned) taxa. A well-developed air sac system that invades bones in a basal diapsid (drepanosaurids) is unexpected and the adaptive value of a lightened axial skeleton in a presumed scratch digger remains to be resolved.

## Macroecology & Macroevolution

### THE INTERPLAY BETWEEN REGIONAL AND GLOBAL CLIMATIC TRENDS IN CROCODYLIFORM FAUNAL CHANGE

Brochu, Christopher A.<sup>1</sup>, Adams, Amanda<sup>1</sup>, Drumheller, Stephanie K.<sup>2</sup>, Miller-Camp, Jess<sup>3</sup>, Rubin, Margaret<sup>1</sup>

<sup>1</sup>University of Iowa, Iowa City, Iowa, U.S.A., <sup>2</sup>University of Tennessee, Knoxville, Tennessee, U.S.A., <sup>3</sup>Indiana University, Bloomington, Indiana, U.S.A.

The relationship between changes in diversity and climate provides windows into how environmental conditions might drive evolution. Cenozoic crocodyliforms are an excellent clade with which to explore this interplay, as their observed diversity appears to track global temperature proxies, with peaks coinciding with mid-Paleogene and early Miocene thermal highs. This would be the predicted pattern for a clade of large ectotherms, but we do not know the extent to which regional changes in diversity reflect local and global environmental changes. To explore this, we catalogued Cenozoic crocodyliforms across western North America, Europe, and Africa based on direct observations in museum collections. In the North American Western Interior, units up to Uintan (middle Eocene) age preserve as many as five crocodyliforms; this drops to one in the overlying Duchesnean, well before the cooling event at the end of the Eocene, and remaining low thereafter, with only *Alligator* persisting and evolving to resemble the generalized crocodyloids found in the earlier Paleogene. This also appears to be true for deposits formed away from the paleocoast in western and central Europe, where within-unit diversity drops well before the end-Eocene climatic transition. The lack of a recovery to multi-species assemblages in the early Miocene in these regions

might be related to lower temperatures at higher latitudes, but faunal turnover also occurs at low latitudes during the Neogene. Diversity in the late Cenozoic of East Africa is unlikely to correlate with temperature, as lower altitudes remained within crocodyliform thermal tolerance levels throughout the period. However, regional trends reveal other potential drivers. In the Turkana Basin, extinct relatives of forest-dwelling dwarf crocodiles (*Osteolaemus*) are replaced by groups with broader ecological tolerances (e.g., *Crocodylus*) during the middle Miocene. This was when continuous forest cover gave way to open savannas and grasslands. Similar taxonomic changes are not observed in the western (Gregory) branch of the African Rift Valley, where dwarf crocodile relatives and their preferred forests persisted into the Pliocene. Here, diversity changes appear to reflect changes in rainfall and aridity more than temperature. Evidence from all three continents suggests that concentrating on only one aspect of climate masks a more complex interplay between regional and global environmental change.

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### **Biomechanics & Functional Morphology**

#### **SHOULDER JOINT RANGE OF MOTION IN FOSSIL SYNAPSIDS AND THE ORIGINS OF MAMMALIAN LOCOMOTOR DIVERSITY**

Brocklehurst, Robert J.<sup>1</sup>, Fahn-Lai, Philip<sup>1</sup>, Regnault, Sophie<sup>2</sup>, Angielczyk, Ken<sup>3</sup>, Pierce, Stephanie E.<sup>1</sup>

<sup>1</sup>Museum of Comparative Zoology and Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts, U.S.A., <sup>2</sup>School of Veterinary Medicine, University of Surrey, Guildford, U.K., <sup>3</sup>Negaunee Integrative Research Center, Field Museum of Natural History, Chicago, Illinois, U.S.A.

Extant mammals are both taxonomically and ecologically diverse, having evolved a remarkable array of locomotor ecologies (e.g., swimming, digging, and flying). Evolution of the therian-type forelimb, with a highly reduced pectoral girdle and ball-and-socket shoulder joint, has been heralded as a key innovation that enabled mammals to co-opt their forelimbs for diverse functions. The acquisition of the mammal forelimb can be traced through their forerunners, the non-mammalian synapsids (NMS), but exactly how this musculoskeletal transformation proceeded and its impact on functional diversification have not been quantitatively tested.

To explore the evolution of forelimb functional diversity in synapsids, we measured shoulder joint osteological range of motion (ROM) in a range of extant amniotes (lizards, monotremes, therian mammals), and compared their patterns of joint mobility to exemplars from each of the

major grades of NMS: ‘pelycosaurs’, basal therapsids, and non-mammalian cynodonts. Three-dimensional models of the shoulder girdles and humeri were digitally aligned in an anatomical ‘neutral pose’ using a semi-automated approach based on articular surface morphology. ROM was then determined for the shoulder joint using a fully automated method, where the humerus was moved in flexion-extension, adduction-abduction, and pronation-supination until bone-to-bone contact occurred. Relative degree and directionality of mobility were then compared across taxa.

We find an increase in total shoulder joint ROM through synapsid evolution, suggesting that more derived NMS could perform a wider range of limb movements. However, we also see more complex trends in directionality of shoulder mobility that may be indicators of forelimb posture. Extant lepidosaurs and monotremes had the greatest ROM in abduction-adduction, whereas therians had more ROM in flexion-extension, likely related to ‘sprawling’ vs. ‘erect’ gaits. Therapsids and cynodonts both had greatest ROM in abduction-adduction, matching previous reconstructions of these taxa as sprawling to semi-erect. However, ‘pelycosaurs’ had the greatest ROM in flexion-extension, despite having abducted forelimbs, suggesting they did not move their forelimbs in same manner as modern sprawling animals. Our results demonstrate the complex nature of forelimb evolution in synapsids and provide novel insights into the functional transformation and diversification of the mammalian forelimb.

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### **Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

#### **DETERMINING PROBABLE CAUSE OF DEATH AND CHANCE OF BONE DISEASE IN A MAMMOTH FROM SOUTHEASTERN IDAHO**

Brooks, Kate  
Geological Sciences, University of Idaho, Moscow, Idaho, U.S.A.

Analysis of a near-complete skeleton of a 11,700 ± 40-year-old mammoth from southeastern Idaho has the potential to show us whether Columbian and Woolly mammoth interbreeding caused introgressive hybridization and genetic diseases in their offspring: the Jeffersonian Mammoth. Understanding the circumstances surrounding this mammoth’s death have raised several questions that have led us to discover that it was a juvenile (between 12–18 years old) and most likely male. In this study, CT (computerized tomography) scans, 3D modeling applications, and optical observation have revealed evidence of internal pore widening in the joints and foot

bones, and potential internal fracturing in a foot of the mammoth. Enlarged pore sizes of up to 3 mm in diameter occur; this is in contrast to normal ranges for pores that are typically less than 0.1 mm. Pore widening can be an indicator of osteoporosis or other skeletal related diseases such as Kashin-Beck disease. The internal fracture is approximately 44.15 mm in length inside the right calcaneum bone and is identified by a thickened callus around the fracture. Internal fractures can be indicators of lameness and may have contributed to the mammoth's eventual death. There is also evidence that osteofibrotic changes can cause increased bone fragility that may have led to this fracture. Unusual markings have also been observed externally on the joints, long bones, and foot bones. Preliminary interpretation of these markings suggest that they are evidence of premortem ulcers or deformation caused by an underlining bone disease. Premortem deformations by ulcers can be identified by an area up to 6 cm<sup>2</sup> with a linear dimension typically no larger than 7 cm. These features are common on the articular surface of subchondral bones. This mammoth presents a feature that matches this description on the distal end of its ulna measuring 4 cm x 4.5 cm. These observations provide insight into possible bone diseases within the mammoth, whether it died because of bone disease or lameness, and the premortem state of the mammoth. The evidence also allows for further study into hybridization of mammoths right before their final demise in North American during the Pleistocene epoch.

## Mesozoic & Early Cenozoic Mammalian Evolution

### NEW LATE CRETACEOUS MAMMALS FROM LA COLONIA FORMATION, PATAGONIA, ARGENTINA SUPPORT MULTITUBERCULATE AFFINITIES FOR FERUGLIOTHERIIDS

Brown, Corinne E.<sup>1</sup>, Cardozo, Mauricio S.<sup>2</sup>, Kuwabara, Nobuyuki<sup>1</sup>, Rougier, Guillermo W.<sup>1</sup>

<sup>1</sup>Anatomical Sciences and Neurobiology, University of Louisville, Louisville, Kentucky, U.S.A., <sup>2</sup>Universidad de La Plata, La Plata, Argentina

Recent field work in the Maastrichtian-Danian La Colonia Formation resulted in a rich microvertebrate collection including numerous mammalian remains. Isolated teeth represent the bulk of the material, but occasionally fragmentary jaws, maxillae, and postcranial elements were recovered via screen-washing. At least five new localities providing mammalian remains have been identified in addition to the previously reported Anfiteatro 1. All of them are in similar stratigraphic position, and with no perceptible differences in faunal content.

Mammals include additional specimens of the meridiolestids *Reigitherium* and *Coloniatherium*, and the multituberculate *Argentodites*. New records for the

formation include small-sized meridiolestids and the controversial taxon *Ferugliotherium*, formerly known only from the approximately contemporaneous and geographically not too distant Los Alamitos Formation.

Two mandibular fragments showing the characteristic blade-like multituberculate p4 can be assigned to *Argentodites*. These specimens preserve no other teeth, but show that *Argentodites* have a large, curved incisor extending posteriorly to the level of p4, not reaching behind the last molar, and a single plagiaulacoid premolar, followed by two molars. The first molar was rectangular in outline while the second was quadrangular, both supported by four roots. There is a reasonable number of isolated *Argentodites* specimens, suggesting the molars of this taxon should be relatively abundant. We have numerous isolated molars of *Ferugliotherium*; they match the size and pattern of alveoli in the jaws attributed to *Argentodites*, and when preserved well enough, have four roots. In our large collection of isolated teeth there are no other potential molar candidates for the jaws. We formally recognize *Argentodites* as a junior synonym of *Ferugliotherium*, supporting earlier suggestions. The lower tooth formula for *Ferugliotherium* was i1 c0 p1 m2. There are a number of isolated upper molar and premolar morphs. The upper molars (M1-2) show the diagnostic transverse crest connecting buccal and lingual cusps. The M1 has two rows and an incomplete third lingual row. At least four premolar positions are identified, which lack transverse crests. Mesial premolars are relatively simple and small, while the two distal are complex multi-row elongated premolars. The tooth formula and dental morphology supports *Ferugliotherium* as a multituberculate, making gondwanatherian affinities unlikely.

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## Symposium: Dietary Reconstruction

### CARBON ISOTOPE ANALYSIS OF CERCOPITHECIDAE FROM THE SHUNGURA FORMATION, 3.3 MA–1.2 MA: DIET DURING THE TRANSITION BETWEEN DOMINANT SPECIES OF THEROPITHECUS IN THE TURKANA BASIN

Brown, Morgan<sup>1</sup>, Uno, Kevin T.<sup>2</sup>, Merceron, Gildas<sup>3</sup>, Boisserie, Jean-Renaud<sup>4</sup>

<sup>1</sup>Ecology, Evolution, and Environmental Biology, Columbia University, New York, New York, U.S.A.,

<sup>2</sup>Division of Biology and Paleo Environment, Lamont-Doherty Earth Observatory, Palisades, New York, U.S.A.,

<sup>3</sup>PALEVOPRIM, CNRS and University of Poitiers, Poitiers, France, <sup>4</sup>CFEE, CNRS and Ministry of Europe and foreign affairs, Addis Ababa, Ethiopia

Understanding the paleodiet of *Theropithecus*, a genus of Old World monkey, can provide insight into the terrestrial ecosystems of Africa in the Plio-Pleistocene. Previous analyses have highlighted the C<sub>4</sub>-dominated diet of the genus; however, the period in which *T. oswaldi* replaced *T. brumpti* as the dominant cercopithecoid in the Turkana Basin (between 3.0 Ma–2.0 Ma) is not well documented. This study aimed to clarify the diet of *Theropithecus* through carbon isotope analysis of enamel samples from the Lower Omo Valley in Ethiopia. First, we compared the diets of five cercopithecoid taxa (*T. oswaldi*, *T. brumpti*, *Papio*, *Paracolobus mutiwa*, and *Rhinocolobus turkanaensis*) to discern dietary niche partitioning of monkeys within the Shungura Formation. Then, we contextualized these new data on *Theropithecus* with previous studies to advance the spatial and temporal understanding of the dietary progression of this genus in eastern Africa. These new data show clear carbon isotope-based partitioning of cercopithecoid diets in the Shungura Formation, with nearly all *Theropithecus* having a C<sub>4</sub>-dominated diet, *Papio* having a mixed C<sub>3</sub>–C<sub>4</sub> diet, and colobines having C<sub>3</sub>-dominated diet. There is no difference in diet between *T. oswaldi* and *T. brumpti* where they are coeval. Extending into the Turkana Basin, the data show an increasingly C<sub>4</sub>-based diet of *T. brumpti* in the region whereas *T. oswaldi* shows no such shift. As the first isotopic analysis of contemporaneous samples of *T. brumpti* and *T. oswaldi*, these findings necessitate a revision of our understanding of the dietary patterns of *Theropithecus*, as the diet of these two species may not be as different as previously thought. Future analyses of Turkana Basin paleoecology should consider this information on cercopithecoid diet, especially in regard to C<sub>3</sub> and C<sub>4</sub> resource availability and competition between terrestrial species for the C<sub>4</sub> niche.

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## Evolution & Biology of Non-Avian Theropods

### REEVALUATION OF DINOSAUR MATERIAL FROM THE ATLANTIC COASTAL PLAIN ILLUMINATES A BIZARRE NEW ASSEMBLAGE

Brownstein, Chase D.  
Collections & Exhibitions, Stamford Museum and Nature Center, Stamford, Connecticut, U.S.A.

One key discovery in Mesozoic vertebrate biogeography was the existence of continental or hemispheric vertebrate assemblages. This biogeographic split has perhaps most famously been illustrated using dinosaur skeletons from northern Africa and Patagonia that belong to lineages

entirely different from those that dominated contemporaneous North American and Asian ecosystems. During the Late Cretaceous, the eastern half North America was isolated for approximately thirty million years as a landmass known as Appalachia. Mesozoic dinosaur faunas from eastern North America are poorly known compared to those from the American west, primarily because eastern finds often consist of fragmentary specimens unable to be identified at low taxonomic levels. This situation has made it difficult to understand how geographic isolation influenced the evolution of life on Appalachia. Recent discoveries and the reevaluation of previously collected eastern North American dinosaur material have provided new information on the dinosaur assemblages of this region. I review recent research of Appalachian dinosaur material from the Atlantic Coastal Plain and provide an analysis of what these fossils suggest about the composition and biogeography of late Mesozoic vertebrate assemblages. Appalachian dinosaurs are currently represented by several genera of tyrannosauroids, hadrosaurids, non-hadrosaurid hadrosauroids, nodosaurids, ornithomimosaurs, and avians. Additional material has substantiated several other clades of dinosaurs, including dromaeosaurids, allosauroids, and ceratopsians, although some of these specimens remain problematic. Almost all Appalachian dinosaurs known from fragmentary and partial skeletons included in phylogenetic analyses are found in basal positions among their respective parent groups. Some, like the latest Cretaceous tyrannosauroid *Dryptosaurus aquilunguis*, show bizarre body plans that differ extensively from western North American and Asian relatives. Along with other members of Appalachian assemblages, these dinosaurs evince that this landmass probably harbored a distinctive, potentially relictual vertebrate fauna and demonstrate that the Cretaceous 'fauna' of the northern hemisphere was highly heterogeneous.

## Mesozoic Herpetology

### GREATER DIVERSITY OF ELASMOSAURID PLESIOSAURS FROM ANTARCTICA REVEALED BY NEW FOSSILS FROM THE CAMPANIAN OF THE SNOW HILL ISLAND FORMATION, JAMES ROSS BASIN, ANTARCTICA

Brum, Arthur<sup>1</sup>, Simões, Tiago<sup>2</sup>, Piacentini, André<sup>3</sup>, Figueiredo, Rodrigo<sup>4</sup>, Sayão, Juliana<sup>5</sup>, Kellner, Alexander W.<sup>1</sup>

<sup>1</sup>Laboratório de Paleobiologia e Paleogeografia Antártica, Geologia e Paleontologia, Museu Nacional, Rio de Janeiro, Rio de Janeiro, Brazil, <sup>2</sup>Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A., <sup>3</sup>Faculdade de Formação de Professores, Universidade do Estado do Rio de Janeiro,

São Gonçalo, Rio de Janeiro, Brazil, <sup>4</sup>Departamento de Biologia, Universidade Federal do Espírito Santo, Alegre, Espírito Santo, Brazil, <sup>5</sup>Laboratório de Paleobiologia e Microestruturas, Universidade Federal de Pernambuco, Vitória de Santo Antão, Pernambuco, Brazil

The vertebrate fossil record of Late Cretaceous outcrops from the James Ross Island Basin mostly comprises marine reptiles, especially mosasauroids and elasmosaurid plesiosaurs. Aristonectines are the most common elasmosaurid plesiosaurian from that locality, mostly known from the upper Maastrichtian, whereas the lower Campanian diversity is still obscure, with only a few occurrences of polycotylids plesiosaurs and indeterminate elasmosaurids. The 2018–2019 fieldwork for the PALEOANTAR Project in James Ross Island prospected in the Snow Hill Formation (Campanian) at Santa Marta Cove and recovered five associated cervical vertebral centra and four centrum fragments referable to elasmosaurids. We performed a phylogenetic analysis and linear morphometrics with a bivariate analysis, utilizing height/length ratio (HI); breadth/length ratio (BI); and rate of vertebral elongation (VLI) indices. We also conducted nonparametric tests (Kruskal-Wallis Test [KWT]) and Mann-Whitney tests) to recover significant difference between VLI means among elasmosaurid ontogenetic stages and plesiosaur morphotypes, and group membership of the James Ross specimen. Our dataset included 87 juvenile elasmosaurids to determine ontogenetic stage grouping. To evaluate morphotype membership, we evaluated 69 Aristonectinae, 165 Elasmosaurinae (Em), and 91 ‘*Cimoliasaurus*’ morphotypes. The centra are anteroposteriorly elongated, with low BI and HI, and high VLI. Nonparametric analyses showed the James Ross specimen is significantly different from all juveniles, suggesting that it was not a juvenile at time of death. We also found the specimen to be significantly distinct from all morphotypes except Em, indicating it has cervical proportions of elasmosaurines. Phylogenetic analysis assigns the specimen within Elasmosauridae based on the following unambiguous synapomorphies: centra longer than higher; lateral surface with a longitudinal lateral keel; and a rounded midline ridge on the median ventral surface of the centra. The James Ross specimen was found as an early elasmosaurid and a sister taxon to *Zarafasaura oceanis* (outside Euelasmosaurida), by the breadth subequal to the height or less. It also shares with the non-euelasmosauridan elasmosaurids the plesiomorphic subcylindrical centra without a ventral notch. These new remains suggest a higher diversity of elasmosaurids, and the occurrence of a non-Euelasmosaurida in the Campanian fossil record of James Ross Basin.

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## Symposium: Paleoneurology

### BRAINS, GIANT DINOSAURS, AND SWIMMING CROCODYLOMORPHS: NEUROSENSORY CHANGES DURING MAJOR EVOLUTIONARY TRANSITIONS IN MESOZOIC ARCHOSAURS

Brusatte, Stephen<sup>1</sup>, Young, Mark T.<sup>1</sup>, Schwab, Julia A.<sup>1</sup>, Witmer, Lawrence<sup>2</sup>, Herrera, Yanina<sup>3</sup>, Walsh, Stig<sup>4</sup>, McKeown, Matthew<sup>1</sup>, Muir, Amy<sup>1</sup>, Williamson, Thomas E.<sup>5</sup>, Carr, Thomas D.<sup>6</sup>

<sup>1</sup>School of GeoSciences, University of Edinburgh, Edinburgh, Lothian, U.K., <sup>2</sup>Ohio University, Athens, Ohio, U.S.A., <sup>3</sup>Museo de La Plata, La Plata, Argentina, <sup>4</sup>National Museums Scotland, Edinburgh, U.K., <sup>5</sup>New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, U.S.A., <sup>6</sup>Carthage College, Kenosha, Wisconsin, U.S.A.

Archosaurs originated ca. 250 million years ago and diverged into two lineages: one including birds and dinosaurs, the other leading to crocodylians. Both lines diversified in the Mesozoic, experienced spates of dominance, and underwent evolutionary changes as they faced changing environments and two mass extinctions, ultimately surviving as 10,000+ species today. Little is known, however, about how brains and sensory systems related to, and perhaps underpinned, major evolutionary transitions in archosaurs. We here focus on neurosensory changes during two of the most remarkable transformations in Mesozoic archosaurs: the development of enormous body size in tyrannosauroid dinosaurs and the transition from terrestrial ancestors to open-ocean swimmers in thalattosuchian crocodylomorphs. We used high-resolution computed tomography scanning to construct digital endocasts of the endocranium (approximating the brain), nerves and vasculature, and associated pneumatic sinuses of over two dozen fossil and extant archosaurs, focusing particularly on metriorhynchids (the thalattosuchian subgroup, which were the only archosaurs to ever develop fully pelagic lifestyles) and tyrannosauroids from the mid-to-Late Cretaceous that span the acquisition of gigantic size (>ca. 1 ton). For thalattosuchians, we find there was little change in overall brain shape or relative size as metriorhynchids evolved from nearshore semiaquatic species into pelagic forms. The brains of close thalattosuchian outgroups (e.g., *Eopneumatosuchus*) and teleosauroids share with metriorhynchids an elongate, tubular shape and a long, horizontal pituitary fossa with enlarged orbital arteries. Metriorhynchids, however, have an expanded dural venous sinus system, particularly pronounced in taxa like *Metriorhynchus brachyrhynchus*, which may be related to diving or thermoregulation. For tyrannosauroids, we find

that the large, tubular brain with an expanded dorsal peak but reduced flocculus, characteristic of the largest Late Cretaceous species, first developed in smaller, more basal taxa like *Timurlengia*. Voluminous air sinuses surrounding the brain evolved later, in concert with a great increase in body size in taxa such as *Bistahieversor*. In both thalattosuchians and tyrannosauroids, there is no marked change in brain anatomy associated with their major ecological and evolutionary transitions, although there are associated sinus changes. Brains, thus, were not evidently drivers of these transitions.

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### **Mammalian Skeletal Morphology**

#### **STERNAL STRUCTURE PREDICTS FEEDING STYLE IN MYSTICETE CETACEANS**

Buchholtz, Emily A., Siegel, Claire  
Biological Sciences, Wellesley College, Wellesley, Massachusetts, U.S.A.

The mammalian sternum lies at the intersection of the head, forearm, and torso, and provides regionally defined attachment sites for muscles acting on all of these structures. This geometry predicts that sternum shape will reflect differences in the relative size and use of these peripheral structures. Interspecific variation of the sternum has received limited examination since the 19<sup>th</sup> century, and intraspecific variation has been essentially ignored. Here we examine sternal shape in mysticete cetaceans, a clade showing extreme modification of multiple peripheral structures that articulate and/or interact with the sternum: there is no clavicle, the forelimb is restructured as a flipper, the head is exceptionally large, and there is a single costosternal articulation (with rib 1). Further, mysticetes display disparate feeding styles that depend on the highly specific structure and action of the mandibles and tongue, both of which have direct or indirect muscular connections to the sternum. Specimens of mysticete sterna were photographed in museums and collected from the primary literature. Sternal shape was documented using geometric morphometrics, and was analyzed statistically using principal components analysis. Despite extensive ontogenetic change, our results indicate that sternal shape is highly correlated ( $p < 0.001$ ) with species identification, with feeding style (skim vs. suction vs. lunge), and with relative forelimb length. Further expansion of the database will allow more extensive comparisons among individuals of a wider range of total body length and sternum length (as proxies for ontogenetic stage), and across the different subcategories of lunge feeding found in baleenopterids.

This approach also offers the possibility of predicting feeding style in fossil taxa.

### **Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

#### **GLACIAL CYCLES DRIVE QUATERNARY POPULATION DYNAMICS IN THE SAGEBRUSH VOLE, *LEMMISCUS CURTATUS* (RODENTIA, ARVICOLINAE)**

Burroughs, Robert W.  
Committee on Evolutionary Biology, University of Chicago, Chicago, Illinois, U.S.A.

The fossil record of the extant sagebrush vole, *Lemmys curtatus*, records a purported anagenetic evolutionary event consisting of stepwise increases in the number of closed enamel triangles on the lower first molar over the past 2 million years. Previously elucidated developmental mechanisms provide the framework for understanding the developmental mechanism underlying this evolutionary transition, leaving the question of population dynamics through the event as an area ripe for investigation. Using a combination of DNA markers (two mitochondrial and one nuclear), I investigated the recent population dynamics of 19 individuals representing 16 distinct geographic localities. My results indicate that extant populations of *Lemmys* function as a single large metapopulation, suggesting that interrogation of gene-trees via molecular clock analysis can reveal the population dynamics of ancient populations. The gene-trees revealed that distinct mitochondrial markers (CytB and CO1) preserve two levels of geographic patterns, with one being more ancient than the other. The more ancient pattern, recorded by CytB, suggests that *Lemmys* populations were once more disparate and geographically regionalized. Subsequently, this regionalization was homogenized, resulting in the modern metapopulation dynamic indicated by the CO1 sequences. The timing of divergence events in both gene-trees is consistent with phylogeographic range shifts that are forced by glacial-interglacial cycles. Limited diversification events from 1.8 million years ago to 850 thousand years ago (ka) suggests that the geographic range was contracted by extensive glaciation. Following 850 ka, diversification pulses over the next 840 thousand years are timed with interglacials. Following the end of the last glacial maximum, four diversification events are detected, suggesting that range expansion is active. These results corroborate a previous hypothesis that *Lemmys* utilized high elevation glacial refugia. Range contraction associated with these refugia facilitated remixing of once geographically- and genetically-distinct populations, with subsequent redispersal coinciding with the ends of glacial cycles and leading to new genetic differentiation. These

results in concert with the fossil record of *Lemmiscus* provide a contextual basis for investigating how anagenetic evolution occurred within this species and an exemplification for how these types of events may have occurred in other species.

**Funding Sources** University of Chicago Hinds Fund.

### **Late Cenozoic Mammalian Macroecology & Macroevolution**

#### **UPDATED POPULATION STRUCTURE OF *TAPIRUS POLKENSIS* AT THE EARLIEST PLIOCENE GRAY FOSSIL SITE, TENNESSEE, BASED ON NEW MNI CALCULATIONS**

Bushell, Matthew, Wallace, Steven, Haugrud, Shawn  
Don Sundquist Center of Excellence in Paleontology and  
Department of Geosciences, East Tennessee State  
University, Johnson City, Tennessee, U.S.A.

*Tapirus polkensis* outnumbers all other mammalian taxa at the earliest Pliocene Gray Fossil Site of eastern Tennessee by an order of magnitude. Previous work reported a Minimum Number of Individuals (MNI) of at least 75; however, ongoing excavations continue to yield new material, affording an updated count. As expected because of its robust nature, the astragalus yielded the highest value among elements examined: currently at 135 individuals. In addition to basic left/right designations, all astragali are classified following seven age classes (1–7) originally established for the taxon using tooth eruption/replacement. Astragali directly associated with cranial material thereby served as a baseline for placement of isolated specimens into developmental 'stages' (corresponding to the age classes). Initial results supported the creation of an additional age class (fetal to 9 months) to include those individuals clearly younger than class 1. Again primarily based on cranial material, earlier work hypothesized that the lack of specimens younger than age class 1 could be the result of tapirs birthing at another location and only bringing young tapirs to Gray once they had reached a certain age. Results presented here could refute that idea, should many of our age class 0 specimens represent newborn individuals. However, better differentiation of fetal vs. newborn material is needed. Additionally, this new, 'young' age class is heavily represented in the fossil sample (class 0–33%, 1–9.7%, 2–5.8%, 3–5.8%, 4–10.7%, 5–14.6%, 6–10.7%, and 7–9.7%), suggesting that the Gray site is mostly an attritional deposit, resulting from rapid burial (ensuring the survival of fragile, infant bones). Such results also support previous anecdotes that Gray was not likely a natural trap (at least for this taxon). Worth noting is that even with nearly 20 years of excavation, only a small proportion of the site has been explored, so all conclusions rely on the assumption that what has been uncovered is a

close proxy for the whole site. Moreover, detailed geospatial analyses could reveal additional patterns not recognized here. Continued excavations should shed additional light on these, and other, hypotheses.

### **Biomechanics & Functional Morphology**

#### **FINITE-ELEMENT MODELING OF FOSSIL TAXA: HOW CLOSE IS CLOSE ENOUGH? SENSITIVITY ANALYSES ON THE SKULL OF *MEGAPNOSAURUS KAYENTAKATAE***

Button, David J.<sup>1</sup>, Porro, Laura B.<sup>2</sup>, Barrett, Paul M.<sup>1</sup>

<sup>1</sup>Earth Sciences, Natural History Museum, London, U.K.,

<sup>2</sup>Cell and Developmental Biology, University College London, London, U.K.

Finite-element analysis (FEA) is now a widely used tool in paleontology, allowing testing of mechanical hypotheses in extinct taxa. However, accurately modeling the tissues of extinct taxa is difficult. In particular, properties of skull sutures are poorly characterized, and modeling them can be time-consuming. Validation studies on extant mammals indicate that suture inclusion has little impact on overall stress and strain patterns, suggesting that their exclusion represents a reasonable tradeoff between model accuracy and complexity. However, most of these studies have been performed on mammals, whose box-like skulls are unlike those of sauropsids, which include many long, overlapping sutures.

We present results from cranial FEA of the Early Jurassic theropod *Megapnosaurus kayentakatae*. This taxon retains many unfused cranial sutures, including a loose premaxilla-maxilla junction. This is common in early theropods and has been hypothesized to have: been a functional constraint; modified strain transmission in the snout; or facilitated passive kinesis during biting. The skull was restored in Avizo, with jaw musculature reconstructed from osteological correlates. FEA models were built in Strand7, with material properties of bone, dentine, and sutures based on extant analogs. Models were solved both with and without sutures, and for unilateral and bilateral bites at multiple positions along the toothrow.

Results indicate that cranial sutures acted as strain sinks in *Megapnosaurus*. Further, the loose premaxilla-maxilla articulation acts to locally redistribute stresses and strains in the snout. However, high bending stresses are observed in the firmly sutured descending processes of the nasals, preventing kinesis in this region. Results are consistent with hypothesized feeding behavior, with prey handling and dispatch/processing performed by the premaxillary and maxillary dentition, respectively. Comparison between models with and without sutures reveals significant differences in absolute magnitudes of stresses and strains. However, there is little difference in the distribution of

relative stresses and strains, corroborating validation studies on extant taxa. This indicates that, if relative performance is of interest, exclusion of cranial sutures is a reasonable compromise, but fine-scale functional information will be lost. This highlights the importance of considering research questions thoroughly before deciding on model complexity.

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## Evolution & Biology of Non-Avian Theropods

### USING 2D GEOMETRIC MORPHOMETRICS AND LINEAR DISCRIMINANT ANALYSIS TO CLASSIFY DINOSAUR FOOTPRINTS FROM THE LOWER JURASSIC EAST BERLIN FORMATION, DINOSAUR STATE PARK, ROCKY HILL, CONNECTICUT

Bykowski, Richard<sup>1</sup>, Farlow, James O.<sup>2</sup><sup>1</sup>Department of Biology, Georgia State University, Atlanta, Georgia, U.S.A., <sup>2</sup>Department of Biology, Purdue University Fort Wayne, Fort Wayne, Indiana, U.S.A.

The rocks of the east coast of North America preserve an incredible record of early dinosaur diversity. However, unlike the fossil fields of the western regions, dinosaur remains from the east are predominantly trace fossils, with one of the more incredible sites located in Dinosaur State Park (DSP) in Connecticut. Preserved at DSP is an excellent series of Lower Jurassic dinosaur footprints; however, reaching a consensus as to the identity of the specific trackmakers and ichnogenera has been an ongoing endeavor since the site's discovery in 1966. In this project, our goal is to utilize geometric morphometric analyses of shape (GMA) and discriminant functions analysis (DFA) to assess the potential ichnotaxonomic affinities of the prints at DSP. We subjected 77 well-preserved individual footprints (38 previously identified prints from the Newark Group and other ichnofaunas of varying age and 31 test prints from DSP) to a standard 2D GMA. Results of this analysis found significant differences among the known ichnogenera ( $F = 1.818$ ,  $p = 0.021$ ) based on shape; however, among likely candidates from the Lower Jurassic, only *Anchisauripus* and *Kayentapus* were significantly different ( $p = 0.003$ ), with the former having a much more mediolaterally compressed print, with longer pedal claws. We then carried out a DFA to assess the similarity of DSP prints to potential candidate ichnotaxa based on our landmark configuration. Results from the DFA correctly classified footprints from sites other than DSP to their previously identified ichnogenic assignments with 95% efficacy. The most common print morphotypes identified at DSP include specimens similar to *Dilophosauripus* (9), *Kayentapus* (8), *Anchisauripus* (5),

and *Eubrontes* (3), with no specimens being more like *Grallator* and only one like *Anomoepus*. Surprisingly, 4 prints were most like footprints from later Jurassic or Lower Cretaceous prints identified as *Megalosauripus* (2) and *Irenesauripus* (2), which may indicate conservatism or convergence of form between the trackmakers in the Lower Jurassic and those in the later Mesozoic. It may also indicate the presence of more than one large theropod taxon in the ecosystem of the East Berlin Formation. Analyses such as these may prove essential in documenting the biodiversity following the extinction of the Triassic pseudosuchians and the radiation of dinosaurs.

## Dinosaur Systematics, Diversity & Ecology

### PERINATAL HADROSAURS FROM THE EL GALLO FORMATION (LATE CRETACEOUS), EL ROSARIO, BAJA CALIFORNIA, MEXICO

Cabrera Hernández, Jonathan S., Montellano-Ballesteros, Marisol, Hernández-Rivera, René  
Instituto de Geología, Tequila, Jalisco, Mexico

Near El Rosario, Baja California, outcrops of the Campanian El Gallo formation comprise a non-marine sedimentary sequence. Recently, remains of perinatal hadrosaurs were collected from different sites, including isolated limb bones and a nest with at least one egg and partial skeletons of at least two individuals.

One isolated humerus is almost complete, and is identified to belong to Hadrosaurinae due to its ratio of the width of the delta pectoral crest and the minimum diameter of the humerus shaft at 1.61. The curvature of the deltopectoral crest differs from the subsquare profile of perinates of *Maiasaura* and *Saurolophus*, being more similar to juvenile *Edmontosaurus*. The new humerus, however, differs from the latter in that the humerus presents torsion of its condyles with respect to the proximal region.

The perinatals from the nest are represented by fragmentary left and right premaxilla, one left maxilla, two left dentaries, several vertebral bodies lacking neural arches, one almost complete left scapula, a distal blade of a right scapula, complete left and right femurs, one incomplete right femur, one left tibia, and several isolated teeth. Because of the characters present mainly in the maxilla, such as the angle between the rostradorsal region and the ventral alveolar margin, the curvature of the dorsolateral margin of the rostral region of the premaxillary shelf, a prominent flange on the medial margin of the premaxillary shelf, and the number and location of the foramina, these perinatal remains are identified as *Magnapaulia laticaudus*, which has been previously described from the area. Like perinatals of *Hypacrosaurus stebingeri*, the dorsal process of the maxilla is poorly developed; the coronoid process is nearly vertical; reduced

number of teeth in both dentary and maxilla; the scapula has a narrow neck and the deltoid crest is not well developed; and the tibia has a short cnemial crest. Unlike the condition in *H. stebingeri*, the perinatals and the adults of *M. laticaudus* possess different morphology of the maxillary tooth denticles and share a similar angle of the premaxillary shelf of the maxilla.

Most of the perinatal remains can be only assigned to a family or subfamily level. The specimens from the nest represent the first perinatal record of *M. laticaudus* and also the first record of perinatal lambeosaurine in Mexico. The presence of a nest and perinatal remains may raise the possibility of finding a nesting site in future prospecting.

**Funding Sources** PAPIIT projects IN 100913, IN103616 and the CONACyT scholarship.

### **Mammalian Skeletal Morphology**

#### **MORPHOLOGICAL CORRELATES OF KNUCKLE-WALKING: ASSESSING CARPAL CONVERGENCE TO UNDERSTAND THE ORIGINS OF HUMAN BIPEDALISM**

Calamari, Zachary T.<sup>1</sup>, Ragni, Anna J.<sup>2</sup>

<sup>1</sup>Department of Natural Sciences, Baruch College, City University of New York, New York, New York, U.S.A.,

<sup>2</sup>Department of Anthropology, Smithsonian Institution National Museum of Natural History, Washington, District of Columbia, U.S.A.

An enduring mystery of human evolution is whether obligate bipedal locomotion arose from knuckle-walking (KW), a mode of locomotion in which the dorsal aspect of the middle phalanges bears weight in the forelimb, or from some other type of movement. Species of *Pan* (chimpanzees and bonobos) and *Gorilla* both exhibit KW. They also share morphological features such as ridges and keels on the bones of the wrist and hand, especially the magnum, that may provide stability to weight-bearing wrist joints during KW. The similarity of these features in *Pan*, *Gorilla*, and *Homo* has been used to argue for the homology of KW in *Pan* and *Gorilla*, and thus evidence for the evolution of bipedal humans and their relatives from a KW ancestor. In contrast, some of the proposed stabilizing features, such as a narrow 'waist' of the magnum, may not appear in all individuals within either genus, and the timing of their development seems at odds with the onset of KW locomotion, which may support multiple evolutions of KW behavior in Primates. KW also has evolved in multiple non-primate mammals, possibly to prevent long fingers or claws from obstructing movement. Despite the importance of understanding KW as a potential basis for the evolution of human bipedalism, there have been few quantitative tests comparing wrist and hand morphology between primates and non-primates to assess

the necessity of these features for KW. We focused on extinct giant ground sloths, such as *Megatherium* (Mammalia, Pilosa), and Chalicotheriine chalicotheres (Mammalia, Perissodactyla), both of which may have engaged in some form of KW, to test for convergence in carpal shape among KW species. In order to address the question of KW homology in *Gorilla* and *Pan*, we tested the hypothesis that morphology of the magnum in KW species is more similar to that of KW species in other families than to non-KW species from the same order (i.e., Primates, Pilosa, Perissodactyla), using morphometric approaches. We show that KW chalicotheres, like primates, have a greater degree of 'waisting' in the magnum than non-KW chalicotheres and primates, yet the magnitude of difference is generally not statistically significant between most KW and non-KW species. Convergence in KW magnum morphology across diverse taxa suggests similar wrist-stabilizing carpal features may not alone support a single origin for KW behavior in Primates.

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### **Late Cenozoic Mammalian Macroecology & Macroevolution**

#### **CLIMATIC DRIVERS OF BODY SIZE IN LIVING GEOMYIDS AND OLIGOCENE PALEOENVIRONMENTS**

Calede, Jonathan

Evolution, Ecology, and Organismal Biology, The Ohio State University, Marion, Ohio, U.S.A.

The recent discoveries of several species of the entoptychine gopher *Gregorymys* across Arikareean-aged deposits of western North America have showed its existence from Montana to Mexico. My analysis of these fossils using paleolatitude estimates reveals a strong latitudinal gradient in body size akin to that observed in taxa that follow Bergmann's rule. Yet, living geomyoids (including the families Heteromyidae and Geomyidae) do not display a latitudinal gradient in body size. In fact, living heteromyids are one of two mammal families that do not show a latitude cline at both the interspecific and the intraspecific levels. I use the body mass records of over 7,100 individual geomyoids to explore the relationship between climate and their body mass. Specifically, I calculated a genus-level average mass for 686 geolocalized sites with more than four individuals from a given taxon. Each site is associated with 14 different climatic and environmental variables selected for their purported effects on the distribution and mass of geomyoids.

My multiple regression analyses show a consistent pattern across six of the seven geomyoid genera studied so far (*Cratogeomys*, *Thomomys*, *Dipodomys*, *Chaetodipus*, *Perognathus*, and *Microdipodops*), regardless of their diverse ecologies. The only exception to that pattern is found in the tropical taxon *Heteromys*. The dominant control on the body size of all temperate genera is precipitation seasonality. This result is consistent with limited data on select species of the extant kangaroo rat *Dipodomys*. I interpret this pattern as a consequence of burrowing capabilities in geomyids and water balance physiology in heteromyids. Interestingly, the relationship between body size and precipitation seasonality is the opposite in the pocket gopher *Thomomys* of what it is in its relative *Cratogeomys*, and all other geomyoids. This may reflect different soil affinities with body size that will require further analyses. The results for *Heteromys* suggest that in tropical environments, geomyoid size appears to be associated with temperature seasonality, a hypothesis that remains to be more broadly tested in other taxa for which data collection is ongoing.

The ubiquity of fossil geomyoids across western North America may provide a useful tool to estimate precipitation seasonality during the Oligocene and Miocene. Estimates based on over 100 fossil specimens currently suggest more seasonal precipitations during the Arikarean than observed today.

## Bird Biology & Evolution

### TAXONOMIC AND ECOLOGICAL ASSOCIATIONS OF THE AVIFAUNA WITHIN THE 8ABC SITE FROM THE EARLY EOCENE CLARKS FORK BASIN, WILLWOOD FORMATION, WYOMING

Camarena, Dakota, Houde, Peter  
Biology, New Mexico State University, Las Cruces, New Mexico, U.S.A.

Acid etching of especially fossiliferous limestone nodules from the locality 8ABC have vastly expanded the scope of avifaunal diversity from the early Eocene Clarks Fork Basin (CFB) of the Willwood Formation in Northwestern Wyoming (Wasatchian, 56.0–53.3 Ma). The mixed avian assemblage from 8ABC is mostly disarticulated but three-dimensionally preserved, allowing for ecomorphological comparisons with osteological collections not possible with flattened fossils. Limestone nodules in the CFB are known to represent a protective preservation environment unsampled in the contiguous and coeval fluvial mudstones where surface-collected fossils are more susceptible to diagenetic distortion and erosion. We contextualized the CFB avifauna by making taxonomic associations and ecological comparisons with better sampled assemblages of a similar age. The most geographically proximal

assemblages considered are the younger North American Green River and Nanjemoy formations of Wyoming and Virginia respectively. European assemblages also considered are the Fur Formation of Denmark, Messel Oil Shale of Germany, and the London Clay of England, the latter of which is the most taphonomically and temporally comparable to the 8ABC birds.

There is considerable taxonomic overlap between the birds in the CFB and the other Holarctic assemblages, which reaffirms the established homogenization of early Eocene avifauna with the onset of widespread paratropical forests. Like the other Holarctic assemblages, the CFB contains representatives that are now restricted to the Southern Hemisphere within warmer environments. The most striking differences within the known CFB avifauna relative to other early Eocene Holarctic avifauna are the apparent lack of zygodactylous birds and presence of accipitrimorphs. Like the Messel and Fur Formation assemblages, there is preservation bias against aquatic birds in the CFB. The local 8ABC avifauna is dominated by small-bodied arboreal members of terrestrial avian clades. The most numerous remains are limb elements belonging to two species of *Plesiocathartes*, inferred from features of the hypotarsus and trochleae of the tarsometatarsus. Isolated elements identifiable to *Lithornis* and *Sandcoleus* are also present. An isolated humerus compares most closely with charadriiform and strisorean aerial specialists. One associated skeleton represents a new species of a medium-sized accipitrimorph with a vulturine beak.

## Fishes & Chondrichthyans: Evolution & Distribution

### LUNGFISH TOOTH PLATES AS A TEST CASE FOR POST-DEVONIAN DIPNOAN PHYLOGENY: AN AUSTRALIAN EXAMPLE

Hartnett, Nicholas R.<sup>1</sup>, Campione, Nicolás E.<sup>1</sup>, Bell, Phil R.<sup>1</sup>, Brougham, Tom<sup>1</sup>, Smith, Elizabeth T.<sup>2</sup>

<sup>1</sup>Earth Sciences, University of New England, Armidale, New South Wales, Australia, <sup>2</sup>Australian Opal Centre, Lightning Ridge, New South Wales, Australia

The Grimman Creek Formation (GCF; Cenomanian) is one of the most diverse Cretaceous fossil deposits in Australia, preserving a unique assemblage of mostly terrestrial vertebrates. Subsurface outcrops of this deposit, made accessible by over a century of opal mining near the town of Lightning Ridge, New South Wales, are renowned for containing opalised fossil material. Among the most common aquatic taxa preserved in the GCF are lungfish (Dipnoi), represented almost exclusively by their toothplates, but which have led to the identification of three fossil species: *Ceratodus diutinus*, *Metaceratodus wollastoni*, and the extant species *Neoceratodus forsteri*.

The aim of this study is to explore the systematics of Dipnoi from the GCF, incorporating recent discoveries, and to place them into a phylogenetic framework for the first time. In addition to GCF Dipnoi, this study includes the most complete set of post-Devonian Dipnoi from Australia. In total, the morphology of 100 specimens, representing 16 species were examined, with an emphasis on toothplate features. These were coded into a recently published phylogenetic character-taxon matrix and analysed using traditional parsimony criteria. Safe taxonomic reduction (STR) was also used to increase the resolution of the phylogeny and evaluate character sampling. The phylogenetic analysis resulted in 90 most parsimonious trees and revealed an overall lack of species-level resolution, which we attribute to poor character sampling. For instance, STR identified *Mioceratodus gregoryi* and *Archaeoceratodus djelleh* as taxonomically equivalent, despite significant differences in toothplate morphology, particularly the denticulations, which highlights the need for better toothplate character sampling to differentiate otherwise identically coded species. As such, the characters used in this study are insufficient to resolve the phylogenies to the species level amongst post-Devonian Dipnoi. Future studies could increase resolution by utilising previously ignored toothplate characters, such as those that differentiate between the upper and lower jaw. Nevertheless, our preliminary phylogenetic results reveal that Australian Dipnoi, specifically those from the Griman Creek Formation, were part of two post-Devonian radiation events, one at the start of the Triassic, which would eventually lead to the long-lived extant *N. forsteri*, and the other in the mid-Cretaceous, associated with both *C. diutinus* and *M. wollastoni*.

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## Quantitative Methods

### CAN KERATAN SULFATE BE USED TO DISCRIMINATE MEDULLARY BONE IN NON-AVIAN DINOSAURS?

Canoville, Aurore, Zheng, Wenxia, Zanno, Lindsay E., Schweitzer, Mary  
Biological Sciences, North Carolina State University,  
Raleigh, North Carolina, U.S.A.

The ability to sex the skeletons of extinct dinosaurs would revolutionize our understanding of their paleobiology; however, to date, definitive sex-specific traits remain elusive or controversial. Although living dinosaurs (i.e., extant birds) exhibit a sex-specific tissue called medullary bone (MB) that is unique to females, the confident identification of this tissue in non-avian archosaurs has

proven a challenge. Tracing the evolution of MB is complicated by existing variation of MB tissues in living species; hypotheses that MB structure or chemistry varied during its evolution; and a lack of studies aimed at distinguishing MB from other types of endosteal tissues with which it shares microstructural/developmental characteristics, such as pathological tissues.

A recent study attempted to capitalize on the molecular signature of MB, which contains specific markers such as the sulfated glycosaminoglycan keratan sulfate (KS), to definitively identify the purported MB of a non-avian dinosaur specimen (*T. rex* MOR 1125). Purported MB samples of MOR 1125 reacted positively to histochemical analyses and the single pathological control tested (avian osteopetrosis) did not, suggesting the presence of KS might serve to definitively discriminate these tissues for future studies.

To further test these results, we sampled 20 avian bone pathologies of various etiologies (18 species), and several MB samples. Our new data universally supports KS as a reliable marker of MB in birds. However, we also find that reactivity varies among pathological bone tissues, with reactivity in some pathologies indistinguishable from MB. In particular, some pathologies comprised of chondroid bone (often a major constituent of skeletal pathologies and developing fracture calluses in vertebrates) contain KS. We note that beyond chemistry, chondroid bone shares many characteristics with MB (highly calcified, fibrous matrix, numerous, large cell lacunae, potential endosteal origin, trabecular architecture) and MB has even been considered by some to be a type of chondroid bone.

Our results suggests that the presence of KS is not exclusive evidence for MB, but rather must be used as one in a suite of criteria available for identifying MB (and thus gravid females) in non-avian dinosaurs specimens. Future studies should investigate whether there are definite chemical or microstructural differences between MB and reactive chondroid bone that can discriminate these tissues.

**Funding Sources** National Science Foundation award #1552328.

## Fishes & Chondrichthyans: Evolution & Distribution

### A LONG-SNOUDED MARINE BONYTONGUE (TELEOSTEI: OSTEOGLOSSIDAE) FROM THE EARLY EOCENE OF MOROCCO: GLIMPSE INTO THE UNDERAPPRECIATED DIVERSITY OF AN EARLY PALEOGENE MARINE RADIATION OF PREDATORY FISHES

Capobianco, Alessio, Friedman, Matt  
Department of Earth and Environmental Sciences,  
University of Michigan, Ann Arbor, Michigan, U.S.A.

The fossil record of osteoglossid fishes (commonly known as bonytongues) includes several marine taxa found in early Paleogene deposits worldwide. This is particularly remarkable as extant bonytongues are strictly freshwater and nest within a larger clade (Osteoglossomorpha) of freshwater fishes. Whether marine osteoglossids represent a clade descended from a single colonization of marine environments or a polyphyletic assemblage resulting from multiple independent marine invasions remains unclear.

Here we describe a new species of osteoglossid from marine early Eocene (Ypresian) deposits of Morocco, represented by an articulated and three-dimensionally preserved skull with pectoral girdle. Besides displaying unique anatomical features such as an elongated preorbital region that likely reflects a peculiar feeding ecology among bonytongues, this specimen exhibits a tantalizing combination of characters shared with different extant osteoglossid subclades. Phylogenetic analyses including the new taxon as well as other previously described marine bonytongues support a single marine invasion from a freshwater ancestor for Osteoglossidae. Moreover, some freshwater taxa, both extant and extinct, are recovered as nested within the marine radiation, suggesting that reverse transitions from the sea to riverine and lacustrine environments might have occurred multiple times during the early Paleogene. Overall, the bonytongue fossil record indicates a remarkable first 20 million years of the Cenozoic for osteoglossids, with a diverse marine radiation after the K–Pg mass extinction and a complex biogeographical and ecological history including intercontinental dispersal and several major environmental transitions.

#### **Fishes & Chondrichthyans: Evolution & Distribution**

##### **RAISING ENDOCRANIAL DATA: A NEW CARBONIFEROUS ACTINOPTERYGIAN AND REVISION OF *KANSASIELLA EATONI***

Caron, Abigail M., Venkataraman, Vishruth, Coates, Michael I.

University of Chicago, Chicago, Illinois, U.S.A.

The origin of crown Actinopterygii has been dated to near the Devonian–Carboniferous boundary; however, poor phylogenetic signal from existing data on late Paleozoic ray-fins obstructs investigation of the early evolution of modern biodiversity. Actinopterygian neurocrania are rich in constrained morphological characters ideal for revealing occluded relationships between taxa at large time scales. Unlike external features (e.g., dermal bones, squamation, dentition, body shape) known to repeatedly undergo convergent evolution, braincase morphology is constrained by the integration of multiple critical systems such as the brain, sensory organs, vasculature, jaw suspension, and respiratory musculature into one complex unit. Despite the

emergence of abundant actinopterygian taxa, the phylogenetic pattern of cladogenesis within the post-Hangenberg extinction recovery remains poorly resolved. The scarcity of well-preserved neurocrania recovered from this interval may be responsible: a mere handful are known from the Carboniferous, only one of which (*Lawrenciella schaefferi*) has been thoroughly described using modern microcomputed tomography ( $\mu$ CT). Here we present a new actinopterygian from the Bashkirian of Readycon Dean, Yorkshire, U.K., based on a  $\mu$ CT-scanned undistorted braincase and associated dermal bones. Morphological similarities to the Virgilian *Kansasiella eatoni* prompted comparative revision of *Kansasiella* via specimens from the Field Museum. The revised *Kansasiella* is broadly consistent with Poplin's 1974 description though proportions differ, and newly revealed details link it to our Bashkirian specimen while confirming a distinctive genus-level diagnosis. Preliminary comparative work highlights synapomorphies characterizing the vascular foramina, fossae and myodomes, cranial fissures, and articulation surfaces for the visceral skeleton that link these taxa to *Lawrenciella* and the Triassic *Pteronisculus*, weaving previously disparate parts of the tree together. These new data triple the number of complete Carboniferous neurocrania known from  $\mu$ CT and provide a vital framework for future testing of large-scale hypotheses regarding the diversification and origin of ray-finned fishes.

**Funding Sources** NSF DEB-1541491: Fishlife.

#### **Marine Reptile Diversity & Biology**

##### **SOFT TISSUE PRESERVATION AND PALEOECOLOGY OF A NEW GIANT PLIOPATECARPINE MOSASAUR FROM THE BEARPAW SHALE OF MONTANA (U.S.A.)**

Carr, Richard<sup>1</sup>, Lindgren, Johan<sup>2</sup>, Schweitzer, Mary<sup>3</sup>, Woodward, Holly<sup>4</sup>, Scannella, John<sup>5</sup>

<sup>1</sup>Geosciences, Fort Hays State University, Bozeman, Montana, U.S.A., <sup>2</sup>Geology, Lund University, Lund, Sweden, <sup>3</sup>Biological Sciences, North Carolina State University, Raleigh, North Carolina, U.S.A., <sup>4</sup>Center for Health Sciences, Oklahoma State University, Tulsa, Oklahoma, U.S.A., <sup>5</sup>Museum of the Rockies; Montana State University, Bozeman, Montana, U.S.A.

Many of the largest mosasaurs from the Campanian stage of the Cretaceous, including the notable genera *Prognathodon*, *Tylosaurus*, and *Mosasaurus*, are found in the Bearpaw Shale of Canada. A new wave of exploration of this formation in Montana, U.S.A., has resulted in the discovery of an exceptionally large mosasaur represented by a nearly complete skull and pectoral girdle (Museum of the Rockies [MOR] specimen 10855). Phylogenetic analysis tentatively recovers MOR 10855 as a novel taxon

within the subfamily Plioplatecarpinae. Putative autapomorphies include ventrally ridged postorbitofrontals, medially curved teeth in both dentaries, anterior-posterior changes in medial parapet height of the dentaries, a bracket-shaped posterior margin of the splenial, and a postero-ventrally hooked scapular blade. Comparison with related taxa suggests that MOR 10855 represents the largest plioplatecarpine on record, approaching the size of coeval mosasaurines. The disparity in size between this specimen and other related species found in the Bearpaw Shale is not morphologically consistent with ontogenetic trends for this group. The coexistence of both large and small-sized plioplatecarpines in the Bearpaw Shale compares favorably with the size disparity observed among extant physeteroid whales. MOR 10855 preserves two partially healed bite marks on the right side of the skull; representing the first record of non-lethal face biting among plioplatecarpine mosasaurs. The dentition of MOR 10855 is unique and may indicate an innovative division of ecological roles amongst coeval mosasaurs in the Bearpaw Shale. In addition to shedding light on the paleoecology of this group in the Western Interior Seaway, this specimen also provides a unique taphonomic window. Ultrastructural and molecular analysis of preserved cartilage and bone supports the presence of nucleated chondrocyte- and osteocyte-like microbodies, together with vessel-like structures and fibrous tissues that are chemically distinct from one another. Although most molecular studies on Mesozoic soft tissues have been conducted on dinosaurs deposited under terrestrial conditions, MOR 10855 supports similar preservation in marine environments, suggesting new avenues of recovery of molecular data from ancient fossils. Overall, MOR 10855 contributes to an unfolding view of a complex Cretaceous marine ecosystem and a highly productive environment capable of sustaining a rich diversity of trophically demanding apex predators.

## Evolution & Biology of Non-Avian Theropods

### JUVENILE TYRANNOSAURID FRONTAL FROM THE TWO MEDICINE FORMATION (CAMPANIAN, LATE CRETACEOUS) SHOWS ONTOGENETIC RECAPITULATION OF PHYLOGENETIC CHARACTER ACQUISITION

Carr, Thomas D.<sup>1</sup>, Sedlmayr, Jayc C.<sup>2</sup>

<sup>1</sup>Biology, Carthage College, Kenosha, Wisconsin, U.S.A.,

<sup>2</sup>School of Medicine, Louisiana State University Health Sciences Centre, New Orleans, Louisiana, U.S.A.

MOR 573 is a small (length: 70.8+ mm, width: 40.3 mm) frontal from the Two Medicine Formation (MT). It is probably referable to *Daspletosaurus horneri*, but its gross morphology is different from adults (MOR 590, MOR

1130): it is dorsoventrally thin and bulges upwards over the position of the cerebral hemispheres.

Its identity was tested in a phylogenetic analysis of 33 frontal characters and 13 theropod taxa; *Alligator mississippiensis* was the outgroup. The matrix was assembled in Mesquite and executed in PAUP under a branch-and-bound search. Thirteen Most Parsimonious Trees were recovered, each with a length of 39 steps, a Consistency Index of 0.83 and a Rescaled Consistency Index of 0.79. MOR 573 was recovered as the sister taxon of a set of adult tyrannosaurids (*Albertosaurus libratus* + *Daspletosaurus* spp. + *Tyrannosaurus rex*).

MOR 573 was united with the adults based on the extensive coverage of the bone made by the dorsotemporal fossa, a rostrocaudally long joint surface for the postorbital and its differentiation into a rostral buttress and a caudal shelf.

The characters that differentiate it (recovered as autapomorphies) include a flat interorbital region (in troodontids), a slot-like joint surface for the prefrontal (in ornithomimids), and a convex rostromedial corner of the dorsotemporal fossa (in deinonychosaurs). The first two reflect the shallow condition, whereas the third reflects the large cerebral hemispheres of juveniles that produce deeply concave fossae. Later in growth they are shallow depressions. Also, the fossae of more mature juveniles are unaffected by the increase in bone depth (DDM 344.1) and so the shallow condition in adults is from a different, possibly exclusively endocranial process.

The adults were diagnosed by their great depth, caudal end of the subcutaneous surface that is pinched out by opposite dorsotemporal fossae (reaches the parietal in MOR 573, separating the fossae), an elevated interorbital region, dorsoventrally deep joint surface for the lacrimal (shallow in MOR 573), presence of a sagittal crest (absent from MOR 573), and presence of a sagittal foramen (absent from MOR 573).

As such, several hallmark characters of tyrannosaurids (deep frontals and joint surfaces, confluent dorsotemporal fossae, sagittal crest and foramen) are absent early in growth. These are naively interpreted as recapitulatory, where the growth pattern is congruent with the phylogenetic acquisition of their phylogenetic homologues.

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## Dinosaur Systematics, Diversity & Ecology

### DOES THE LATE CAMPANIAN-EARLY MAASTRICHTIAN HERBIVOROUS DINOSAUR FAUNA OF THE ANTARCTIC PENINSULA REPRESENT THE SOUTHERN END OF A LATITUDINAL CLINE FROM SOUTH AMERICA?

Case, Judd A.<sup>1</sup>, Lamanna, Matthew C.<sup>2</sup>

<sup>1</sup>Biology, Eastern Washington University, Cheney, Washington, U.S.A., <sup>2</sup>Section of Vertebrate Paleontology,

Carnegie Museum of Natural History, Pittsburg, Pennsylvania, U.S.A.

The late Campanian–early Maastrichtian non-avian herbivorous dinosaur faunas of southern South America and West Antarctica exhibit consistent differences along a latitudinal cline that extends from the Neuquén Basin (~37°S) in northern Patagonia to the James Ross Basin (~64°S) of the Antarctic Peninsula. Specifically, although a small-bodied ankylosaur is also known from this unit, the herbivorous dinosaur fauna of the Allen Formation of the Neuquén Basin is dominated by large-bodied species: multiple ( $\geq 5$ ) titanosaurian sauropods and at least two hadrosaurid ornithopods. By contrast, upper Campanian–lower Maastrichtian strata of the Lago Colhué Huapi Formation of the Golfo San Jorge Basin (~45°S) have yielded at least two titanosaurs, a hadrosaur, and an elasmarian ornithopod; consequently, this fauna is characterized by the presence of this medium-sized ornithopod and decreased titanosaur diversity relative to the Allen Formation. Similarly, laterally equivalent strata of the Chorrillo (Argentina) and Dorotea (Chile) formations of the Austral Basin (~52°S) have produced a titanosaur, a hadrosaur, and an elasmarian, again hinting at an overall decrease in average body size among the herbivorous dinosaur community relative to more northern Patagonian regions. Finally, the fauna of the Snow Hill Island Formation of the James Ross Basin includes a titanosaur, two elasmarians, and a small ankylosaur. Consequently, there appears to be a trend of decreasing diversity (and perhaps abundance) of large herbivorous dinosaurs such as titanosaurs and a concomitant increase in elasmarian diversity along a latitudinal gradient from north to south. Nevertheless, data limitations and substantial differences in sampling intensity (e.g., the Neuquén Basin being more heavily prospected than the others) and depositional environment between the localities (e.g., the Snow Hill Island Formation being marine and the Patagonian formations continental) render this hypothesis tentative.

Interestingly, however, a north-south transition from sauropod-dominated to small ornithopod-dominated faunas is also noted for the Cretaceous of Australia, on the basis of four general localities spanning a vast latitudinal and temporal range. Consequently, the latitudinal cline hypothesized for Patagonia/Antarctica may have had a counterpart in eastern Gondwana, thereby providing tantalizing evidence of a potential pattern in dinosaur paleobiogeography across the southern supercontinent.

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#### Preparators

## A TEST OF THE STATE OF THE ART IN 3D COLOR PRINTING

Cavigelli, Jean-Pierre<sup>1</sup>, Kerr, Tyler<sup>2</sup>, Connely, Melissa<sup>5</sup>, Vietti, Laura A.<sup>3</sup>, Hoff, Helen<sup>1</sup>, Hutchen, Chad<sup>4</sup>

<sup>1</sup>Tate Geological Museum, Casper College, Casper, Wyoming, U.S.A., <sup>2</sup>Department of Engineering Makerspace, University of Wyoming, Laramie, Wyoming, U.S.A., <sup>3</sup>Geological Museum, University of Wyoming, Laramie, Wyoming, U.S.A., <sup>4</sup>Coe Library, University of Wyoming, Laramie, Wyoming, U.S.A., <sup>5</sup>Geology Department, Casper College, Casper, Wyoming, U.S.A.

Replicating fossils for a variety of reasons is almost as old as collecting and preparing fossils. Silicone molds have been the norm, but in the past decade or so, 3D printing has started to replace actual casts. 3D printing comes in many forms and uses digital models to guide the printing. The digital models can be created from a variety of technologies including laser and structured-light scanners, photogrammetry, and CT scanning. Common concerns with printing copies of fossils with 3D printers are visible ‘topo lines’, scars left by support struts, and the lack of realistic color. New advances are bringing high resolution color 3D printing to the public that also deals with these concerns.

The University of Wyoming’s Engineering Makerspace recently added a full color Stratasys J750 polyjet 3D printer capable of printing over 360,000 color combinations at a 14 micron (0.00055 in.) resolution scale. The J750 is capable of producing full color, high resolution copies without the use of breakaway supports, instead using a removable water-soluble support. The UW program is free and available to the public to use with appropriate training, a short 90-minute course.

Staff and volunteers from the Tate Geological Museum recently spent time at UW to attend the training and print a ‘fossil’. The Tate Geological Museum borrowed the University of Wyoming’s type specimen of *Corosaurus alcovensis* (UW-5485) in hopes of creating an affordable replica for display. Using photogrammetry, a digital model of the specimen was made without actually threatening the delicate teeth. This digital model was used to make a full color 3D copy at UW on the J750 printer. The final product has none of the of low-resolution ‘topo lines’ on the model, no strut scars, and is in full color. Digital models of UW-5485 were also generated using two structured-light scanners (*Creaform20* and *HP 3D Scan*); however, these scanning technologies generated pixelated texture overlays and were unsuitable for printing on the J750. Model comparisons suggest that digital models generated with high resolution texture overlays, like photogrammetry, are better suited for color 3D printing. With the introduction of these new polyjet 3D printers, and the recent announcement of a new, affordable Stratasys J55 for museums and educators, replicating full-color, high

resolution, accurate fossil specimens through 3D printing may be within the realm of possibility.

### Symposium: Dietary Reconstruction

#### CH<sub>4</sub>/CO<sub>2</sub> RATIOS AND ISOTOPE ENRICHMENT BETWEEN DIET AND BREATH IN MAMMALS

Cerling, Thure E.<sup>1</sup>, Bernasconi, Stefano<sup>2</sup>, Hofstetter, LS<sup>2</sup>, Jaggi, M<sup>2</sup>, Wyss, F<sup>3</sup>, Rudolf von Rohr, Claudia<sup>4</sup>, Clauss, Marcus<sup>5</sup>

<sup>1</sup>Geology and Geophysics, University of Utah, Salt Lake City, Utah, U.S.A., <sup>2</sup>Geological Institute, ETH-Z, Zurich, Zurich, Switzerland, <sup>3</sup>Basel Zoo, Basel, Basel, Switzerland, <sup>4</sup>Zurich Zoo, Zurich, Zurich, Switzerland, <sup>5</sup>University of Zurich, Zurich, Zurich, Switzerland

Breath and diet samples were collected from 25 taxa of animals at the Zurich and Basel Zoos to characterize the isotope enrichment between breath and diet. Diet samples were measured for  $\delta^{13}\text{C}$  and breath samples for CH<sub>4</sub>/CO<sub>2</sub> ratios and for the respired component of  $\delta^{13}\text{C}$  using the Keeling plot approach. Different digestive physiologies included hindgut coprophagous, hindgut non-coprophagous, foregut non-ruminants, and foregut ruminants. Isotope enrichments were  $0.8 \pm 0.9\%$ ,  $3.5 \pm 0.8\%$ ,  $2.3 \pm 0.4\%$ , and  $4.1 \pm 1.0\%$ , respectively. CH<sub>4</sub>/CO<sub>2</sub> ratios were strongly correlated with isotope enrichments for both foregut and hindgut digestive strategies, although CH<sub>4</sub> production was not the sole reason for isotope enrichment. Average CH<sub>4</sub>/CO<sub>2</sub> ratios per taxon ranged over several orders of magnitude from  $10^{-5}$  to  $10^{-1}$ . The isotope enrichment values for diet-breath can be used to further estimate the isotope enrichment from diet-enamel because Passey and colleagues found a nearly constant isotope enrichment for breath-enamel of about 11.4‰ for all diverse mammalian taxa. The understanding of isotope enrichment factors from diet to breath and diet to enamel will have important applications in the field of animal physiology, and also in interpreting the paleontological record.

**Funding Sources** US National Science Foundation.

### Marine Reptile Diversity & Biology

#### NEW SPECIMENS FOUND IN XINGYI FAUNA PROVIDE EVOLUTION INFORMATION OF THALATTOSAURIFORMES

Chai, Jun, Jiang, Dayong, Sun, Zuoyu  
Department of Geology and Geological Museum, Peking University, Beijing, China

Thalattosauriformes are some of the important marine reptiles found in the Middle to Late Triassic. It is classified

into two clades, namely Askeptosauridae and Thalattosauridae. They were discovered in North America and Europe, and more recent discoveries in the Xingyi Fauna, southwest China have provided new information about their evolution. XNGM WS-22-R5, a newly prepared specimen, had a different type of rostrum with the local *Xinpusaurus*. Its strongly ventrally deflected contour assembles the same type found in North America and Europe, and it is the first thalattosaur with this design found in China. Phylogenetic analysis indicates that this specimen forms a polytomy with *Hescheleria ruebeli* and *Clarazia schinzi*. As the turned-downward rostrum appear in XNGM WS-22-R5, *Hescheleria ruebeli* and *Nectosaurus halius*, and the resolution of current phylogenetic tree is low, it is hard to determine whether this feature is related to phylogeny. It is more likely an adaptation as *Nectosaurus* does not have a close affinity with this new specimen, while a similar design occurred in proterosaurs. A complete specimen, XNGM XY-PVR2013-R2, is described. According to the characters of jugal, surangular, angular, humerus, dorsal neural spines, and carpals, it can be identified as *Anshunsaurus cf. A. huangguoshuensis*. We compared the currently known three species of *Anshunsaurus*, and found that the previous diagnosis is not diagnostic enough. The ratio in diagnosis varies among the specimens of the same species. The only distinct diagnostic character is the development of ect- and entepicondyles on the humerus of *A. wushaensis*. As this is the most unambiguous character among *Anshunsaurus* and is related to the locomotion of the forelimbs, we suppose that this difference may be a sexual dimorphism.

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### Taphonomy & Stratigraphy

#### PUTATIVE ERYTHROCYTE STRUCTURES REVEAL FOR THE FIRST TIME THE EFFECT OF PYRITIZATION ON PROTEIN PRESERVATION IN A 250 MILLION YEARS OLD FOSSIL AMPHIBIANS FROM THE PANCHET FORMATION, EASTERN INDIA

Chakravorti, Sanjukta  
Geological Studies Unit, Indian Statistical Institute, Kolkata, West-Bengal, India

Recent advances in paleontology reveal excellent preservation of soft tissues in vertebrate fossils, including erythrocytes. This study reveals the evidence of putative erythrocytes in amphibian fossils, dated to 250 Ma, for the first time. Fossilized bones of temnospondyl amphibians from the Early Triassic Panchet Formation were studied

here. Although the fossils are disarticulated and fragmented in nature, their surfaces are not weathered and show very well-preserved muscle scars on the surfaces of the bones. The Panchet Formation is important because the Permo-Triassic Boundary passes through the Panchet Formation, and the temnospondyl bones from the Panchet Formation are small and miniaturized in form, which is an added advantage to this study involving nanotechniques. Scanning Electron Microscopy (SEM) and Elemental Energy dispersive X-ray Spectroscopy (EDS) were performed on a well-preserved temnospondyl humerus, and the results were compared to SEM studies of fixed blood samples from extant amphibians such as frogs and salamanders. SEM of the fossilized temnospondyl humerus revealed putative erythrocyte-like structures. The aggregated structures show the characteristic biconcavity present in an extant erythrocyte of frog or salamander fixed blood sample. Elemental Energy dispersive X-ray Spectroscopy revealed that these structures have a high carbon content in addition to oxygen, silica, calcium, aluminium, sodium, iron, magnesium, sulphur, and potassium, in decreasing order of abundance. Iron, though present, decreases from the surface of the blebs (0.27 wt%) inwards towards the concavity (0.16wt%). Ordinarily, an erythrocyte contains 0.3% iron by weight and is thus in coordination with the iron level in the said structures. The difference in structure between an extant erythrocyte and the 250 million year old putative erythrocyte along with the increase in concentration of iron away from the diagnostic biconcavity is an effect due to the taphonomic process of paleo-substitution of the biconcave erythrocyte disc shape by pyrite via organic pyritization. This study will lead to the synergistic approach of novel nanotechnical methods in the future, to determine the cellular behavior of extinct animals in the deepest interval of time on Earth.

**Funding Sources** Project 8, Geological Studies Unit, Indian Statistical Institute, Kolkata, West-Bengal, India.

### **Romer Prize**

### **ONTOGENY OF THE EARLY JURASSIC DINOSAUR *MASSOSPONDYLUS CARINATUS* AND ITS IMPLICATIONS FOR SAUROPODOMORPH EVOLUTION**

Chapelle, Kimberley (Kimi)  
Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, Gauteng, South Africa

Sauropodomorph dinosaurs were the dominant large-bodied herbivores for much of the Mesozoic Era. While paleobiological extremes in the largest sauropods are well-studied, evolution of these multi-tonne, quadrupedal animals from smaller, bipedal Triassic/Early Jurassic basal

sauropodomorphs is poorly understood. The Stormberg Group of South Africa preserves a remarkable basal sauropodomorph fossil record, best represented by the Early Jurassic *Massospondylus carinatus*. *M. carinatus* is a crucial taxon for understanding sauropodomorph evolution, and the discovery of their nests provides important information on early development in the group. *M. carinatus* perinates have been proposed to be quadrupedal and adults bipedal, suggesting potential pedomorphic aspects to sauropod origins despite their enormous size.

Although rich, the Stormberg dinosaur record was taxonomically problematic, with even the basic identity of *M. carinatus* being unclear. My revision establishes a robust diagnosis for *M. carinatus*, allowing confident referral of hundreds of specimens from embryo to mature adult. With this sample, I collected an unprecedented breadth of data for nearly every major stage of development of a sauropodomorph taxon, including cranial CT scans, skeletal measurements, and osteohistological sections.

Sample size limits most studies of dinosaur life history to single-proxy comparisons, and histological studies often sample only a single element between individuals. A comprehensive dataset for *M. carinatus* permits extensive analysis of growth in this taxon, allowing more rigorous testing of hypotheses such as ontogenetic postural changes. Comparing stylopodial circumference ratios across a broad sample of amniote ontogenetic series, I found postural shifts from quadrupedal to bipedal in the dinosaurs *Mussaurus* and *Psittacosaurus*, but not in *M. carinatus*. These results were reinforced by geometric morphometric analyses of the inner ear in *M. carinatus* that show no evidence of postural change through ontogeny. A large inter-element histological study of *M. carinatus* also revealed no notable differences in growth pattern between fore and hind limb elements, further supporting bipedality throughout development. The histological study did however reveal evidence of developmental plasticity, also seen in penecontemporaneous dinosaurs like *Plateosaurus*, hinting at successful strategies to deal with environmental turbulence in the wake of the End-Triassic Extinction Event.

**Funding Sources** National Research Foundation of South Africa (NRF), Department of Science and Innovation and NRF Centre of Excellence in Palaeosciences, and PAST.

### **Biomechanics & Functional Morphology**

### **BIRD TO THE BONE: MECHANICAL ADAPTATION IN THE AVIAN WING**

Chase, Hila Tzipora, Tobalske, Bret W.  
University of Montana, Missoula, Montana, U.S.A.

To understand the evolution of avian flight it is necessary to resolve the functional morphology of the flight stroke. Though birds have long been admired for having lightweight bones with specialized ‘reinforcements,’ little work has been done to investigate the internal substructure (i.e., trabecular matrix) of wing bones. Trabecular bone mechanically adapts to an organism’s behavior over its lifetime, which has facilitated great success in mammalian fossil interpretation. Despite this, the approach has yet to be explored in relation to avian flight. We thus collected high-resolution microCT scans of the humerus across a broad, comparative set of museum specimens (51 spp.), including four corvid species (n = 5) that vary in flight mode on a continuum from flapping to soaring. Segmentation was done on whole bones and trabecular parameters were measured for the humeral head. We developed a new parameter (Trabecular Extent, Tb.Ex) to holistically assess the extent of trabeculae across the bone, and performed mechanical tests on a comparative set of 3D-printed samples. Increases in trabecular thickness, ellipsoid factor, and the degree of anisotropy significantly covaried with increases in soaring behavior across corvids, with similar preliminary patterns found across the phylogeny. Tb.Ex was shown to scale allometrically within, but not across clades and varied with ecology. Tb.Ex also varied significantly with flight mode, whereas mid-shaft cortical geometry did not. Truss- and ridge-like trabecular structures within the diaphysis also did not correlate with flight mode, contrary to long-held assumptions, and preliminary mechanical testing showed no significant difference in the relative contribution of these ‘reinforcing’ structures. Along with finding direct functional signals within the trabecular matrix of the avian shoulder, our results support the need for a more holistic approach to the functional morphology of bird flight – one which integrates whole-bone mechanics with broadly comparative structural analysis. Using these results, we are currently applying our approach to 3D-preserved paravian fossil humeri. In pursuing a comparative and holistic study of trabecular bone in the bird wing, we are gaining significant insight into extant flight mechanics and providing a robust, novel approach to the interpretation of extinct taxa, both of which are crucial to understanding the evolution of avian flight.

**Funding Sources** GRFP, University of Montana Flight Lab.

### **Education & Outreach**

#### **DECOLONIZING INTERDISCIPLINARITY: A ROOTS-BASED INTEGRATION APPROACH THROUGH**

Chase, Hila Tzipora  
University of Montana, Missoula, Montana, U.S.A.

In our pursuit to assuage issues pertaining to science and society, we often separate between a focus on educating public, underserved communities and addressing issues of diversity within academic careers. Often, minority students from these communities must assimilate to succeed in the dominant academic system. This harms the student, distances them from their underserved communities, increases distrust in academia, and ultimately invalidates the very goals of diversity initiatives. Systemic changes like decolonizing academia are thus necessary, allowing minorities to not only access academic careers but affect the system of academia itself. In order to address such complex and integrated issues, however, a deeply integrative paradigm is necessary. After a decade working to create such a paradigm, called Roots-Based Integration, I have started an initiative at the University of Montana. This paradigm uses a systems-based, relational approach to find existing connections between things rather than bridge artificially categorized disciplines. The initiative provides hands-on training to effectively guide the design, execution, and impact of interdisciplinary projects, and has already begun to form a network of resources and support that expands beyond campus to public schools, community organizations, local reservations, and beyond. I created and taught a graduate seminar called “Integrating Art and Science” to jump-start the initiative and test its efficacy, with a cohort of eleven students from nine difference disciplines. The course included both practical training in professional skills and theoretical training in non-Western approaches to learning and knowledge, relational thinking, and other basic Roots-Based principles. This enabled students to not only create interdisciplinary projects with extensive impacts that benefitted their careers, but design and pursue their work in a way that consciously and holistically aids in the decolonization and diversification of academia. A key factor in facilitating this was training students from a basis of respect: respect for different disciplinary approaches within the dominant academic system, and respect for different cultural approaches to learning and knowledge that promote exchange and collaboration, rather than the ‘bestowal’ model often used in serving minority communities.

**Funding Sources** Graduate School at University of Montana.

### **Anatomical & Developmental Explorations of the Mammalian Skull**

#### **MANDIBULAR DISPARITY OF EARLY SABERTOOTHED FELIDS FROM THE LATE MIOCENE OF SPAIN**

Chatar, Narimane<sup>1</sup>, Fischer, Valentin<sup>1</sup>, Siliceo, Gema<sup>2</sup>, Antón, Mauricio<sup>2</sup>, Morales, Jorge<sup>2</sup>, Salesa, Manuel J.<sup>2</sup>

<sup>1</sup>Evolution & Diversity Dynamics Lab, University of Liège, Ans, Liège, Belgium, <sup>2</sup>Paleobiología, Museo Nacional de Ciencias Naturales (MNCN-CSIC), Madrid, Spain

Machairodontinae is a subfamily of extinct felids that gathered much attention thanks to their iconic saber teeth. Unfortunately, how this morphology evolved is unclear because of the patchy fossil record of early machairodontines. The Batallones localities (Madrid, Spain) have the potential to shed light on this issue, as two cavities (Batallones-1 and Batallones-3) contain hundreds of fossils of the early machairodontines *Machairodus aphanistus* and *Promegantereon 102gygia* from the late Miocene (MN10). Previous analyses suggested that these two cavities are not contemporaneous and that a morphological drift could be observed between the different sites; characterizing this intraspecific variability is thus important to better understand the evolution of early machairodontines. To tackle this issue, we modelled 45 mandibles of *Machairodus aphanistus* and *Promegantereon 102gygia*, six mandibles of more derived machairodontines, and 11 mandibles of extant felines in 3D using a laser surface scanner. We applied linear morphometry and 3DGM on these models to test for differences in populations and to better characterize the morphology of early machairodontines. All our analyses (PCA, PcoA, clustering, Procrustes ANOVA and PERMANOVA) converge in finding no morphological change in the mandibular shape between Batallones-1 and Batallones-3 questioning the hypothesis of a morphological drift between the cavities. The morphospaces derived from 3DGM were compared to those obtained via linear morphometry and a Mantel test confirmed that the position of each individual was not significantly different between the two morphospaces. The morphospace occupation of Batallones species is closer to extant felines than to other machairodontines, suggesting the existence of a morphological gap between primitive and derived machairodontines. Also, we reveal that the peculiar orientation and large size of the mandibular condyle is a unique feature of Machairodontinae among Felidae.

**Funding Sources** Fonds de la Recherche Scientifique – FNRS; Consejo Superior de Investigaciones Científicas – CSIC.

### Bird Biology & Evolution

#### PHYLOGENETIC UTILITY OF THE AVIAN PECTORAL GIRDLE AND FORELIMB SKELETON

Chen, Albert<sup>1</sup>, Benson, Roger B.<sup>2</sup>, Field, Daniel J.<sup>3</sup>

<sup>1</sup>Biology and Biochemistry, University of Bath, Cambridge, U.K., <sup>2</sup>Department of Earth Sciences,

University of Oxford, Oxford, U.K., <sup>3</sup>Department of Earth Sciences, University of Cambridge, Cambridge, U.K.

Although recent phylogenomic analyses have clarified the interrelationships among crown-group birds, the results of these studies nonetheless exhibit notable incongruities with each other and with morphology-based hypotheses. However, evaluating the merits of applying morphological data to avian phylogenetics is challenging, because existing crown-avian morphological datasets are often limited by restricted taxon or character sampling, inconsistent character construction, incorrect scoring, or a combination of several of these factors. This in turn hampers our understanding of the early evolution of crown-birds and the affinities of enigmatic fossil avians.

As part of a broader effort to produce a novel crown-avian morphological dataset, we focused on identifying phylogenetically informative characters of the avian pectoral girdle and forelimb skeleton, elements of which are commonly preserved as avian fossils. A dataset of 172 characters was assembled based on personal observations and previous literature. Each character was vetted against established criteria for formulating morphological characters and revised as necessary.

The characters were scored for a phylogenetically diverse range of 36 extant avian taxa and analysed in preliminary phylogenetic analyses. Although these analyses do not recover identical topologies to recent molecular analyses, implementation of molecular scaffolds allows identification of diagnostic character combinations for several clades previously only recognized through molecular data, and potentially provides an independent avenue with which to assess support for alternative molecular topologies. Future work will greatly expand the sampling of extant and fossil taxa to further elucidate the phylogenetic utility of osteological characters and the effects of different analytical parameters on morphological tree topology.

**Funding Sources** Paleontological Society Student Research Award, University Future Leaders Fellowship, and Royal Society Research Grant.

### Mesozoic Herpetology

#### NEW ANATOMICAL INFORMATION ON *DSUNGARIPTERUS WEII* WITH A FOCUS ON THE PALATAL REGION

Chen, He<sup>1</sup>, Jiang, Shunxing<sup>1</sup>, Kellner, Alexander W.<sup>2</sup>, Cheng, Xin<sup>3</sup>, Xinjun, Zhang<sup>1</sup>, Qiu, Rui<sup>1</sup>, Li, Yang<sup>1</sup>, Wang, Xiaolin<sup>1</sup>

<sup>1</sup>Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China, <sup>2</sup>Department of Geology and Paleontology, Laboratory of Systematics and Taphonomy of Fossil Vertebrates, Museu Nacional/UFRRJ,

Rio de Janeiro, Brazil, <sup>3</sup>College of Earth Sciences, Jilin University, Changchun, China

Pterosaur specimens with complete and well preserved palatal region are rare. Here we describe new and previously undescribed specimens of the pterodactyloid pterosaur *Dsungaripterus weii* that are three-dimensionally preserved and provide new anatomical information for this species. Among the unique features is a lateral process of the pterygoid divided into two parts: an anterior thin, parabolic arc shaped element that separates the secondary subtemporal and the subtemporal fenestrae, followed by a dorsoventrally flattened portion that is directed inside the subtemporal fenestrae. The interpterygoid fenestrae join, forming an irregular oval shape with two symmetrical posterior notches and a smooth anterior margin. Among all pterosaurs where the palate is known, the posterior configuration of the palate of *D. weii* is similar to some azhdarchoids, which is consistent with the suggested phylogenetic position of the *Dsungaripteridae* as closely related to the *Azhdarchoidea*. Furthermore, we identify symmetrical grooves on the lateral surface of the upper and lower jaws, which likely represent the impression of the edge of a keratinous sheath that would cover the upturned toothless rostrum during foraging activity, with food most likely consisting of hard elements, as has been previously assumed. Wear facets on the teeth also support this feeding mode.

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#### **Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

#### **THE FIRST LEOPARD FOSSILS FROM TAIWAN INFERRED BY THE INTEGRATION OF MORPHOLOGICAL AND GEOMORPHOMETRIC ANALYSES**

Chi, Tzu-Chin, Gan, Yi, Yang, Tzu-Reui, Chang, Chun-Hsiang  
Department of Geology, National Museum of Natural Science, Taichung, Taiwan

Longshia-dong Cave, a limestone cave located in the Kenting area within the Kenting National Park of southern Taiwan, has yielded numerous terrestrial mammalian fossils. Many of them were not reported in the historical literature and were not known to be present in Taiwan. For instance, no historical literature mentions leopards inhabiting Taiwan, and thus their existence remained

unknown. This study describes three fossil leopard (*Panthera pardus*) teeth uncovered from the Longshia-dong Cave. Two isolated lower premolars and one molar (p3, p4, and m1) exhibit a progressive increase in size and would have belonged to the same individual under the subfamily of Pantherinae. Traditional linear measurement analysis and two-dimensional geomorphometric analysis of the occlusal surface outlines were conducted on the fossil teeth and extant pantherines from Asia, including clouded leopards, leopards, and tigers. Results show that the fossil teeth are similar both in size and morphology to the teeth of extant leopards, supporting the assignment of the fossil teeth to leopard. This study reported, for the first time, the presence of leopards in the late Pleistocene of Taiwan. Furthermore, the smaller size of the fossil teeth relative to Chinese fossil leopards putatively suggests insular dwarfism, yet more studies are required.

**Funding Sources** Ministry of Science and Technology (MOST), Taiwan (102-2116-M-178-004- to C.-H. Chang and 108-2116-M-178-003-MY2 to T.-R. Yang).

#### **Romer Prize**

#### **COMBINING EARTH SYSTEM AND ECOLOGICAL MODELLING REVEALS THE CLIMATIC DRIVERS BEHIND MESOZOIC DINOSAUR DISTRIBUTION AND EXTINCTION**

Chiarenza, Alfio A.  
Paleontology, Perot Museum of Nature and Science, Dallas, Texas, U.S.A.

The fossil record preserves the signature of ancient biodiversity and climate, but geological and sampling artifacts hinder our understanding of their interplay. Here I developed a quantitative, multidisciplinary approach to account for problems pertaining to data absence (true versus false absences) and spatial heterogeneity in the fossil record, combining dinosaur fossil occurrences with Earth System and Ecological Niche Modelling (ENM). ENM correlates spatial occurrences with paleoclimatic conditions to generate explicit models of climatic suitability in paleogeographic settings. This tool-set was developed to evaluate several macroecological questions regarding climatic drivers of the distribution of non-avian dinosaur diversity, using a dataset of 14,355 fossil occurrences. Regression models reveal unprecedentedly detailed evidence of geographic partitioning between the main three clades of Dinosauria. Uniquely among dinosaurs, temperature exerted a stronger constraint on the paleolatitudinal ranges of sauropods, with median values in the tropics, and never extending beyond 65°, a distributional pattern closer to crocodylomorphs than to ornithischians and theropods, whose ranges extended to >80°. In the lead-up to the Cretaceous/Paleogene (K/Pg) mass extinction, 66 million years ago, dinosaurs are argued

to have been either in gradual decline or thriving until their sudden demise. In North America, ENM shows a climatic habitability decrease in areas with present-day rock outcrop towards the K/Pg, mirroring a decline in species diversity. However, a continent-wide projection demonstrates that habitat was either stable or increased towards the K/Pg, but is not preserved. This suggests that Maastrichtian North American dinosaur diversity is underestimated, with the apparent long-term, climatically-driven decline likely due to sampling bias. Given this support for a sudden extinction, global climate and ENM simulations were focused on the K/Pg event to determine whether asteroid impact or volcanism was the main kill-mechanism. Asteroid-induced cooling entirely removes dinosaur habitability at conservative (10–15%) solar dimming scenarios. By contrast, Deccan volcanism was a mitigating event that potentially protected against a worse extinction, and might have supported biotic recovery. This work highlights the potential for integrating Earth System Modelling with the paleontological record to provide a new perspective on deep-time macroecological questions.

**Funding Sources** Janet Watson Departmental Ph.D. studentship awarded to AAC at the Department of Earth Science and Engineering, Imperial College London.

### Dinosaur Systematics, Diversity & Ecology

#### TAXONOMIC RE-EVALUATION OF *PROTOCERATOPS* (DINOSAURIA: CERATOPSIA) SPECIMENS FROM UDYN SAYR, MONGOLIA

Chiba, Kentaro<sup>1</sup>, Ryan, Michael J.<sup>2</sup>, Saneyoshi, Mototaka<sup>1</sup>, Konishi, Satoshi<sup>1</sup>, Yamamoto, Yudai<sup>1</sup>, Mainbayar, Buuvei<sup>3</sup>, Tsogtbaatar, Khishigjav<sup>3</sup>

<sup>1</sup>Department of Biosphere-Geosphere Science, Okayama University of Science, Okayama, Okayama, Japan,

<sup>2</sup>Department of Earth Sciences, Carleton University, Ottawa, Ontario, Canada, <sup>3</sup>Institute of Paleontology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia

Numerous specimens of *Protoceratops* have been collected from the Gobi Desert in Mongolia and China since the first discovery of this dinosaur in the 1920s. Two species, *Protoceratops andrewsi* and *P. hellenikorhinus*, have been described to date, but the former species is known only from the Djadochta Formation in Mongolia and the latter only from the putatively time equivalent Bayan Mandahu Formation in Inner Mongolia, China. Additional specimens assigned to *P. andrewsi* and *Protoceratops* sp. Have been reported from the Djadochta Formation at Udyn Sayr, Mongolia, but the taxonomic uncertainties of some of the specimens have not been resolved yet. In this study, we re-evaluate the taxonomic status of the Udyn Sayr specimens and describe new specimens from Udyn Sayr and an adjacent locality, Bor Tolgoi.

Our examination indicates that the two *Protoceratops* species can be differentiated by three cranial characters. First, *P. andrewsi* has a pair of premaxillary teeth on both sides, but *P. hellenikorhinus* lacks premaxillary teeth. Second, *P. andrewsi* has a smooth, unmodified texture on the dorsal surface of the nasals, but *P. hellenikorhinus* possesses unique ornamentation composed of multiple short ridges running anteroposteriorly. Third, the dorsal margin of the posterior flange of the squamosal is angled dorsally in *P. andrewsi*, whereas the margin is straight or slightly ventrally curved in *P. hellenikorhinus*. Importantly, these three characters do not change ontogenetically. Identification of the differential characters indicates that specimens from the Udyn Sayr and Bor Tolgoi include both *P. andrewsi* and *P. hellenikorhinus*, suggesting that two closely related species lived in the same area contemporaneously, which is a rare occurrence amongst ceratopsians. The co-occurrence of the two species might be explained by the paleoenvironmental differences of the localities; the facies of classic *P. andrewsi* localities, such as Tugrikin Shire and Bayn Dzag, are composed of aeolian sediments deposited by large sand dunes, whereas those of Bayan Mandahu, where *P. hellenikorhinus* is found, comprises a mixture of aeolian and fluvial facies. The facies at Udyn Sayr is also a mixture of aeolian and fluvial facies suggesting that this may have been the preferred habitat of *P. hellenikorhinus* in the Djadochta Formation. The taxonomic re-evaluation of *Protoceratops* in this study provides an intriguing opportunity to investigate the paleoecology of this well-known ceratopsian.

**Funding Sources** Grants-in-Aid for Scientific Research by JSPS; Private University Research Branding Project by MEXT, Japan.

### Evolution & Biology of Non-Avian Theropods

#### ORNITHOMIMOSAUR SPECIMENS FROM THE UPPER CRETACEOUS EUTAW FORMATION (SANTONIAN) OF MISSISSIPPI: NEW DATA ON APPALACHIAN THEROPOD DINOSAURS

Chinzorig, Tsogtbaatar<sup>1</sup>, Philips, George<sup>3</sup>, Cullen, Thomas M.<sup>1</sup>, Lamb, James<sup>4</sup>, Larson, Peter L.<sup>5</sup>, Rolke, Richard<sup>6</sup>, Zanno, Lindsay E.<sup>2</sup>

<sup>1</sup>Biological Sciences, North Carolina State University, Raleigh, North Carolina, U.S.A., <sup>2</sup>Paleontology, North Carolina Museum of Natural Sciences, Raleigh, North Carolina, U.S.A., <sup>3</sup>Paleontology, Mississippi Museum of Natural Science, Jackson, Mississippi, U.S.A., <sup>4</sup>Black Belt Museum, University of West Alabama, Livingston, Alabama, U.S.A., <sup>5</sup>Geological Research, Black Hills Institute, Hill City, South Dakota, U.S.A., <sup>6</sup>Dow Chemical Company, Baton Rouge, Louisiana, U.S.A.

Reconstructing the evolution, diversity, and paleobiogeography of North America's Late Cretaceous dinosaur assemblages requires spatially and temporally contiguous data. Currently, our knowledge of eastern North American (Appalachian) dinosaurs, as compared to western North American (Laramidian) neighbors, is poor. Similarly, rare preservation of terrestrial ecosystems between the Turonian–Santonian (early Late Cretaceous) presents a persistent challenge for studies of North American dinosaur evolution. Here we report on a collection of fossil materials recovered as individual clasts from a mile-long exposure of Luxapallila Creek, Columbus, Mississippi. The specimens derive from the Eutaw Formation and represent multiple individual medium and large-sized theropods from the Santonian of Appalachia.

Materials recovered consist mainly of pedal elements and vertebral centra belonging to theropods with estimated femoral lengths ranging from 0.5–1m. Surprisingly, no comparably sized theropod teeth are yet represented. Among the material, elements referable to Ornithomimosauria include a distal metatarsal IV exhibiting a mediolaterally constricted, dorsoventrally high midshaft with no medial expansion and distal condyles expanded cranially and caudally beyond the shaft margins, and pedal unguals bearing a laterally straight ventral surface and weakly ridged flexor tubercle. Log-transformed linear regression analysis using the partial MTIV to predict a minimum femoral length for the Eutaw ornithomimosaur yields a FL of ~600mm, similar to *Beishanlong*. Additional pedal elements share some intriguing features with ornithomimosaur, yet suggest a larger-body size closer to *Deinocheirus*, and require additional study. This includes a large, pathological second metatarsal bearing a large callus across most of the diaphysis. Although tentative, the presence of a giant ornithomimosaur in this region at this time would not be surprising, given that the relatively recent discoveries of *Arkansaurus* (U.S.A.) and *Beishanlong* (China) confirm the presence of large-bodied ornithomimosaur in mid-Cretaceous strata of Laurasia. Published records of pre-Campanian ornithomimosaur from North America are sparse. Because previous reports of ornithomimosaur materials from the Santonian (e.g., the Milk River Formation of Alberta) have been re-evaluated as undiagnostic, the Eutaw materials currently represent the oldest definitive record of Late Cretaceous ornithomimosaur on the continent.

## Bird Biology & Evolution

## MICROSTRUCTURAL AND CRYSTALLOGRAPHIC EVOLUTION OF PALEOGNATH (AVES) EGGSHELLS

Choi, Seung<sup>1</sup>, Hauber, Mark<sup>2</sup>, Kim, Noe-Heon<sup>1</sup>, Varricchio, David<sup>3</sup>, Lee, Yuong-Nam<sup>1</sup>

<sup>1</sup>Seoul National University, Seoul, Korea (the Republic of),

<sup>2</sup>Department of Evolution, Ecology, and Behavior, University of Illinois, Urbana-Champaign, Illinois, U.S.A.,

<sup>3</sup>Montana State University, Bozeman, Montana, U.S.A.

Palaeognathae is an ancient lineage forming one of the major clades of modern birds. Their phylogeny has been revised drastically due to the advancement of genome-wide comparative analyses, and the updated phylogeny shows that many of the similar morphological characters of paleognaths, which had been used for prior morphological systematics, might have been acquired independently. The recent progression in the paleognath phylogeny thus provides a chance to trace the evolution of eggshell macro- and microstructure. Here, eggshells of all major clades of paleognaths (including fossil taxa) and selected eggshells of neognath and non-avian dinosaurs are analyzed to quantify structure and crystallography. Our results show diverse microstructures and crystallography amongst paleognath eggshells that can be categorized into three morphotypes: ostrich-, rhea-, and tinamou-styles. These diverse structures have been acquired independently despite their similarities, as is the case of shared body shape evolution among paleognaths. Our findings imply that differentiating homology from homoplasy should be a critical consideration in morphology-based interpretation of fossil eggshell research and other fields of paleontology in general without genome-based phylogenies. The results of the current study can be a helpful starting point for future field-based analyses of eggshells in paleontology and archaeology because diverse fossil paleognath eggs are present in many Cenozoic deposits.

**Funding Sources** National Research Foundation of Korea Grant 2019R1A2B5B02070240; Harley Jones Van Cleave Professorship.

## Permo-Triassic Tetrapods

## TAXONOMICALLY RICH LATE TRIASSIC FAUNAS FROM SOUTH AFRICA'S LOWERMOST ELLIOT FORMATION

Choiniere, Jonah N.<sup>1</sup>, Benson, Roger B.<sup>2</sup>, Botha, Jennifer<sup>3</sup>, Barrett, Paul M.<sup>4</sup>, Bordy, Emese<sup>5</sup>, Chapelle, Kimberley (Kimi)<sup>1</sup>, Dollman, Kathleen<sup>1</sup>, Suarez, Celina<sup>6</sup>, Viglietti, Pia A.<sup>7</sup>, Sciscio, Lara<sup>8</sup>, Butler, Richard J.<sup>9</sup>

<sup>1</sup>Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, Gauteng, South Africa,

<sup>2</sup>Earth Sciences, University of Oxford, Oxford, U.K.,

<sup>3</sup>Palaeontology, National Museum, Bloemfontein, Free State, South Africa, <sup>4</sup>Earth Sciences, Natural History Museum, London, London, U.K., <sup>5</sup>Geological Sciences,

University of Cape Town, Cape Town, Western Cape, South Africa, <sup>6</sup>Geosciences, University of Arkansas,

Fayetteville, Arkansas, U.S.A., <sup>7</sup>Field Museum of Natural History, Chicago, Illinois, U.S.A., <sup>8</sup>Geological Sciences, University of Johannesburg, Johannesburg, South Africa, <sup>9</sup>Geography, Earth, and Environmental Sciences, University of Birmingham, Birmingham, U.K.

The Elliot Formation of Southern Africa is an important continental sedimentary succession for studying the end-Triassic mass extinction (ETE). The formation is divided into informal lower (LEF) and upper sections (UEF) that are distinguished lithostratigraphically, biostratigraphically, and, more recently, magneto- and chronostratigraphically. These subunits are respectively considered to be Upper Triassic and Lower Jurassic. While the UEF fauna has become increasingly well-characterized, the LEF has lagged behind in new knowledge of its diversity. This shortcoming is a hindrance to understanding the effects of the ETE and to regional and global biostratigraphic correlations. In 2017, members of our research team were shown a series of sites in the lowermost LEF in the Eastern Cape Province of South Africa, discovered by the local community. We report here on the preliminary findings from our excavations of those sites, which have unearthed a trove of vertebrate fossils. These fossils were excavated from at least five distinct bonebeds and bone accumulations at two stratigraphic levels, including some of the stratigraphically lowest in the Elliot Formation yet known. The identifiable remains collected so far include three distinct non-sauropodan sauropodomorph species, two theropods, the skull of a non-crocodylomorph pseudosuchian, a medium-large sized early branching crocodylomorph, a stahleckeriid dicynodont and other dicynodont material, and gomphodont cynodonts. As yet unidentified remains of small-bodied vertebrates are also present. One of the first specimens to be fully prepared is the partial skull and postcranial skeleton of the gomphodontosuchine *Scalenodontoides macrodotes*. By incorporating this specimen into a revised biostratigraphic database for the Elliot Formation, we are able to show that *Scalenodontoides* is an ideal index fossil for correlating disparate LEF outcrops regionally. This specimen also allows us to provide a limb-based estimate of the body mass of this taxon at approximately 300 kg, showing that close mammalian relatives attained large body masses in the Late Triassic (Norian) of southern Africa. Taken together, our preliminary discoveries nearly double the known taxonomic diversity of the LEF, including its first theropod and crocodylomorph material, and the first well-provenanced occurrence of dicynodonts. These discoveries are an important step in understanding how the ETE affected continental faunas.

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## Mesozoic & Early Cenozoic Mammalian Evolution

### TESTING THE COMPETITION HYPOTHESIS: DID COMPETITION WITH CARNIVORAMORPHANS RESULT IN EXTINCTIONS AMONG CREODONTS DURING THE EOCENE IN NORTH AMERICA?

Christison, Brigid E.<sup>1</sup>, Fraser, Danielle<sup>2</sup>

<sup>1</sup>Biology, Carleton University, Ottawa, Ontario, Canada, <sup>2</sup>Palaeobiology, Canadian Museum of Nature, Ottawa, Ontario, Canada

Carnivoramorphans and creodonts are two groups of ancestrally carnivorous mammals, which emerged in the Paleocene and quickly occupied most North American terrestrial carnivore niches. During the Eocene, however, creodont diversity declined while carnivoramorph diversity increased. Creodonts subsequently went extinct in North America in the Oligocene and worldwide in the Miocene, while Carnivoramorphans persists to modern day. The 'Competition Hypothesis' proposes that carnivoramorphans outcompeted creodonts during the Eocene in North America, leading to their extinction from the continent. Previous studies examining genera at the continental scale found that reduced niche overlap between the groups at the end of the Eocene relative to the beginning. We tested the competition hypothesis at the species and locality level by assessing how carnivoramorph and creodont species divided dietary niche space at the start and the end of the Eocene at four localities in central North America.

To determine how species divided niche space, we analyzed locomotory mode, dental indicators of carnivory, cranial measurements corresponding to prey-size preference, body mass, and prey-focus mass using regressions, Linear Discriminant Analyses, and Principal Component Analyses. Prey-focus mass regressions, which approximate the prey-size preference of each species based on their body mass, suggest that body mass was the main mechanism of niche partitioning. In the early Eocene, we found that both carnivoramorphans and creodonts were likely mesocarnivores that targeted medium-sized prey, though hyaenodontid creodonts and carnivoramorphans targeted some smaller prey as well. By the end of the Eocene, oxyaenids were extinct and hyaenodontids had specialized to larger prey, with some becoming hypercarnivores, while carnivoramorphans remained mesocarnivores (with some exceptions), which targeted small-medium prey.

Our results support the Competition Hypothesis as an explanation for oxyaenid creodont extinction, but not for hyaenodontid creodonts, who may have become extinct due to hyperspecialization instead. Though specialization may have helped hyaenodontids avoid niche overlap and

competition with carnivoramorphan in the short term, it likely led to their extinction when their large-bodied prey went extinct in the late Eocene. Further combination with other morphological indicators of prey preference may provide insight into how these mesocarnivores partitioned niche space.

**Funding Sources** Natural Sciences and Engineering Research Council of Canada; Carleton University.

### Fishes & Chondrichthyans: Evolution & Distribution

#### A NEW ASSEMBLAGE OF LUNGFISHES (DIPNOI: LEPIDOSIRENIDAE) FROM THE LATE OLIGOCENE NSUNGWE FORMATION, RUKWA RIFT BASIN, SOUTHWESTERN TANZANIA

Claeson, Kerin<sup>1</sup>, Ngasala, Sifa<sup>2</sup>, Gottfried, Michael D.<sup>2</sup>, Roberts, Eric<sup>3</sup>, O'Connor, Patrick M.<sup>4</sup>, Stevens, Nancy J.<sup>4</sup>  
<sup>1</sup>Philadelphia College of Osteopathic Medicine, Philadelphia, Pennsylvania, U.S.A., <sup>2</sup>Michigan State University, East Lansing, Michigan, U.S.A., <sup>3</sup>James Cook University, Townsville, Queensland, Australia, <sup>4</sup>Ohio University, Athens, Ohio, U.S.A.

Extant lungfish are separated into two families: Lepidosirenidae, represented by *Protopterus* in Africa and *Lepidosiren* in South America, and Neoceratodontidae, represented by a single genus (*Neoceratodus*) in Australia. Given the sparse record of Lepidosirenidae fossils from continental Africa, any new materials are important for understanding diversification of the clade. Here we describe new lungfish fossils referable to *Protopterus annectens* and *Protopterus aethiopicus*, collected from the late Oligocene Nsungwe Formation in the Rukwa Rift Basin (RRB) of southwestern Tanzania further demonstrating that African lungfishes were more geographically and phylogenetically diverse on the continent in the past than they are today, with only 5% of extinct taxa recorded from the sub-Saharan fossil record. The late Oligocene Nsungwe Formation represents a sequence of continental rift-fill deposits of the Songwe sub-basin of the Rukwa Rift Basin and is subdivided into the lower Utengule and upper Songwe members. All lungfish material described herein was recovered from the Songwe Member, assigned a late Oligocene age, between 25–26 Ma based on biostratigraphy and high-precision U-Pb and Ar/Ar dating of intercalated ashbeds. Recovery of such material from the Paleogene of Africa below the equator addresses a sizable gap in the lungfish fossil record. It also expands the Nsungwe Formation fauna that includes invertebrates, alestid fishes, ptychadenid anurans, snakes, and several clades of mammals, deepening paleoecological insights into the late Oligocene record of the continental African interior.

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### Late Cenozoic Mammalian Macroecology & Macroevolution

#### A NEW SPECIES OF *GREGORYMYS* FROM THE ARIKAREEAN OF SOUTH DAKOTA AND THE PHYLOGENETICS OF ENTOPTYCHINAE (MAMMALIA, RODENTIA, GEOMYIDAE)

Claxton, Alexander, Caledo, Jonathan  
Department of Evolution, Ecology, and Organismal Biology, The Ohio State University, Columbus, Ohio, U.S.A.

Rodent ecological and taxonomic diversity throughout the Cenozoic has been linked to large-scale changes in habitat. In particular, several studies have suggested that burrowers became more abundant and taxonomically diverse as habitat aridity and openness increased during the Oligocene. This hypothesis remains to be rigorously tested for several groups of burrowers. One of them, the Entoptychinae, an extinct subfamily of gophers from North America, includes over 35 species distributed throughout the American west ranging from the beginning of the Arikareean to the early Clarendonian. Although numerous species of this clade have been described, the timing of its diversification remains elusive. Here, we provide new data that help refine the evolutionary history of this important group of rodents. We present a new species of entoptychine gopher within the genus *Gregorymys* from the Monroe Creek Formation of South Dakota (ca. 26.5 Ma), represented by two partial crania. This new species was recovered from the same deposits as the large taxon *Gregorymys formosus*. We scanned the new material using a micro-CT and reconstructed 3D models that enabled the study of obscured parts of the morphology (e.g., cheek tooth roots) as well as minute structures (e.g., foramina). We scored the two crania as individual OTUs in a phylogenetic matrix that includes 36 other taxa and 98 craniodental characters. The resulting analysis was run using TNT. The two specimens were recovered as sister OTUs and form a clade with the coeval *G. formosus*. It is likely that these two crania represent a single, novel, taxon. This new species is the smallest known member of the genus *Gregorymys*. It is also distinguished from *G. formosus* by several discrete dental characters, including the presence of a fourth cusp on the metalophs of the upper fourth premolar and upper third molar. The relationships recovered for other entoptychine taxa help resolve the pattern of diversification of the subfamily. In particular, the time calibration of the phylogenetic analysis shows three

successive diversification events 30, 28, and 26 million years ago. The first two affected the genera *Pleurolicus*, *Gregorymys*, and *Entoptychus*, whereas the last one only affected *Entoptychus*. The inclusion of biogeographic information will be necessary to resolve the association of these events with the heterochronous environmental changes across the western U.S.A.

**Funding Sources** Paleontological Society Norman Newell Early Career Award and OSU College of Arts and Sciences, Regional Campus Faculty Research Activity Grant.

### Symposium: Paleoneurology

#### BRAIN-BRAINCASE RELATIONSHIPS ACROSS THE FISH-TETRAPOD TRANSITION

Clement, Alice<sup>1</sup>, Challands, Tom<sup>2</sup>, Trinajstić, Kate<sup>3</sup>, Houle, Laurent<sup>4</sup>, Cloutier, Richard<sup>4</sup>, Long, John<sup>1</sup>

<sup>1</sup>Flinders University, Adelaide, South Australia, Australia, <sup>2</sup>School of Geosciences, University of Edinburgh, Edinburgh, U.K., <sup>3</sup>Curtin University, Perth, Western Australia, Australia, <sup>4</sup>Université du Québec à Rimouski, Rimouski, Quebec, Canada

The water-land transition by the early tetrapods in the Devonian Period is seen as one of the greatest steps in evolution. The Sarcopterygii first evolved limbs with digits, a group which contains other lobe-finned fishes such as lungfishes and coelacanths. However, while a great deal is understood about changes of the postcranial skeleton during this time, relatively little is understood concerning changes in brain morphology over this transition.

Several confounding factors likely contribute to this problem: 1) the assumption that braincases of 'lower' vertebrates yield little information regarding brain morphology; 2) many of the groups closest to the fish-tetrapod transition are extinct; 3) relatively few fossil sarcopterygian fish braincases are known in detail; and 4) while fossils can provide rich data, the rarity of soft tissue preservation means osteological correlates must be used to infer soft tissue anatomy, and the precise relationships between the two are not always well understood.

Thus, 'endocasts' are studied in lieu of preserved brains to provide insight into early neural evolution. However, few studies have attempted to determine the reliability of endocasts as proxies of brain size in non-mammalian taxa. We aim to determine the brain-braincase relationship in fishes and basal lissamphibians to elucidate the changes that occurred over the fish-tetrapod transition.

Thus, we herein investigate six basal extant sarcopterygians spanning coelacanths to salamanders (*Latimeria*, *Neoceratodus*, *Protopterus aethiopicus*, *P. dolloi*, *Cynops*, *Ambystoma*) via micro-CT or MRI and quantify the brain-braincase relationship in extant taxa

spanning the fish-tetrapod transition. We detail the use of our 'distance heat map' approach to quantify and visualize the brain-braincase relationship in taxa whose brain does not fill the entirety of their cavity.

Our results also allow brain-endocast disparity to be considered in several key Paleozoic sarcopterygians. New data from fossil material, including coelacanth (sp. nov.), porolepiform (*Quebecius*), lungfish (numerous taxa), and tetrapodomorphs (*Cladarosymblema*, *Koharalepis*, *Elpistostege*) shed further light on the changes manifesting in the braincase approaching the fish-tetrapod transition. Finally, we propose that the basal tetrapod neurocranial Bauplan is distinct from other sarcopterygians, yet has been conserved from basal tetrapods to modern salamanders.

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### Symposium: Dietary Reconstruction

#### COMPOSITIONAL ANALYSIS OF MODERN AND FOSSIL BONE USING RAMAN SPECTROSCOPY (1064 NM)

Clementz, Mark<sup>1</sup>, Cooper, Lisa N.<sup>2</sup>, Thewissen, J. G. M.<sup>2</sup>  
<sup>1</sup>Geology & Geophysics, University of Wyoming, Laramie, Wyoming, U.S.A., <sup>2</sup>Anatomy and Neurobiology, Northeast Ohio Medical University, Rootstown, Ohio, U.S.A.

Within vertebrate skeletons, bone is considered more susceptible to alteration than other types of bioapatite (dentin, enamel) because of its high organic content, small crystallite size, and elevated porosity. However, not all bone types match this description and there is a considerable range in the composition of bone in relation to function and phylogeny. We examined skeletal bone from six orders of mammals (Artiodactyla, Carnivora, Chiroptera, Cetacea, Eulipotyphla, and Rodentia) spanning a range of organic contents (5 wt% to 50 wt%) and porosities. Using a non-destructive method of assessment (Raman spectroscopy), we quantified the compositional qualities of these bone types along with dentin and enamel samples from recent and fossil specimens (late Neogene and Quaternary) to determine how these characters impact preservation.

For most specimens (n = 50), we were able to analyze the whole bone without modification. For larger specimens (i.e., bones from artiodactyls and cetaceans), analyses were made on either thick sections or powders taken from skeletal bones (n = 30). For recent specimens, position and peak width of the primary phosphate (PO<sub>4</sub>) band (960 cm<sup>-1</sup>) were easily measured parameters that could provide

information on composition and crystallinity, respectively. Organic content was determined from the intensity of the amide I (1636 cm<sup>-1</sup>), amide III (1245 cm<sup>-1</sup>), and CH<sub>2</sub> (1450 cm<sup>-1</sup>) peaks within the spectra. We noted that modern bones were characterized by low positions (960 cm<sup>-1</sup> to 962 cm<sup>-1</sup>) and greater widths for the primary phosphate band whereas this band was located at higher peak positions (964-966 cm<sup>-1</sup>) and had smaller peak widths for most fossil specimens. These differences were associated with decreased intensity of the carbonate band (1070 cm<sup>-1</sup>) in these fossil specimens and reduced organic peak intensities, indicating a decrease in carbonate content, an increase in crystallinity, and loss of nearly all organic matrix. Within fossil specimens of bone types consisting of extremely dense bone (i.e., tympanic bullae), however, the position of the primary phosphate band and intensity of the carbonate band fell within the observed range for modern specimens and outside of that of other fossil bone recovered from the same deposits. Likewise, crystallinity values were more similar to those of fresh rather than fossil bone suggesting that tympanic bullae may be more resistant to compositional alteration than other bone types.

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#### Fishes & Chondrichthyans: Evolution & Distribution

#### A NEW SYMMORIFORM FROM THE LATE DEVONIAN OF MOROCCO: NOVEL JAW FUNCTION IN ANCIENT SHARKS

Coates, Michael I.<sup>1</sup>, Frey, Linda<sup>4</sup>, Tietjen, Kristen<sup>2</sup>, Rücklin, Martin<sup>3</sup>, Klug, Christian<sup>4</sup>

<sup>1</sup>University of Chicago, Chicago, Illinois, U.S.A.,

<sup>2</sup>University of Kansas, Lawrence, Kansas, U.S.A.,

<sup>3</sup>Naturalis Biodiversity Center, Leiden, Netherlands,

<sup>4</sup>University of Zurich, Zurich, Switzerland

The fossil record of early chondrichthyans (sharks, rays, chimaeras, and their extinct relatives) is poor because of their predominantly cartilaginous skeletons. 3D preserved fossils of these animals are consequently rare, restricting accurate and detailed knowledge of anatomy and models of likely biomechanical performance and function. Here we report a new symmoriiform shark from the Late Devonian of the Moroccan Anti-Atlas. Computed tomography scanning reveals the barely distorted shape of the jaws and hyoid arch, which are of a kind often used to represent primitive conditions for all jawed vertebrates. Remarkably, the jaw proportions and articulation surfaces are such that they can be fitted precisely to the corresponding articulation surfaces of the neurocranium of the Permian symmoriiform, *Dwykasselachus*. Of critical importance, these closely fitting cartilages, both as preserved in the new

taxon and when fully rearticulated in a composite new taxon-*Dwykasselachus* 3D model, preclude the repeatedly hypothesized presence of a complete gill between mandibular and hyoid arches. Symmoriiforms are not aphethochoidean. In addition, the articulated feeding apparatus of the 3D model reveals that the jaw hinge, involving the articular cotylus and the mandibular knob (or mesial process), drives mandibular rotation outward when the mouth opens (Meckel's cartilage depressed), and inward upon closure (Meckel's cartilage raised). This previously unknown jaw action rolls the mandible to present a greater number of teeth to prey through the bite-cycle, and there is reason to suggest that this unfamiliar mode of jaw function was widespread among early chondrichthyans. Within a new, time-calibrated phylogeny, this adds to an emerging picture of increased functional disparity among chondrichthyans both preceding and surviving the end-Devonian extinction event.

**Funding Sources** NSF DEB-1541491: Fishlife SNF 200021\_156105 NWO 864.14.009.

#### Taphonomy & Stratigraphy

#### TAPHONOMIC VARIATION AMONG PITS AT RANCHO LA BREA INDICATE LITTLE CHANGE IN DEPOSITIONAL ENVIRONMENT THROUGH THE END OF THE PLEISTOCENE

Cohen, Joshua<sup>1</sup>, Noriega, Nicolas<sup>1</sup>, Pitcher, Ellie<sup>1</sup>, Lindsey, Emily<sup>2</sup>, DeSantis, Larisa<sup>3</sup>, Meachen, Julie<sup>4</sup>, O'Keefe, Frank R.<sup>5</sup>, Southon, John<sup>6</sup>, Binder, Wendy J.<sup>1</sup>

<sup>1</sup>Loyola Marymount University, Los Angeles, California, U.S.A., <sup>2</sup>Tar Pits Museum, Los Angeles, California, U.S.A., <sup>3</sup>Vanderbilt University, Nashville, Tennessee, U.S.A., <sup>4</sup>Des Moines University, Des Moines, Iowa, U.S.A., <sup>5</sup>Marshall University, Huntington, West Virginia, U.S.A., <sup>6</sup>University of California Irvine, Irvine, California, U.S.A.

Rancho La Brea (RLB) is an asphaltic site that preserves millions of fossils spanning the last 50,000 years, and has been used to reconstruct the paleoecology of North American Pleistocene megafauna. RLB comprises more than 130 fossiliferous deposits that formed via active entrapment of organisms in surficial asphalt seeps and fluvial deposition. Differences in depositional environments among pits, however, are largely unknown, which hinders researchers' ability to draw comparisons among deposits from different temporal periods. Thus, in order to accurately address paleoecological changes through time at RLB, documenting potential taphonomic biases among deposits is essential. Until now, taphonomy at RLB has only been described from a single deposit – Pit 91 (45–26 ka) – leaving a gap in our knowledge of

taphonomic processes at most RLB pits through time. We quantified taphonomic variables, including weathering, abrasion, pit wear (a taphonomic feature presumably caused by bone-on-bone contact in asphaltic deposits), and minimum number of individuals (MNI) for mammalian megafauna in four RLB deposits, pits 91, 13, 3, and 61/67, ranging in age from approximately 45–11 ka. Overall, weathering in all pits was low, suggesting burial occurred relatively quickly at RLB. Weathering was highest in Pit 3, suggesting burial in this deposit occurred more slowly. Abrasion was also relatively low in all pits, with the highest average abrasion from Pit 13. Higher abrasion indicates more fluvial activity, so the relatively low abrasion suggests little movement of sediments and fossils during deposition of most pits, with Pit 13 having the highest fluvial activity. Pit wear differed substantially between pits, ranging from the highest incidence of pit wear in Pit 13 (40.5% of specimens) to the lowest in Pit 61/67 (3.8% of specimens). Pit wear has been suggested to be a function of fossil concentration within a deposit; however, we found no positive correlation between pit wear and number of fossils per grid. Pit wear and abrasion, however, are positively correlated ( $R^2 = 0.97$ ), suggesting pit wear may be related to fluvial activity. MNIs for the most abundant taxa differed between Pit 13 and all other pits, with a relative decrease in *Smilodon fatalis* and *Equus occidentalis*. Overall, the four deposits at RLB have similar taphonomic signatures, suggesting that differences in MNI among pits are ecologically driven, and not reflective of changes in the depositional environment.

### Mesozoic Herpetology

#### **‘WALKING IN THE RAIN’: A NEW PTEROSAUR TRACKSITE SHOWING SUBAERIAL PERAMBULATIONS.**

Connely, Melissa<sup>2</sup>, Cavigelli, Jean-Pierre<sup>1</sup>

<sup>1</sup>Tate Geological Museum, Casper College, Casper, Wyoming, U.S.A., <sup>2</sup>Geology Department, Casper College, Casper, Wyoming, U.S.A.

Pterosaur tracks now known as *Pteraichnus* were first reported in the fossil record by Ambroggi and Lapperent in 1954 from Morocco. They were slow to be accepted by the paleontological community. Subsequent reports were decades apart; from Utah by Stokes in 1957 and central Wyoming by Logue in 1977. Since then, *Pteraichnus* has been reported from numerous places around the world. They generally feature long four-toed pes and a shorter ‘double comma’ wrist impression. These tracks have been used to define a standing/walking position for pterodactyloid pterosaurs, and to confirm the presence of pterosaurs in layers where body fossils are rare or non-existent. They have alternately been interpreted as

swimming crocodile tracks. A new *Pteraichnus* site, the Strohecker Ranch Tracksite, from the Windy Hill Member of the Sundance Formation in central Wyoming preserves numerous pterosaur tracks. A sample from the site has been collected by Tate Geological Museum crews. The productive layer is at the base of a 1.5 meter tall massive sandstone cliff. Collecting was limited by the risk created by collecting from the base of the cliff. The cumulative slab collected is 4 meters long and about 30 to 50 cm wide. It includes 31 pes prints and 23 manus prints. None of these can be considered as obvious trackways as the prints are fairly randomly directed. Prints are all subequal in size; pes prints are 6.5 cm long and manus prints are 5.5 cm. The imprint layer is a 3 cm thick, well indurated sandstone with impressions. The infilling layer is a 1 cm shale layer. The preservation is far superior on the infilled layer, preserving more details. The Strohecker Ranch Tracksite is preserved on a rippled surface and also preserves countless raindrop impressions. Some raindrop impressions are interrupted by footprints, and some raindrop impressions were deposited after the animal walked by suggesting that the tracks and raindrop impressions were formed roughly simultaneously; the pterosaurs were walking in a light rain. *Pteraichnus* was considered by some to be crocodylian swimming tracks. While that idea has faded, the presence of raindrop impressions shows that these tracks were formed on a subaerial surface, not underwater, ruling out the possibility of these being swimming traces. The Strohecker Ranch track site is approximately 50 kilometers north of other known *Pteraichnus* sites, geographically expanding the occurrence of *Pteraichnus* in the Windy Hill of Wyoming.

### Romer Prize

#### **CRANIAL MORPHOLOGY IN WHALES: A STUDY SPANNING THE EVOLUTIONARY HISTORY AND DIVERSITY OF THE CETACEAN SKULL**

Coombs, Ellen

Genetics, Evolution, and Environment, University College London, London, U.K.

The extant clades of whales, Odontoceti (toothed whales) and Mysticeti (baleen whales), diverged ~39 Ma. Odontocetes evolved high-frequency echolocation and cranial asymmetry, while mysticetes evolved larger masses and filter feeding. Despite an excellent fossil record and unique morphology, there has been little quantitative study of shape evolution spanning cetacean diversity. To quantify morphological disparity and evolutionary rate in cranial shape and to identify ecological correlates of shape variation across Cetacea, I gathered 3D scans of specimens representing 84 living (72 odontocetes, 12 mysticetes) and 72 Eocene to Pliocene fossil (45 odontocetes, 17 mysticetes, 10 archaeocetes) cetaceans. I then digitized 123

landmarks and 64 curves on these scans and conducted high-dimensional geometric morphometric and macroevolutionary analyses within a phylogenetic framework.

The largest component of cranial variation (PC1 = 39.9%) reflects a posterior shift in the nares and separates odontocete and mysticete modes of cranial telescoping. Rostrum length is the major component of variation on PC2 (20.7%) with dolicocephalic (e.g., *Pontoporia blainvillei*) and brachycephalic (e.g., *Kogia sima*) crania representing the extremes. Allometry is a significant aspect of cranial variation ( $r^2 = 0.18$ ,  $p < 0.001$ ), but, after accounting for phylogeny, habitat ( $p = 0.40$ ) and diet ( $p = 0.20$ ) had no significant effect on skull shape. The highest morphological disparity (Procrustes variance) in odontocetes is in the premaxilla (3.21), nasal (2.45), and frontal (2.36), with the highest evolutionary rate ( $\sigma^2_{\text{mult}}$ ) in the frontal (3.17). In mysticetes, the highest disparity and evolutionary rate is in the premaxilla (4.39 and 1.39, respectively). Disparity and rate of evolution is lowest in the basisphenoid and basioccipital.

Cranial asymmetry in archaeocetes is high in the rostrum, squamosal, jugal, and orbit, possibly reflecting preservational deformation. In odontocetes, it is highest in the naso-facial region. Mysticetes show levels of asymmetry similar to terrestrial artiodactyls. Significant rate shifts in asymmetry are observed in the stem odontocetes Xenorophidae (~30 Ma), Physeteroidea (~27 Ma), Squalodelphinidae (~27 Ma), and Monodontidae (~7 Ma). Rapid evolution of both cranial shape and asymmetry in cetaceans occurred in the middle-late Oligocene and peaks in the middle late Miocene, largely due to subclade-specific diversification of rostrum and facial morphology.

**Funding Sources** London Natural Environment Research Council Doctoral Training Partnership (London NERC DTP) training grant NE/L002485/1.

## Education & Outreach

### EXPLOREMOS: SUPPORTING THE ADVANCEMENT OF MINORITIES IN STEM

Cortes, Celine<sup>1</sup>, Smith, Kent<sup>1</sup>, Czaplewski, Nicholas<sup>2</sup>, Whitten, Reggie<sup>3</sup>, Hargrave, Jeff<sup>3</sup>

<sup>1</sup>Oklahoma State University Center for Health Sciences, Tulsa, Oklahoma, U.S.A., <sup>2</sup>Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma, U.S.A., <sup>3</sup>Native Explorers Foundation, Oklahoma City, Oklahoma, U.S.A.

Hispanics are highly under-represented minorities (URMs) in science in the U.S.A. In Oklahoma, Hispanics are the largest minority group, followed by American Indians. The student population at Oklahoma State University Center for Health Sciences (OSU-CHS) is very diverse and includes Hispanics and American Indians. In 2010, the

Native Explorers Program (NEP) was created to increase the number of American Indians who pursue STEM careers. The program introduces participants to various scientific disciplines, with an emphasis on vertebrate paleontology. It has been incredibly successful, with most former participants earning science degrees. In spring 2020, a novel program called “Exploremos” was created as an opportunity for two Hispanic college students to participate in the 2020 NEP. The NEP and Exploremos were canceled due to COVID-19.

The targeted population for Exploremos is Hispanic college-age students with a high-school degree or equivalent and a desire to continue their education. Despite Hispanics representing 16% of the U.S. workforce, they hold only 7% of STEM jobs. Exploremos was created to address their paucity in STEM. In efforts to recruit participants, we contacted campus diversity officers and distributed program materials to Oklahoma colleges and universities. Despite our efforts, we received fewer applications than anticipated. We are evaluating recruiting methods to increase applications for 2021.

Studies on STEM workforce diversity have indicated Hispanics lack encouragement to pursue STEM early in life, as well as educational resources and opportunities in STEM. Exploremos participants will learn from URM and non-minority OSU-CHS faculty, graduate and medical students, and scientific professionals. They will engage in activities within anatomy and vertebrate paleontology labs, and prospect for and collect vertebrate fossils at multiple field sites in Oklahoma. Exploremos will allow Hispanic students, regardless of scientific background, to explore STEM fields with support from URM mentors and peers. We hope this enrichment program will empower participants to pursue STEM, and become the next generation Hispanic STEM educators, researchers, and leaders.

**Funding Sources** Native Explorers Foundation.

## Cenozoic Herpetology

### INTRASPECIFIC VARIABILITY IN AN ONTOGENETIC SEQUENCE OF THE BASAL CROCODYLIAN *BOREALOSUCHUS FORMIDABILIS* AND ITS IMPLICATIONS FOR THE RECOGNITION OF FOSSIL SPECIES

Cossette, Adam P.  
Basic Sciences, NYIT College of Osteopathic Medicine,  
Jonesboro, Arkansas, U.S.A.

In the summer of 1970 the Science Museum of Minnesota began exploration of the late Paleocene Tongue River Formation of western North Dakota at the Wannagan Creek site. The following 27 field seasons yielded an unparalleled *Borealosuchus formidabilis* collection

representing the remains of more than 80 individuals. The complete skeleton is known for the species and this sample provides unique insights into intraspecific variation among basal crocodylians while informing on anatomical changes as they grow. The objective of this study is to document differences between the specimens and compare to modern species of crocodylians.

Morphological variability is present throughout the skeleton of *B. formidabilis*. The elements, sutural contacts, and foramina of the posterior skull demonstrate the most variability, some of which result in divergent character state codings in published matrices. Among the lower jaws, intraspecific differences are concentrated in and around the jaw joint. Variability in postcranial skeletal morphology is pronounced in the limb girdles but is present in the vertebral column as well.

Historically, determining numbers of fossil species has been open to interpretation of the author and operational species likely outnumber real species. As fossils are often found in isolation, two specimens of similar age from different localities, which demonstrate slight variation, are oftentimes assigned to different species. But studies of modern crocodylians indicate that considerable morphological variation may be present within a species (i.e., *Alligator mississippiensis*). It is likely that intraspecific variation in fossil species is proportional to that of their modern counterparts, and this variation complicates efforts in the recognition of fossil species.

Until now, intraspecific variation among basal crocodylians using an expansive, single site, single taxon sample has not been undertaken. This collection allows for the comparison of variation not only among individuals of the same life history stage but also over ontogeny. Insights from the fossils in this project, in concert with studies of modern species, will guide efforts in recognizing fossil diversity in named, and yet to be named, species.

## Marine Reptile Diversity & Biology

### PARANASAL SINUS SYSTEM EVOLUTION IN METRIORHYNCHOID CROCODYLOMORPHS

Cowgill, Thomas<sup>1</sup>, Young, Mark T.<sup>1</sup>, Schwab, Julia A.<sup>1</sup>, Walsh, Stig<sup>2</sup>, Witmer, Lawrence<sup>3</sup>, Herrera, Yanina<sup>4</sup>, Brusatte, Stephen<sup>1</sup>

<sup>1</sup>School of Geosciences, University of Edinburgh, Ipswich, U.K., <sup>2</sup>National Museum of Scotland, Edinburgh, Scotland, U.K., <sup>3</sup>Department of Biomedical Sciences, Ohio University, Athens, Ohio, U.S.A., <sup>4</sup>División Paleontología Vertebrados, Unidades de Investigación Anexo Museo, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Buenos Aires, Argentina

During the Mesozoic, metriorhynchoid crocodylomorphs adapted to life in marine ecosystems, transitioning from semi-aquatic predators into fully pelagic forms

(Metriorhynchidae). Until recently this transition has largely focused on the osteological changes, with the endocranial changes being poorly studied. This is especially true for the paranasal sinus system. In extant crocodylians the rostrum has numerous pneumatic diverticula originating from both the nasal cavity and nasopharyngeal ducts, that become more extensive (in terms of size and number of diverticula) during ontogeny. To investigate the evolution of this sinus system we digitally segmented  $\mu$ CT scans of skulls of two basal metriorhynchoids (*Pelagosaurus typus* and *Eoneustes gaudryi*), four derived pelagic metriorhynchids (*Metriorhynchus superciliosus*, *Cricosaurus araucanensis*, *Cricosaurus schroederi*, and *Torvoneustes coryphaeus*), and two adult and juvenile longirostrine crocodylians (*Gavialis gangeticus* and *Tomistoma schlegelii*) for comparison. We found metriorhynchoids to have exceptionally reduced paranasal sinus systems, solely comprising the antorbital sinus. In basal metriorhynchoids the paranasal sinus extent and morphology is most similar to juvenile longirostrine crocodylians, suggesting evidence of pedomorphosis in Metriorhynchoidea. The antorbital sinus is largely indistinguishable from the dorsal alveolar canal in basal metriorhynchoids, and we propose that they shared the same cavity. In Metriorhynchidae, the antorbital sinus has a conical morphology and extends posteriorly through the postnasal fenestra into the orbit, creating an accessory suborbital sinus. The function of the suborbital sinus is unknown, but its association with the dorsal pterygoideous muscle possibly allowed active ventilation of the paranasal sinus system indicating a respiratory function. Alternatively, expansion and contraction of the sinus through the postnasal fenestra could have enabled metriorhynchids to cope with water pressure changes when diving. The nasopharyngeal ducts in basal metriorhynchoids are similar to extant crocodylians, but in metriorhynchids they are dorsoventrally enlarged and bordered ventrally by thickened palatines. The larger transverse area of the ducts could have enabled stronger ventilation, especially if metriorhynchids had increased lung capacity. The nasal cavity posterior in most metriorhynchoids is dorsolaterally expanded, likely for housing the enlarged salt glands.

**Funding Sources** This project is supported by a Leverhulme Trust Research Project grant (RPG-2017-167).

## Late Cenozoic Mammalian Macroecology & Macroevolution

### PALEOENVIRONMENT AND CHRONOLOGY OF THE LATE MIDDLE MIOCENE (SERRAVALLIAN) MAMMAL SITE OF QUEBRADA HONDA, SOUTHERN BOLIVIA

Croft, Darin A.<sup>1</sup>, Saylor, Beverly<sup>2</sup>, Strömberg, Caroline<sup>6</sup>, Engelman, Russell K.<sup>3</sup>, Catena, Angeline<sup>7</sup>, Deino, Alan<sup>9</sup>, Gibert, Luis<sup>5</sup>, Hembree, Daniel<sup>4</sup>, Anaya, Federico<sup>8</sup>

<sup>1</sup>Anatomy, Case Western Reserve University, Cleveland, Ohio, U.S.A., <sup>2</sup>Earth, Environmental, and Planetary Sciences, Case Western Reserve University, Cleveland, Ohio, U.S.A., <sup>3</sup>Biology, Case Western Reserve University, Cleveland, Ohio, U.S.A., <sup>4</sup>Geological Sciences, Ohio University, Athens, Ohio, U.S.A., <sup>5</sup>Geoquímica, Petrologia i Prospecció Geològica, Universitat de Barcelona, Barcelona, Spain, <sup>6</sup>Biology, University of Washington, Seattle, Washington, U.S.A., <sup>7</sup>Geology, Diablo Valley Community College, Pleasant Hill, California, U.S.A., <sup>8</sup>Universidad Autónoma Tomás Frías, Potosí, Bolivia, Plurinational State of, <sup>9</sup>Berkeley Geochronology Center, Berkeley, California, U.S.A.

Quebrada Honda (QH) is among the best-characterized middle Miocene terrestrial vertebrate sites of South America, with >40 spp. (mainly mammals) documented. Our work clarifies its paleoenvironmental and geochronological context. The studied section (~180 m) can be divided into: (1) a lower unit of reddish mudstone and minor sandstone with basal alluvial gravels; (2) an intermediate unit of mudstone with intercalated beds of soil carbonate; and (3) an upper unit of reddish mudstone with local sandstone and conglomerate channels. Most vertebrate fossils derive from near the base of unit 1. Paleosols and ichnofossils from this unit suggest deposition in a seasonal, sub-humid to semi-arid savanna with MAP of ~100 cm, an interpretation supported by ecological diversity analysis of QH mammals. Paleosol MAP variation is consistent with changes over time scales >10<sup>2</sup>–10<sup>3</sup> years, and well-preserved, several m-thick sedimentary cycles likely reflect ~20 ka cycles in MAP due to precessional orbital forcing (Milankovitch Cycles). We generated three local paleomagnetic sections for the QH basin (based on 60 samples) and seven high-precision Ar<sup>40</sup>–Ar<sup>39</sup> dates for intercalated tuffs, including the first from the Rio Rosario (RR) and Huayllajara (HU) local areas. Our global GPTS correlation indicates that the most fossiliferous intervals at QH are coeval with the Monkey Beds at La Venta, Colombia (Chron C5AA; >13.03 Ma). Fossils at HU derive from strata lithostratigraphically similar to units 2 and 3 of the QH local area; tuff ages and paleomagnetic zones from both areas are concordant with correlation to the younger part of Chron C5A (12.74–12.049 Ma). Phytolith assemblages can be divided into two types using PCA: one with moderately abundant palms and other forest indicators and warm-adapted, presumably open-habitat PACMAD grasses, and the other typically dominated by closed-habitat grasses (e.g., bamboos). Assemblages rich in palm and open-habitat grass morphotypes are associated with laminated sandy layers, primarily in the middle of unit 1, suggestive of more open, riparian vegetation. In contrast, assemblages of mainly closed-habitat grass phytoliths are from mudstones

associated with soil carbonate, primarily in unit 2, potentially representing more terra firme plant communities. A chi-squared comparison of vertebrates of the QH and RR local areas reveals no major taxonomic differences, but turtle and rodent abundances suggest RR samples a less mesic microhabitat.

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## Symposium: Dietary Reconstruction

### AN INITIAL INVESTIGATION OF NICHE PARTITIONING AMONG HISPANIOLA'S RECENT RODENT RADIATION USING STABLE ISOTOPES

Crowley, Brooke<sup>1</sup>, Cooke, Siobhan<sup>2</sup>

<sup>1</sup>University of Cincinnati, Cincinnati, Ohio, U.S.A., <sup>2</sup>Johns Hopkins University, Baltimore, Maryland, U.S.A.

The island of Hispaniola has one extant endemic rodent: Cuvier's hutia (*Plagiodontia aedium*). At least 10 additional caviomorph rodent species lived on the island until the Holocene, and some persisted until just several hundred years ago. These taxa have only been cursorily described (based solely on cranial features) and little is known about their foraging adaptations. We use a suite of carbon ( $\delta^{13}\text{C}$ ), nitrogen ( $\delta^{15}\text{N}$ ), and oxygen ( $\delta^{18}\text{O}$ ) isotopes in incisor enamel and bone collagen to conduct an initial investigation of niche partitioning among endemic rodent taxa as well as introduced *Rattus* from two fossil deposits in the Tiburon Peninsula of southwest Haiti (Trou Jean Paul and Trouing Jérémie 5). These preliminary isotope data support both dietary or spatial niche partitioning among taxa and support what we know about extant taxa. Enamel  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values suggest varying reliance on foliage, fruit, and potentially grasses, and that some species lived in the forest understory, while others likely frequented canopy and more open habitats. Collagen  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values provide further evidence for niche partitioning among taxa. Six species, including extant *P. aedium*, form a cluster of lower  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, while three taxa, including *Rattus*, have higher  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values. The combination of intermediate enamel  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values and low collagen  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for extant *P. aedium* align with observations of a scansorial and generalist herbivore lifestyle for living individuals. Likewise, high  $\delta^{13}\text{C}$ ,  $\delta^{18}\text{O}$ , and  $\delta^{15}\text{N}$  values for *Rattus* are consistent with some trophic omnivory and use of open habitats. A previously undescribed species of *Isolobodon* has higher enamel  $\delta^{13}\text{C}$  than any other taxon, which likely reflects moderate reliance on a C<sub>4</sub> food, such as grass seeds. Conversely, low  $\delta^{13}\text{C}$ ,  $\delta^{18}\text{O}$ , and  $\delta^{15}\text{N}$  values for *Plagiodontia spelaeum*, and possibly *Isolobodon portoricensis*, suggest terrestrial foraging under a relatively

dense forest canopy and some degree of folivory. Comparable isotope values for *Rattus*, *Plagiodontia velozii*, and the undescribed *Isolobodon* species may reflect competition. Alternatively, it is possible that *Rattus* fills a recently vacated niche. Additional isotope data will help validate these preliminary results. Radiocarbon dating specimens will further clarify when species may have disappeared regionally and if there are any temporal isotopic trends.

**Funding Sources** This project was supported with faculty startup funds to Crowley from the University of Cincinnati and to Cooke from Johns Hopkins University School of Medicine.

### Biomechanics & Functional Morphology

#### ESTIMATION OF HINDLIMB LIMB MUSCLE AREAS FROM SKELETONS IN EXTANT AND EXTINCT ARCHOSAURS

Cuff, Andrew R.<sup>2</sup>, Bishop, Peter<sup>1</sup>, Michel, Krijn B.<sup>1</sup>, Wiseman, Ashleigh<sup>1</sup>, Gagnet, Raphaelle<sup>1</sup>, Hutchinson, John R.<sup>1</sup>

<sup>1</sup>Comparative Biomedical Sciences, Royal Veterinary College, North Mymms, U.K., <sup>2</sup>Hull York Medical School, York, U.K.

Does the size of ‘muscle scars’ on bones correspond to the cross-sectional areas of muscles? This question is vital for understanding morphology (e.g., musculoskeletal integration/evo-devo), biomechanics (e.g., mechanobiology) and for reconstructing musculoskeletal form and function in extinct taxa. Archosaurian reptiles famously evolved disparate skeletal forms with differences in body size, posture, gait and other aspects of locomotion reflected by variations of muscle attachments. They are therefore a suitable group to test the question of how well hindlimb muscle areas can be predicted from skeletal morphology. With a high-precision manual digitiser ( $\pm 0.01$  mm), we digitised the bony attachment areas (AA) of all major hindlimb muscles in five juvenile Nile crocodiles and seven Elegant-crested tinamous. Additional, lower-precision ( $\sim \pm 1$  mm) older digitised data from an adult ostrich, emu, turkey and chicken were added to our avian dataset for comparison. We measured the physiological cross-sectional areas (PCSAs) of the same muscles for all specimens via dissection. Logistic regression analysis and stepwise Discriminant Function Analysis were used to predict PCSA from AA after examining variation of PCSAs within crocodiles and between crocodiles vs. birds with Principle Components Analyses. We found that only some homologous muscles in Crocodylia and Aves preserve consistent PCSA:AA ratios, but intriguing trends

related to muscle/bone morphology are evident. Overall, statistically significant conservation of PCSA:AA ratios exists for archosaurian hindlimb muscles; albeit with substantial variation. Finally, we applied this method to the small ( $\sim 13$  kg) Triassic theropod dinosaur *Coelophysis bauri* to estimate its PCSAs from digitised AAs. Comparing these estimates to prior estimates using other assumptions for biomechanical modelling, we found intriguing similarities and differences that are cause for both concern and optimism. Preliminary data from crocodylian forelimbs also indicate useful data for estimating plesiomorphic forelimb muscle morphology in archosaurs, albeit with some deviations even from published data on other amniotes’ forelimb muscles. This dataset and methodology provides a new way to estimate limb muscle architecture in extinct archosaurs that is synergistic with other methods, such as 3D volumetric reconstruction.

**Funding Sources** ERC Horizon 2020 Advanced Investigator Grant (695517, to J.R.H.).

### Fishes & Chondrichthyans: Evolution & Distribution

#### NEW DATA ON *GUALEPIS ELEGANS* (CHONDRICHTHYES) FROM THE LOCHKOVIAN (LOWER DEVONIAN) OF QUJING, YUNNAN, SOUTHWESTERN CHINA

Cui, Xindong<sup>1</sup>, Qu, Qingming<sup>2</sup>, Andreev, Plamen<sup>3</sup>, Zhu, Min<sup>1</sup>, Friedman, Matt<sup>4</sup>

<sup>1</sup>Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, Beijing, China, <sup>2</sup>School of Life Sciences, Xiamen University, Xiamen, Fujian, China, <sup>3</sup>Research Center of Natural History and Culture, Qujing Normal University, Qujing, Yunnan, China, <sup>4</sup>Museum of Paleontology and Department of Earth and Environmental Sciences, University of Michigan, Ann Arbor, Michigan, U.S.A.

*Gualepis elegans* is a scale-based taxon from the Early Devonian Xitun Formation of Qujing, Yunnan, China, originally interpreted as a chondrichthyan. This study examined new material of *Gualepis* comprising more than 1,200 scales isolated via acid digestion. We applied lab-based micro-CT and traditional histological thin sectioning to determine the growth pattern and tissue structure of a sample of these scales. Previous studies of *Gualepis* identified putative old, adult and juvenile scales based on their morphology and size. Our larger sample and more detailed analyses provide a refined picture of growth patterns in *Gualepis*. Tiny scales devoid of secondary odontodes and with a thin base or a large, open basal cavity appear to represent genuine juvenile scales. Scales previously identified as belonging to juvenile *Gualepis* might belong to another taxon. Growth of *Gualepis* can be

divided into four ontogenetic stages. Scales from the two youngest stages possess a basal cavity opening, which gradually shrinks and eventually closes for scales in the two oldest stages. Our scans and sections reveal that *Gualepis* scale crowns have a complex canal system and a single row of areally deposited odontodes (appositional growth pattern). The latter is found in some stem chondrichthyans including *Kathemacanthus*, *Serotolepis*, *Brochoadmones* and *Parexus*. A phylogenetic analysis based on a dataset of 277 characters scored for 87 taxa places *Gualepis* in a clade with *Kathemacanthus* and *Brochoadmones*. This study provides the first 3D virtual growth model of stem chondrichthyan scales, offering new insights into the evolution of squamation within the chondrichthyan total group.

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## Evolution & Biology of Non-Avian Theropods

### THEROPOD BIODIVERSITY PATTERNS IN THE DINOSAUR PARK FORMATION (LATE CRETACEOUS: CAMPANIAN) OF ALBERTA REVEALED THROUGH MORPHOMETRICS AND BIOSTRATIGRAPHY

Cullen, Thomas M.<sup>1</sup>, Larson, Derek W.<sup>2</sup>, Zanno, Lindsay E.<sup>1</sup>, Currie, Philip J.<sup>3</sup>, Evans, David<sup>4</sup>

<sup>1</sup>Paleontology, North Carolina Museum of Natural Sciences, Raleigh, North Carolina, U.S.A., <sup>2</sup>Philip J Currie Dinosaur Museum, Wembley, Alberta, Canada, <sup>3</sup>Biological Sciences, University of Alberta, Edmonton, Alberta, Canada, <sup>4</sup>Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario, Canada

Despite over a century of research on the extremely fossil-rich deposits of the Dinosaur Park Formation (DPF), small-bodied theropod dinosaurs are still only known from a relative dearth of skeletal materials. As a result, the number of named theropod taxa in the DPF has fluctuated, with taxonomic assessments often based on isolated, fragmentary, and/or non-overlapping remains. We combine morphological comparisons, high-resolution biostratigraphy, and morphometric analyses to study DPF theropod biodiversity, with a particular focus on re-assessing specimens/taxa originally described from isolated material, and testing if DPF theropods preserve faunal zonation/turnover patterns similar to those previously documented among ornithischians.

Geometric morphometric analyses performed on a broad sample of DPF and non-DPF frontals readily distinguishes theropod subclades. A frontal previously identified as cf. *Erlikosaurus* plots most closely to troodontids, distinct from non-DPF therizinosauroid frontals. We note that this

placement is supported by a suite of troodontid characters, such as separation of frontal and postorbital components of the depression medial to the orbital margin by an oblique rim, narrow olfactory lobes rimmed by rounded, thickened crista cranii, and caudal buttressing of rostrally-positioned lacrimal articular facets. Postcranial material referred to cf. *Erlikosaurus* is also re-assessed and found to be most similar in morphology to caenagnathids. Among troodontids, there is considerable morphospace overlap between *Stenonychosaurus* and the recently described *Latenivenatrix*. Our analyses, which incorporate frontals not included in the initial description of *Latenivenatrix* results in a variable distribution of putatively autapomorphic characters and stratigraphic overlap between *Latenivenatrix* and *Stenonychosaurus*, which when combined with the morphometric results calls the taxonomic validity of the former into question.

Biostratigraphically, while some non-overlapping ranges exist, there do not appear to be broad-scale patterns of faunal zonation such as those previously documented in ornithischians from the DPF, and many taxa appear to range throughout much of the formation or overlap extensively (e.g., *Gorgosaurus* vs. *Daspletosaurus*). The lack of zonation may reflect a comparative lack of sensitivity to environmental changes among theropods when compared to ornithischians, or may be related to other cryptic ecological or evolutionary factors.

**Funding Sources** Natural Sciences and Engineering Research Council of Canada; National Science Foundation.

## Dinosaur Systematics, Diversity & Ecology

### NEW PROTOCERATOPSID SPECIMENS IMPROVE THE AGE CORRELATION OF THE UPPER CRETACEOUS GOBI DESERT STRATA

Czepinski, Lukasz

Faculty of Biology, University of Warsaw, Warsaw, Poland

Protoceratopsid dinosaurs are abundant in Late Cretaceous localities of the Gobi Desert. A specimen of *Protoceratops andrewsi* from the Zamyn Khond locality enables its correlation with other sites of the Djadokhta Formation. *P. andrewsi* is also common in the Üüden Sair locality, variously assigned to the Djadokhta or Baruungoyot formations. However, one new ceratopsian specimen from that site exhibits a fused nasal horn and a sharp buccal crest of the dentary. With these apomorphic features, it resembles *Bagaceratops rozhdestvenskyi*, known from the Baruungoyot and Bayan Mandahu formations. It may be evidence for: sympatric evolution of *B. rozhdestvenskyi* and *P. andrewsi*; a dispersal of *Bagaceratops* to Üüden Sair; hybridization between the two parapatric taxa; or the

anagenetic evolutionary transition from *P. andrewsi* to *Bagaceratops*. The anagenetic explanation appears to be most strongly supported by given data. This new record advocates for the age of the sediments from the Üüden Sair locality being intermediate between the Djadokhta and Baruungoyot formations. The observed changes in the frequency of the apomorphic features within protoceratopsid samples from various Late Cretaceous sites of the Gobi Desert potentially enable their correlations and chronological ordering.

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### **Biomechanics & Functional Morphology**

## **BREVIROSTRY AS A MAJOR CAUSE OF TOOTH MODIFICATION, REDUCTION, AND LOSS IN NUMEROUS SAUROPSID LINEAGES**

D'Amore, Domenic C., St.Marie, Lauren  
Natural Sciences, Daemen College, Amherst, New York, U.S.A.

The reduction or total loss of teeth has occurred numerous times in tetrapod evolution. Hypotheses as to the cause of this include lack of tooth use, functional replacement by a beak or rhamphotheca, and mass reduction. We propose that shortening of the rostrum, or brevirostry, influences tooth function in such a way as to necessitate dental modifications. The goal of this study is to present morphological evidence that brevirostry is correlated to certain dental conditions, including edentulism, in both modern and extinct sauropsids. The crania of modern crocodylians, squamates, testudines, and tuataras were photographed from the palatal perspective. The tooth row or jaw margin was outlined with equidistant semilandmarks using geometric morphometric software, and measured in reference to the quadrates. The distances between points on the jaw and the hinge were regressed against head width, and the residuals were used to determine relative rostral length. We also calculated the tangent at each semilandmark to determine the orientation of the jaw margin to the axis of rotation. The most brevirostrine modern taxa were the turtles, agamid lizards, and *Phrynosoma*. Tangents typically became more parallel to the axis as the rostrum shortened, and were closest to parallel in these particular taxa. These taxa all displayed clear dental modifications, including edentulism, acrodonty, or tooth size reduction. Similar adaptations are apparent in taxonomically distant brevirostrine fossils, including flanged acrodont teeth in derived Rhynchocephalia, partial/full tooth loss in Oviraptorosauria (and, outside sauropsids, Dicynodontia), and the shift in tooth position from lingual to palatal in both Rhynchosauria and stem Testudinata. Many of these groups also have anterior, beak-like structures, similar to

the modern turtle tomiodont. We suggest this suite of dental conditions are adaptations to cope with the mechanical limitations of the brevirostrine condition. Due to torque a short snout will impose greater forces upon tooth row overall, and potentially break more gracile crowns. This condition also prohibits labio-lingual compression, especially of tall teeth, as the weaker tooth-face would rotate more so about the axis of rotation. The keratinous beaks, uniform sheering surfaces, and/or stout palatal teeth seen in brevirostrine taxa would hold up much better than the typical sauropsid crowns during a substantial bite.

**Funding Sources** Daemen College.

### **Dinosaur Systematics, Diversity & Ecology**

## **A NEW PHYLOGENETIC ANALYSIS OF SAUROPODS WITH INCREASED EMPHASIS ON NON-NEOSAUROPODS**

D'Angelo, John E.  
Independent, Chicago, Illinois, U.S.A.

Despite much research in recent years, many aspects of sauropod phylogeny remain poorly understood. Titanosaurs have proven especially difficult to study, with recent studies finding widely varying relationships within the group. The relationships of the less-studied non-neosauropod sauropods are also enigmatic. To explore sauropod phylogeny, I constructed a novel phylogenetic dataset comprising 126 taxa and 335 characters, including several new characters, with an emphasis on adequately-known taxa that are newly discovered or rarely included in phylogenetic analyses. I chose *Melanorosaurus* as the outgroup and analyzed the dataset with both maximum parsimony (MP) and Bayesian analysis.

Preliminary results generally support previous hypotheses of sauropod relationships, but some findings merit further attention. *Tonganosaurus* falls outside of Eusauropoda and in the Bayesian results outside of Gravisauria. These results are more consistent with its Early Jurassic age than its previous placement in Mamenchisauridae. *Euhelopus* groups with mamenchisaurids to form a non-neosauropod Euhelopodidae in MP, but is a non-titanosauriform macronarian in the Bayesian results. *Dongbeititan* and *Daxiatitan* clade with mamenchisaurids in both results. These results are sensitive to taxon sampling; in a reduced MP analysis including only two Jurassic mamenchisaurids, *Euhelopus* and *Dongbeititan* are somphospondyls. The affinities of these taxa may need review, as many of the characters that have supported their position in Somphospondyli are also found in Mamenchisauridae. *Bajadasaurus* and *Amargatitanis* form a clade with *Amargasaurus*, which is novel but biogeographically congruent. *Galeamopus pabsti* is a non-diplodocine diplodocid, but this may be due to the exclusion of the largely undescribed *G. hayi*. *Galveosaurus* and *Atlasaurus* are brachiosaurids. Opisthocoelicaudiines, including

*Diamantinasaurus*, *Liaoningotitan*, and *Sonidosaurus* but not *Alamosaurus*, are non-titanosaur somphospondyls, but few other conclusions can be drawn about somphospondyl relationships here.

These results highlight several interesting aspects of sauropod phylogeny that may benefit from further research and emphasize the importance of taxon sampling in sauropod phylogenetics. Increasing taxon sampling in analyses is vital to advancing the understanding of sauropod phylogeny, which can be facilitated by thorough morphological descriptions that allow the global sauropod record to be more fully incorporated.

### **Colbert Poster Prize/Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

#### **ASSESSING MIGRATION IN PLEISTOCENE HERBIVORES AT RANCHO LA BREA – YEA OR NEIGH?**

Davis, Madison<sup>1</sup>, Szymanski, Kathryn<sup>1</sup>, Fuster, Joaquin<sup>1</sup>, Cohen, Joshua<sup>1</sup>, DeSantis, Larisa<sup>2</sup>, Lindsey, Emily<sup>3</sup>, Meachen, Julie<sup>4</sup>, O’Keefe, Frank R.<sup>5</sup>, Southon, John<sup>6</sup>, Binder, Wendy J.<sup>1</sup>

<sup>1</sup>Loyola Marymount University, Los Angeles, California, U.S.A., <sup>2</sup>Vanderbilt University, Nashville, Tennessee, U.S.A., <sup>3</sup>La Brea Tar Pits Museum, Los Angeles, California, U.S.A., <sup>4</sup>Des Moines University, Des Moines, Iowa, U.S.A., <sup>5</sup>Marshall University, Huntington, West Virginia, U.S.A., <sup>6</sup>University of California - Irvine, Irvine, California, U.S.A.

The asphaltic seeps at Rancho La Brea (RLB) in California, U.S.A., have accumulated and preserved the remains of local organisms for 50,000 years. More than 3.5 million fossils have been recovered from RLB preserving large herbivores such as *Bison antiquus*, *Equus occidentalis*, and *Camelops hesternus*. From these fossils, migratory patterns can be investigated, shedding light on paleoecological, climatic, and floral changes through time. Previous research using serially-sampled enamel isotopes has suggested that *B. antiquus* was a seasonal migrant at RLB, while *E. occidentalis* was a year-round inhabitant. Additionally, age profiles of *B. antiquus* show annual clusters of juveniles, interpreted as further evidence of migration. However, such age signals could also be the result of seasonal seep activity and seasonal changes in vegetation. In this study, we sought to clarify the purported migratory behavior of *B. antiquus* by comparing them against the presumed non-migratory taxon, *E. occidentalis*, and to apply these same techniques to investigate migratory patterns in *C. hesternus*. We constructed age profiles of *E. occidentalis* (n = 150), *B. antiquus* (n = 170), and *C. hesternus* (n = 136) using tooth wear and eruption sequences from throughout RLB. *E. occidentalis* age

profiles show a continuous age representation, differing from the annual clusters of juveniles in *B. antiquus*. Our age profiles support year-round entrapment of *E. occidentalis* at RLB, with age profiles of *B. antiquus* consistent with migratory behavior, indicating that age profiles can reliably assess migration. Age profiles of *C. hesternus* differ from both *E. occidentalis* and *B. antiquus* with two main clusters, one of young juveniles  $\leq 1$  years in age and one of adults. The lack of continuous ages in *C. hesternus* suggests migration, supported from serially sampled stable isotopes of *C. hesternus* from the McKittrick tar seeps. Differences in age profiles between *C. hesternus* and *B. antiquus* are likely due to behavioral differences, with evidence from modern New World camels showing that family groups comprise adults and individuals  $\leq 1$  year old. Therefore, age profiles may be a useful proxy for migration in extinct taxa, which can be applied to other paleontological sites to assess migration throughout the fossil record.

### **Late Cenozoic Mammalian Macroecology & Macroevolution**

#### **A NEW HEMINGFORDIAN LOCALITY FROM THE MASCALL FORMATION, CROOKED RIVER BASIN, OREGON**

Davison, Shyla R., Hopkins, Samantha S.  
Earth Sciences, University of Oregon, Eugene, Oregon, U.S.A.

The middle Miocene is a critical time period for understanding the evolution of mammalian faunas with changing habitats, as the climate changes around the middle Miocene Climatic Optimum represent both warming and cooling in a context of the spread of open habitats. The Mascall Formation of Central Oregon preserves a well-described middle Miocene mammalian fauna. The fauna from this formation was first described from North Central Oregon, in the John Day Basin, but also outcrops to the south in the Crooked River Basin, where the fossils are substantially older. The fauna in the type area of the Mascall Formation is a classic Barstovian assemblage, but recent studies of the Crooked River assemblages have proven that these southern outcrops are latest Hemingfordian in age. While the Crooked River Mascall localities have been known for some time, it is only recently that they have been exhaustively collected, revealing a more diverse fauna than described in earlier accounts of the Mascall assemblages. Here we describe a new locality from the Crooked River Basin that produces exceptionally well-preserved fossils, including teeth, jaws, and entire bony elements, which are otherwise rare in the Mascall of the Crooked River, where fossils were exposed and weathered for some time prior to burial. This new assemblage includes several new occurrences and new

material not previously described from these sites, including multiple taxa of testudines and both large and small mammals. Two nearly complete dentaries allow us to identify *Monosaulax typicus* in this site; other known specimens are isolated teeth and could only be identified to genus. We also found scutes of at least two testudines, including numerous specimens of *Hesperotestudo* and a small emydid. The mammalian assemblage is dominated by rhinocerotids that we tentatively identify as *Teleoceros*, but also contains *Merychippus*-grade horses, paleomerycids (?*Dromomeryx*) and a large amphicyonid. The assemblage differs strikingly from the Hawk Rim assemblage described from nearby, and the lithology and stratigraphy suggests that the assemblages in the Crooked River span some temporal range. Continuing work on the Crooked River Mascall sites will contribute to our understanding of the evolution of Oregon's terrestrial vertebrates during the warming into the mid-Miocene Climatic Optimum.

### **Taphonomy & Stratigraphy**

#### **BITE MARKS ON *TRICERATOPS* RIBS ATTRIBUTED TO CROCODYLIAN SCAVENGING**

de Rooij, Jimmy  
Naturalis Biodiversity Center, Leiden, Zuid-Holland, Netherlands

Feeding traces on fossilized bones present direct evidence on the interaction between species in ancient ecosystems. Accordingly, they help in reconstructing the trophic levels within food webs and shed light on the niche occupation of extinct species. An associated skeleton of *Triceratops horridus* from the Lance Formation of Wyoming, U.S.A., was discovered bearing osseous deformations on the sixth and seventh right dorsal rib. The size of its post-cranial material and morphology of skull elements indicate that this animal was of sub-adult ontogenetic age. The depositional environment, as indicated by the sedimentological context and grain-size analyses, is reconstructed as a swamp-like environment in an active fluvial system. In addition, observed weathering of cortical bone suggests exposure of the remains for an extended time period, before final burial occurred. Medical CT scanning did not reveal any signs of active bone healing around the deformations. Furthermore, the overall lack of any additional taphonomic and diagenetic alterations suggest a post-mortem, but pre-burial, origin of the bone marks. The deformations are described as a relatively large ovoid depression that crushed the bone rather than pierced, resulting in fragmentation of the surrounding outer cortex. These characteristics closely resemble crocodylian feeding traces, both extant and fossilized. Following, crocodylian scavenging is regarded as the most parsimonious explanation for the observed marks. While scavenging by

crocodyles would be expected in the proposed setting of Late Cretaceous floodplains, this is the first report of actual evidence. Correct assignment based only on bite marks is difficult, but the relative abundance- and size of *Leidyosuchus*, combined with the described taphonomy and morphology of the bite marks, make it the most parsimonious candidate. This discovery holds implications for future interpretations of pathological lesions and Late Cretaceous food webs. Furthermore, it confirms that crocodylians play a significant role as taphonomic agent, ultimately influencing skeletal remains before final burial and fossilisation.

### **Biomechanics & Functional Morphology**

#### **3D VOLUMETRIC MUSCULOSKELETAL MODELING OF LOCOMOTORY BIOMECHANICS IN *EUPARKERIA CAPENSIS***

Demuth, Oliver E., Bishop, Peter, Hutchinson, John R.  
Department of Comparative Biomedical Sciences, The Royal Veterinary College, Hatfield, Hertfordshire, U.K.

Biomechanical analyses of locomotor function in extinct taxa are challenging, as the information provided by the fossil record is often scarce and incomplete, as important soft-tissue information is seldom preserved. Individual muscles sometimes can be identified based on osteological correlates for attachment sites on the bones. Furthermore, the presence or absence of certain muscles can further be constrained using a phylogenetic bracket approach including osteological correlates across extant and extinct taxa. Here we illustrate the importance of three-dimensional (3D) volumetric myological reconstructions using *Euparkeria capensis*, a Middle Triassic stem-archosaur. The 3D muscle reconstruction, added to a 3D articulated digital skeleton derived from micro-CT scans, was used as tool to infer the line of action of hindlimb muscles. The origin and insertion of each muscle was characterized using muscle scarring/bony landmarks and/or phylogenetically informed. Each muscle path and the spatial organization of the limb musculature was then guided by dissection and tomographic data of extant Crocodylia (*Alligator* and *Crocodylus*). Our method prevents the intersections of different muscles, a problem that can arise in simple 2D or line-segment-based reconstructions, as the muscle shapes are informed directly by that of their neighbors. Additionally, the volume of the musculature can be calculated and therefore provide more precise estimates of individual muscle masses for musculoskeletal modeling and simulation. Here, the combination of the novel 3D muscle reconstruction with the calculation of the body's center of mass (COM) was used to test the bipedal locomotor capabilities of *Euparkeria*. We infer that even 'facultative' bipedalism

was highly unlikely in this taxon given its cranially positioned COM relative to the hips, and relatively short hindlimbs.

**Funding Sources** ERC Horizon 2020 Advanced Investigator Grant (695517, to J.R.H.).

## Mesozoic & Early Cenozoic Mammalian Evolution

### THE CURIOUS CASE OF THE CYRIACOTHERIIDS: AN EVALUATION OF THEIR PHYLOGENETIC POSITION

dePolo, Paige E.<sup>1</sup>, Shelley, Sarah L.<sup>2</sup>, Williamson, Thomas E.<sup>3</sup>, Wible, John R.<sup>2</sup>, Brusatte, Stephen<sup>1</sup>

<sup>1</sup>School of GeoSciences, University of Edinburgh, Edinburgh, U.K., <sup>2</sup>Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A., <sup>3</sup>New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, U.S.A.

Sixty-six million years ago, the world's ecosystems suddenly, and fundamentally, changed with a variety of bizarre mammals evolving to fill niches left by non-avian dinosaurs during the end-Cretaceous mass extinction. Pantodonts, an enigmatic group with distinctive upper premolars, quickly increased in body size in the wake of the extinction and had achieved enormous sizes (~500 kg) by the late Paleocene. Despite lacking the premolar features that traditionally unite Pantodontia, cyriacotheriids, a group known exclusively from isolated teeth and fragmentary jaws, were suggested as highly derived, small-bodied pantodonts on basis of characters such as hypoconulid position. This contention proved controversial and alternative hypotheses of mixodectid or dermopterian affinities were subsequently proposed based on the dilambdodonty of their molariform upper premolars. In recent large-scale analyses of placental mammals, the position of *Cyriacotherium* has been labile, variably appearing as sister to plagiomenids (putative dermopterian relatives) or nested within Pantodontia.

We present a novel phylogenetic analysis of these enigmatic animals' relationships. Prior to this study, the two cyriacotheriid genera, *Cyriacotherium* and *Presbyterium* had not been evaluated in the same cladistic framework. We incorporated the four cyriacotheriid species (*Cyriacotherium argyreum*, *C. psammimum*, *Presbyterium rhodorugatus*, and *P. taurus*) and comparative taxa including representatives of early pantodonts, mixodectids, plagiomenids, and dermopterians into the PalM working group matrix (102 taxa scored for 618 dental, cranial, and postcranial characters).

In a strict consensus of 960 most parsimonious trees, we recovered a clade including both species of *Cyriacotherium* and *Presbyterium rhodorugatus*. *P.*

*taurus*, known from only three isolated upper cheek teeth, behaved as a wildcard taxon and was discarded from the analysis a posteriori. This clade supports the cyriacotheriids as a natural grouping on the basis of features such as a cusped preparacrista and postmetacrista and a pronounced lower molar metaconid. Cyriacotheriids are more closely allied with pantodonts and tillodonts than with dermopterans and plagiomenids. The placement of cyriacotheriids near pantodonts and tillodonts bucks an otherwise consistent trend of evolution towards larger body sizes seen in these lineages and supports the inference of wider variation in ecology for these animals than traditionally surmised.

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## Education & Outreach

### IMPROVING SCIENTIFIC LITERACY THROUGH THE EXPLORATION AND MANIPULATION OF DATA FROM EXTANT AND EXTINCT MAMMALS

DeSantis, Derek<sup>2</sup>, DeSantis, Larisa<sup>1</sup>

<sup>1</sup>Biological Sciences, Vanderbilt University, Nashville, Tennessee, U.S.A., <sup>2</sup>Centennial High School, Franklin, Tennessee, U.S.A.

The ability to understand and interpret scientific data is a critical skill and necessary for a scientifically literate public. Further, advance placement environmental science and biological science assessments often require students to plot, analyze, manipulate, and interpret scientific data on collage board exams. In the midst of the biodiversity, climate, and now the COVID-19 crisis, it is even more important for students and the public to understand and interpret scientific data. As databases with climate data, paleontological specimen data, and extant specimen data, are more readily available, these are often untapped resources for high school classrooms. Here, we use data from the Atlas of Living Australia and Neotoma to examine the movement of mammals over historic and geologic time. Additionally, published paleoecological proxy data (in open access journals) were used to formulate and test student generated hypotheses. The use of cutting-edge primary data is appealing to high school students and provides opportunities to evaluate real, relevant, and timely data. In part one of the module, students focus on interpreting paleontological and ecological data from open access publications, reading press releases associated with open access figures. In part two, students are taught how to download, generate, and plot their own data, after developing clearly articulated hypotheses. Lastly, students present their data via virtual poster or oral presentations, with students assessing and evaluating the degree to which stated hypotheses are supported or rejected, in each

scenario. Extinct charismatic prehistoric animals mixed with modern taxa are often good hooks for engaging high school students. Most notably, paleontological data provides a rare deep-time perspective that allows students to evaluate species responses to changing environments and climates over deeper time than possible, today. Making paleontology relevant to the current biodiversity and climate crisis is important, not only in the scientific arena, but in high school classrooms across the globe.

**Funding Sources** This work was supported by the National Science Foundation (1455198).

### **Symposium: Dietary Reconstruction**

#### **MORE TOOLS AND ISOTOPES ARE BETTER THAN ONE: CLARIFYING THE ECOLOGY OF ANCIENT MAMMALS AT RANCHO LA BREA AND BEYOND**

DeSantis, Larisa<sup>5</sup>, Feranec, Robert<sup>1</sup>, Southon, John<sup>2</sup>, Binder, Wendy J.<sup>7</sup>, Cohen, Joshua<sup>7</sup>, Farrell, Aisling<sup>3</sup>, Lindsey, Emily<sup>3</sup>, Meachen, Julie<sup>4</sup>, O'Keefe, Frank R.<sup>6</sup>, Takeuchi, Gary<sup>3</sup>

<sup>1</sup>New York State Museum, Albany, New York, U.S.A.,

<sup>2</sup>University of California, Irvine, Irvine, California, U.S.A.,

<sup>3</sup>La Brea Tar Pits, Los Angeles, California, U.S.A., <sup>4</sup>Des

Moines University, Des Moines, Iowa, U.S.A., <sup>5</sup>Vanderbilt

University, Nashville, Tennessee, U.S.A., <sup>6</sup>Marshall

University, Huntington, West Virginia, U.S.A., <sup>7</sup>Loyola

Marymount University, Los Angeles, California, U.S.A.

Clarifying the ecology of ancient mammals requires tools such as stable isotopes and dental microwear texture analysis (DMTA). Unlike morphology, which provides insight regarding potential diet, paleoecological proxy data clarifies the realized dietary niches of resident taxa and can be used to assess dietary change through time. Prior work demonstrates that when stable carbon isotopes and DMTA are both employed, the diets of both herbivores and carnivores are more thoroughly understood – with the use of just one method revealing only part of the story. Similarly, the study of multiple isotopes and tissues can be useful to reconciling the dietary ecology of predators from Rancho La Brea (California, U.S.A.). Stable carbon isotopes from bone collagen indicate competition for similar prey while the same isotope from tooth enamel suggests disparate prey were consumed. Reconciling these dietary interpretations is critical to evaluating the ecology of late Pleistocene mammals at Rancho La Brea, and clarifying the isotopic ecology of predators across the globe and through time.

Stable carbon isotope spacing between collagen and carbonate has been characterized as a proxy for inferring the trophic level of mammals for decades. Carbonate-collagen offsets (c-c offsets) are assumed as largely stable among taxa feeding at similar trophic levels, with higher

offset values indicative of more omnivorous/herbivorous diets in secondary consumers. To clarify the stable isotope ecology of carnivores, past and present, we isotopically analyzed bone collagen and enamel carbonate of extinct and extant felids and canids, including *Canis dirus*, *Canis latrans*, *Lycaon pictus*, *Panthera leo*, *Puma concolor*, and *Smilodon fatalis*. Our results reveal that c-c offsets can be predicted via enamel carbonate values in secondary consumers, with lower c-c offsets occurring coincident with lower carbonate values, not trophic levels. These results indicate that the foraging habitat of prey affects c-c offsets in carnivores, similar to the relationship for c-c offsets previously observed in herbivores. Further, variable c-c offset values in secondary consumers appear to reconcile the disparate dietary interpretations of *S. fatalis* and *C. dirus*. Much like the need for multi-proxy approaches, multiple stable isotopes from collagen and carbonate tissues provide clarity to the dietary ecology of ancient predators and their prey – of relevance to extinct and extant taxa across the globe.

**Funding Sources** This work was funded by the National Science Foundation (1757545).

### **Marine Mammals**

#### **CLEANING UP THE RECORD OF FOSSIL SEALS (MAMMALIA, PHOCIDAE) FROM THE NORTH SEA BASIN: TAXONOMY AND TIMING**

Dewaele, Leonard<sup>1</sup>, de Muizon, Christian<sup>2</sup>, Everaert, Stijn<sup>3</sup>

<sup>1</sup>Liège University, Horebeke, Belgium, <sup>2</sup>Centre de

Recherche en Paléontologie, Muséum national d'Histoire

naturelle, Paris, France, <sup>3</sup>Ghent University, Ghent,

Belgium

Starting in the nineteenth century, the record of fossil Phocidae from the Neogene of the North Sea Basin steadily grew over time to include over a dozen taxa representing both commonly accepted subfamilies: Monachinae and Phocinae. In the light of modern-day paleontological approaches, many question marks surround the historical research on fossil phocids from this region, namely the use of syntypes lacking anatomical overlap, and the uncertain stratigraphic context. In recent years, researchers both reviewed parts of the historical collections and presented new material and new taxa. However, an all-encompassing (re-assessment of this fossil record remained much needed so that it can be used to study seal diversity through time at regional and global levels.

In the present study, the entirety of the North Sea fossil record is reviewed in the light of published research cautioning against the use of isolated long bones as type specimens, as well as against grouping isolated specimens that cannot be associated. Many of the historically-described species in the nineteenth century remain easily

separable and identifiable, whereas it remains questionable whether closely-related, recently-described species are distinguishable as separate species given the incompleteness of the fossil record. For other taxa, the present study suggests new subfamily designations differing from previous studies: *Frisiphoca aberratum*, *Frisiphoca affinis*, and *Prophoca rousseaui* are identified as monachine seals instead of phocine seals. This taxonomic reassessment, considering a significant number of described phocid taxa as nomina dubia, and reassigning taxa at the subfamily level, results in an increased diversity of Monachinae in the Neogene North Sea Basin, and a decreased diversity of Phocinae. This juxtaposes the current situation, with Monachinae being entirely absent at high northern latitudes. The present study also compiles all the available data on stratigraphy for the fossil Phocidae from the Neogene of the North Sea Basin, combining both biostratigraphy, lithostratigraphy, and literature research. The early Langhian (early middle Miocene) is the oldest definite age of Phocidae in the North Sea Basin, with certain new discoveries suggesting an extension to the earliest record into the early Miocene.

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## Mesozoic Herpetology

### REPTILIAN TETRAPODS OF UPPER CRETACEOUS (MAASTRICHTIAN) VOLCANIC SEDIMENTS ASSOCIATED WITH OLDEST LAVA PILES OF NORTHEASTERN DECCAN TRAPS: RESPONSE TO DECCAN ERUPTIONS

Dhobale, Anup G., Mohabey, Dhananjay M., Samant, Bandana T., Kumar, Deepesh  
Department of Geology, RTM Nagpur University, Nagpur, Maharashtra, India

We investigated reptilian tetrapods in a series of sediments at different stratigraphic levels below and between the lava flows of Maastrichtian–Paleocene age in Deccan volcanic sequences. The lava piles are designated as Malwa Group, representing the northern-most Deccan volcanic province in India. The reptilian fauna is the earliest Maastrichtian Indian reptiles recorded from the sediments of magnetochron C30N. The reptilian tetrapods before the advent of volcanism are mainly represented by titanosauriform sauropods and abelisaurid theropods, including *Rajasurus narmadensis* and *Rahiolisaurus gujaratensis*, having the acme of their nesting and breeding under semi-arid conditions. These dinosaurs were adversely impacted by the onset of volcanism, with only a couple of titanosaurid species surviving the initial onslaught, and with increasing volcanism they became extinct before reaching the Cretaceous–Paleogene

boundary (K–Pg B). Contemporary snakes are mainly represented by Alethinophidia (*Sanajeh indicus*, *Madtsoia pisdurensis*); turtles, mainly bothremydid, (Kurmadymydinae?), and notosuchid crocodylomorphs. The snakes and turtles survived the advent of volcanism but remarkably declined in diversity and abundance, whereas the crocodylomorphs are indicated to have increased diversity favoured by hot and humid climatic conditions induced by volcanism. The anguimorph and scincomorph lizards represented by dentary, maxilla, vertebrae, and body scales are mainly found associated with multiple intertrappean lake sediments during early volcanism, showing increased abundance and diversity.

## Fishes & Chondrichthyans: Evolution & Distribution

### A REDESCRIPTION OF *CIMOLICHTHYS LEWESIENSIS* LEIDY, 1857 (AULOPIFORMES: CIMOLICHTHYIDAE) BASED ON COMPUTED TOMOGRAPHY WITH COMMENTS ON ITS PHYLOGENETIC POSITION

Díaz-Cruz, Jesús A.<sup>1</sup>, Giles, Sam<sup>2</sup>, Beckett, Hermione<sup>2</sup>, Alvarado-Ortega, Jesús<sup>3</sup>

<sup>1</sup>Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, Ciudad de México, Mexico, <sup>2</sup>Department of Earth Sciences, University of Oxford, Oxford, U.K., <sup>3</sup>Departamento de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

In the exercise of modern paleontology, the use of Computed Tomography (CT) has become a fundamental technique because its non-invasive nature is preferred over traditional destructive preparation procedures. Here we use CT scanning to investigate the anatomy of *Cimolichthys lewesiensis*, a fossil member of the order Aulopiformes. This order comprises bony fishes with a great morphological disparity, occurring in environments ranging from coral-reefs to deep-seas. The evolutionary relationships between extant and fossils aulopiforms are only partially understood mainly because most of phylogenetic investigations focus separately on extinct or extant forms, with few taking an integrative approach. In these analyses, *Cimolichthys* has proved to be a somewhat problematic taxon, despite the fact that it is known from multiple specimens, some exquisitely preserved, and ideal for thorough anatomical studies. We performed a comprehensive morphological examination of acid prepared and CT scanned specimens housed in the Natural History Museum, London, U.K., allowing us to recognize morphological characters previously unknown in this species and not captured in phylogenetic analyses. Our results also provide a better understanding of the tooth distribution pattern in jaws, the articulation of maxillary

bony elements, and the identification of maxillary teeth, which have not been reported before in *Cimolichthys*. These data were added to an expanded aulopiform data matrix and analyzed under Maximum Parsimony (MP) and Bayesian Inference (BI) criteria. Our results broadly agree with those of some previous works regarding the placement of *Cimolichthys* as a member of the superfamily Alepisauroidea, supported by the presence of the palatine as the dominant tooth-bearing bone. However, our findings show that a) in the MP analysis, *Cimolichthys* forms a polytomy with *Anotopterus* [Alepisauridae] + (*Arctozenus* + *Paralepis*) [Paralepidae] and the clade formed by (*Sudis* [Sudidae] + Paralepidae); and b) the BI topology differs from that of the MP in resolving *Cimolichthys* as the sister group of *Anotopterus* [Alepisauridae], with relationships in Alepisauroidea similar to those recovered in the MP analysis. Although both analyses show low support values for the clades where *Cimolichthys* is included, we consistently resolve a close relationship with Alepisauridae. Our exercise also reveals that aulopiform clades may be reorganized when fossils are included since they lack synapomorphies.

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### Romer Prize

#### THE ORIGIN AND EVOLUTION OF TERRESTRIAL LOCOMOTION: FUNCTIONAL ADAPTIVE LANDSCAPES OF THE TETRAPOD HUMERUS ACROSS THE WATER-LAND TRANSITION

Dickson, Blake V.  
Organismic and Evolutionary Biology, Harvard University, Somerville, Massachusetts, U.S.A.

The evolution of limb-driven terrestrial locomotion in stem tetrapods has been a question at the fore of vertebrate paleontology for over a century. The origin of limbs was one key innovation that allowed tetrapods to invade the land, though it remains unclear when tetrapods evolved the ability to perform terrestrial limb-based locomotion. Much of our understanding of stem tetrapod paleobiology is based on qualitative interpretations of a few exceptionally preserved fossils that provide only limited temporal resolution on the evolution of terrestriality. Isolated humeri, however, are far more common throughout this transition and can provide critical functional information on locomotor adaptations, thus serving as an exceptional yet underutilized resource. Here I present a comprehensive quantitative analysis of 40 tetrapodomorph humeri spanning the water-land transition, including 12 specimens

from Romer's Gap – a period historically devoid of tetrapod fossils. Using high resolution 3D geometric morphometrics, biomechanics, and quantitative trait modelling, I implement novel advances in constructing functionally informed ecological adaptive landscapes to predict the functional transition from water to land. I reconstruct the adaptive landscape of the water-land transition and identify the functional locomotor adaptations of tetrapodomorph fishes, stem, and crown tetrapods; and provide novel insight into the timing of the terrestrial invasion. I find that the evolution of tetrapods is defined by two distinct functional adaptive regimes between aquatic fishes and terrestrial crown tetrapods. The 'L'-shaped humeri of stem tetrapods are not adapted to their own locomotor adaptive optima, and instead occupy a transitional zone between water and land. Their position on the transitional landscape indicates that the earliest limbed tetrapods were capable of terrestrial locomotion, utilizing relatively greater stride-lengths and improved locomotor efficiency, but that advanced terrestrial adaptations did not evolve until the diversification of crown group tetrapods and the tetrahedral humerus morphology. This study is the first analysis of its kind on tetrapod evolution and provides new avenues for understanding major biological transitions over macroevolutionary timescales.

**Funding Sources** Robert A. Chapman Fellowship.

### Evolution & Biology of Non-Avian Theropods

#### QUANTITATIVE HETERODONTY IN ALLOSAURUS: PALEOECOLOGICAL IMPLICATIONS OF SHED TEETH

Diepenbrock, Julian E.  
Department of Geosciences, University of Arizona, Rancho Cucamonga, California, U.S.A.

*Allosaurus* is a well-known theropod dinosaur from the Upper Jurassic, with the majority of remains known from the Morrison Formation of Western North America. Much research has been done on the osteology of *Allosaurus*, most recently assigning a new species to the genus after intense study of the skull. Despite the genus' status as a well-known theropod, it has been noted that the genus lacks thorough dental description. Shed teeth are some of the most common theropod elements in the fossil record and can be paleoecologically important. Shed tooth morphology and denticle structure can be useful for identification, as shed teeth may be the only theropod material recovered from a site. Tooth morphology has been well studied in some theropods, particularly *Tyrannosaurus* and *Majungasaurus*, but not *Allosaurus*. Here, 15 specimens are used to describe different tooth morphologies assigned to *Allosaurus* to provide a stronger baseline for the genus. Studied specimens were collected

from multiple Morrison Formation quarries at Warm Springs Ranch, in Hot Springs County, Wyoming. Specimens were measured by digital calipers and put through micro-CT scanning to observe cross-sectional morphology. Preliminary analysis of tooth morphology and structure shows a definite difference between two types of teeth based on cross-section morphology: a lanceolate cross-section and a somewhat asymmetrical salinon shaped cross-section. Salinon-shaped teeth are noted to be present towards the anterior of the mouth. Due to the spatial separation of the two different types of teeth in the mouth, this study finds *Allosaurus* to be pseudoheterodont.

**Funding Sources** George H. Davis Undergraduate Research Fund, through the University of Arizona Geosciences Department.

## Education & Outreach

### “BROADER IMPACTS”, AN EXHIBIT PROGRAM FOCUSING ON BASIC RESEARCH

Dooley, Alton C.<sup>1</sup>, Radford, Darla<sup>1</sup>, Wedel, Mathew J.<sup>2</sup>, Atterholt, Jessie<sup>3</sup>, Nalley, Tierra<sup>4</sup>

<sup>1</sup>Western Science Center, Hemet, California, U.S.A.,

<sup>2</sup>College of Osteopathic Medicine of the Pacific and College of Podiatric Medicine, Western University of Health Sciences, Pomona, California, U.S.A., <sup>3</sup>Graduate College of Biomedical Sciences, Western University of Health Sciences, Pomona, California, U.S.A., <sup>4</sup>Dept of Medical Anatomical Sciences College of Osteopathic Medicine of the Pacific, Western University of Health Sciences, Pomona, California, U.S.A.

Given the importance of public funding to scientific endeavors, dissemination of the process and results of research to the public should be regarded as integral to research programs. Social media phenomena such as #actuallivingscientist and #scientistswhoselfie have highlighted the importance of connecting scientists with their research when communicating with the public. Besides print and digital media, museums are one of the few venues available for scientists to present their work directly to the public. Unfortunately, very few scientists are employed by museums, and museum exhibits often present a refined picture of science, one which largely obscures the sometimes haphazard basic processes, observations, and discoveries that come together to form the more polished ‘end-product’.

In an attempt to make basic research more accessible to the public, in 2019 the Western Science Center (WSC) in Hemet, California launched a new exhibit program, “Broader Impacts”. These small (~20 m<sup>2</sup>) exhibits feature a narrowly focused research project, recently completed or currently underway, and conceptually are similar to an

expanded, public-friendly research poster. One exhibit panel is devoted to photos and short biographies of the scientists conducting the research, while others introduce the basic concepts, preliminary results, significance, and unanswered questions. Emphasis is placed on science as an ongoing process, rather than final answers. Panels are supplemented by specimens or 3D prints, videos, and other interactives when appropriate. Exhibit runs are generally planned to last 3-4 months, with exposure to 8,000-10,000 visitors. Because of their small size and narrow focus, the exhibits can be produced rapidly and inexpensively, and are easily adapted into traveling exhibits that can be displayed in other venues. Following the closure due to the COVID-19 pandemic, WSC intends to premiere the second “Broader Impacts” exhibit upon reopening in 2020.

## Paleozoic Tetrapods & Lissamphibians

### A POSSIBLE TRANSITIONAL SPECIES TO A FROG YOU’VE NEVER HEARD OF: WHERE DID RHINOPHRYNUS GO FOR 30 MILLION YEARS?

Driebergen, Julie

University of Minnesota, Lake Elmo, Minnesota, U.S.A.

The lineage of Rhinophrynidae is estimated to be 190 million years old, but the earliest specimens of the extant genus *Rhinophrynus* (*R. canadensis*) occur in the late Eocene (37.2–33.9 Ma). The only other species of *Rhinophrynus* (*R. dorsalis*) does not appear until the Pleistocene (~0.12 Ma). The hiatus of occurrences of *Rhinophrynus* in the fossil record may highlight preservation or collection biases, as faunal studies of North America tend to focus on mammals and megafaunas.

At the Fitterer Ranch locality in North Dakota (Oligocene, 34.0–32.0 Ma), a single, left *Rhinophrynus* ilium was found (*R. sp.*). It is missing part of the shaft and part of the ventral prominence. Among Anura and even within Rhinophrynidae, the ilia of *Rhinophrynus* are distinct. The ilium from Fitterer Ranch appears to have an intermediate morphology between *R. canadensis* and *R. dorsalis*. Although all species have robust ilia, the ilia of *R. canadensis* have shorter, more rounded dorsal ornamentation compared to the condition in *R. dorsalis* and *R. sp.* *Rhinophrynus sp.* has a larger acetabular fossa than *R. dorsalis*, and its dorsal ornamentation curves more acutely than *R. dorsalis*.

Based on a principle components analysis of five key measurements, *Rhinophrynus sp.* differs from both *R. dorsalis* and *R. canadensis* on all components measured; most of the variance was due to fossa/expansion length. Morphologically (based on outline morphometrics) the ilium of *R. sp.* appears most similar to *R. dorsalis*. *R. dorsalis* is known from the Pleistocene onward and only from Texas, U.S.A. to Costa Rica, while *R. canadensis* is

much closer in geologic time to the Fitterer Ranch specimen and is known from Saskatchewan, Canada. *Rhinophrynus* sp. may fill in the missing record of *Rhinophrynus* between the Eocene *R. canadensis* and the Pleistocene *R. dorsalis* as a transitional form. Transitional forms such as this help us track the ecological changes in North America during the middle to late Cenozoic. Furthermore, *Rhinophrynus* (modernly adapted to arid, subtropical zones) can show that conditions in Northern North America during the Oligocene may have been similar to modern southern North America.

## **Taphonomy & Stratigraphy**

### **BIOSTRATINOMIC ALTERATIONS OF A HADROSAUR ‘MUMMY’ SUGGEST AN UNEXPECTED PATHWAY FOR SOFT TISSUE PRESERVATION**

Drumheller, Stephanie K.<sup>1</sup>, Boyd, Clint A.<sup>2</sup>, Barnes, Becky<sup>2</sup>, Householder, Mindy<sup>3</sup>

<sup>1</sup>Earth and Planetary Sciences, University of Tennessee, Knoxville, Tennessee, U.S.A., <sup>2</sup>Fossil Resource Management Program, North Dakota Geological Survey, Bismarck, North Dakota, U.S.A., <sup>3</sup>State Historical Society of North Dakota, Bismarck, North Dakota, U.S.A.

Dinosaur ‘mummies’ present a unique preservational quandary. Soft tissue preservation is often attributed to a combination of rapid burial and sequestration from scavengers and decomposers. However, soft tissues preserved in these ‘mummies’ often exhibit evidence of desiccation, requiring a contradictory longer-term residence on a landscape prior to burial. Re-examination of a natural mummy of the hadrosaurian dinosaur *Edmontosaurus* from the Cretaceous Hell Creek Formation of North Dakota provides evidence for a different pathway for the preservation of more durable soft-tissues (e.g., skin and nails) outside of the Konservat-Lagerstätten model. Soft tissues are poorly preserved or absent on the torso of this specimen, but the tail and limbs are largely encased in well-preserved skin. Computed tomographic (CT) scans show that the skin is three-dimensionally preserved, and previous chemical analyses identified potential biomolecules, indicating that the skin itself was fossilized and rejecting the possibility of moldic preservation. In many areas the skin is tightly appressed to the underlying bones, appearing deflated and pooling adjacent to the bones owing to the lack of preservation of underlying soft tissues. Additionally, punctures and furrows, consistent with tooth and claw marks, are present on the bones and skin of the right arm and tail, contradicting hypotheses that exposure to scavengers and decomposers hinders the formation of natural mummies. The full set of taphonomic features noted in this specimen comports well with modern

forensic research showing that incomplete scavenging can actually promote mummification by compromising the body wall and providing the fluids, gases, and microbes associated with decomposition a means of escape. This decompositional pathway can result in a natural mummy with a deflated appearance even under moist, temperate conditions. Those findings are especially pertinent for interpreting this specific *Edmontosaurus* mummy, because sedimentological evidence suggests that it formed under warm, humid conditions and was buried at a slow and constant depositional rate. We propose that incomplete consumption of dinosaurian remains by predators and scavengers can serve as a pathway to extend the persistence of more durable soft tissues on a landscape until burial, helping to explain the seeming over-representation of dinosaurian mummies and fossilized skin in the rock record.

**Funding Sources** National Geographic Society and the North Dakota Geological Survey.

## **Dinosaur Systematics, Diversity & Ecology**

### **HISTOLOGICAL ANALYSIS OF PROSAUROLOPHUS MAXIMUS (HADROSAURIDAE, SAUROLOPHINAE) FROM SOUTHERN ALBERTA, CANADA REVEALS EVIDENCE FOR AN EXTENDED JUVENILE GROWTH PERIOD, AND THE EVOLUTION OF GIGANTISM WITHIN A LATE CAMPANIAN (LATE CRETACEOUS) HADROSAURID LINEAGE**

Drysdale, Eamon T.<sup>1</sup>, Chiba, Kentaro<sup>4</sup>, Therrien, François<sup>2</sup>, Erickson, Gregory M.<sup>3</sup>, Zelenitsky, Darla K.<sup>1</sup>

<sup>1</sup>Department of Geoscience, University of Calgary, Calgary, Alberta, Canada, <sup>2</sup>Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada, <sup>3</sup>Department of Biological Sciences, Florida State University, Tallahassee, Florida, U.S.A., <sup>4</sup>Department of Biosphere and Geosphere Sciences, Okayama University of Science, Okayama, Japan

Hadrosaurs, or duck-billed dinosaurs, are a clade commonly used to study dinosaur ontogeny. While most studies of hadrosaur ontogeny have focused on the morphologic changes that occur during growth, recent studies have attempted to reconstruct growth curves in several hadrosaur species, allowing for estimations of hadrosaur growth rates. The initial hadrosaur growth period consists of an extremely rapid growth rate that slows upon reaching an inflection point. This inflection point is used to infer sexual maturity, and occurs around age two to three. However, these estimates have not been compared to other indicators of sexual maturity, such as crest development. Additionally, relatively few hadrosaur species have been examined, limiting our understanding of

hadrosaur ontogenetic diversity, especially in the largest hadrosaur species.

In this study, we examine bone histology of the hadrosaurine *Prosaurolophus maximus*, a large hadrosaur known from the Dinosaur Park Formation of southern Alberta. Histological thin sections were produced from tibiae of four specimens, which range from 45 to 88 percent the taxon's largest known size. These sections were used to identify growth marks and determine the biological age of each individual specimen. Using these growth marks, we reconstructed a growth curve for *P. maximus* and compared it to those of other hadrosaur species to examine possible taxonomic variability in growth rates.

The four examined specimens range from age three to seven, while specimens with developing or developed crest range from age four and seven. All the examined specimens lack an external fundamental system, indicating that they yet to reach skeletal maturity. Our reconstructed *P. maximus* growth curve exhibits a slower growth rate than other hadrosaurines, while the rapid growth period prior to the inflection point is extended relative to other hadrosaurines. Sexual maturity is estimated to have occurred between the ages of four and five, an older age than estimated for other hadrosaur species.

The skeletal immaturity of the largest specimen examined in this study suggests that *P. maximus* reached a gigantic body size, like its sister taxon *Saurolophus*. Additionally, our histological data indicates that *P. maximus* reached this larger body size due to a slower, yet prolonged juvenile growth period, rather than the very rapid growth observed in other hadrosaur species, which may be representative of the growth pattern of larger hadrosaurs.

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## Quantitative Methods

### PLACING PROBABILITIES ON WHETHER A FOSSIL TAXON WAS TRULY ABSENT FROM A SITE OR HAS NOT BEEN FOUND YET

Du, Andrew<sup>1</sup>, Friedlander, Eric<sup>2</sup>, Rowan, John<sup>3</sup>, Alemseged, Zeresenay<sup>2</sup>  
<sup>1</sup>Colorado State University, Fort Collins, Colorado, U.S.A., <sup>2</sup>The University of Chicago, Chicago, Illinois, U.S.A., <sup>3</sup>University of Massachusetts, Amherst, Massachusetts, U.S.A.

Knowing the fossil sites at which a taxon occurs (or does not occur) is a necessary first step in reconstructing its paleobiogeography (e.g., endemism, dispersal ability, habitat preference). While proving a taxon's presence at a site requires only the discovery of a single specimen, demonstrating its absence is a far more challenging issue.

If the taxon has not been discovered at a site after a certain number of specimens have been recovered, this result is consistent with two mutually exclusive outcomes: (1) the taxon never occupied the site, or (2) the taxon occupied the site but has not been sampled yet. To distinguish between these possibilities, we developed a mixture model to explicitly model these two categories as separate mixture components. We use the expectation maximization algorithm to parameterize the model and compute the posterior probability that the first mixture component is true (i.e., the taxon was truly absent) given the data (i.e., the taxon is not recovered after sampling a certain number of specimens) and estimated parameter values. We demonstrate the utility of this method by applying it to the hominin genus *Paranthropus* from eastern Africa (2.7–1.2 Ma). Our results show that probabilities of true *Paranthropus* absence at sites where the genus is currently not found range from 0.49 to 0.92 (median = 0.70). The low probabilities for some sites indicate that these are not sampled well enough to confidently infer *Paranthropus* absence, thereby also identifying high-priority sites that have the best chance of yielding *Paranthropus* remains in the future. Our method also quantifies the number of recovered specimens needed to achieve a certain level of confidence that *Paranthropus* was truly absent from a given site, thus establishing a formalized criterion for determining taxon absence.

## Macroecology & Macroevolution

### ECOLOGICAL NICHE MODELING SUPPORTS FOSSIL EVIDENCE FOR AN APPALACHIAN POPULATION OF NEOCHORISTODERES

Dudgeon, Thomas W.<sup>1</sup>, Landry, Zoe<sup>2</sup>, Callahan, Wayne<sup>3</sup>, Mehling, Carl<sup>4</sup>, Ballwanz, Steven<sup>3</sup>

<sup>1</sup>Earth Sciences, Carleton University, Ottawa, Ontario, Canada, <sup>2</sup>Biology, Carleton University, Ottawa, Ontario, Canada, <sup>3</sup>New Jersey State Museum, Trenton, New Jersey, U.S.A., <sup>4</sup>American Museum of Natural History, New York, New York, U.S.A.

Four neochoristoderan vertebral centra were recently recovered from the latest Cretaceous deposits of New Jersey, and represent the first evidence of neochoristoderes from the Atlantic Coastal Plain. Three of these vertebrae were recovered from the basal lag of the Navesink Formation (uppermost Campanian to the lowermost Maastrichtian) in the area of Holmdel, and the fourth was recovered from the Marshalltown sequence (upper Campanian) of Ellisdale. These vertebrae suggest that a population of neochoristoderes was present in Appalachia during the latest Cretaceous, but they raise the question of why neochoristoderes appear to have been so rare here, while they were common in coeval Laramidia. To

investigate this, we implemented ecological niche modeling (ENM) to predict the ideal habitat range of *Champsosaurus*, the only neochoristodere known from the Late Cretaceous of North America. Maastrichtian occurrence data for *Champsosaurus* were paleorotated and run through the ENM algorithm MaxEnt (Maximum Entropy), with Maastrichtian near-surface air temperatures during the warmest and coldest seasons, precipitation during the wettest and driest seasons, and air temperature standard deviation as predictor variables. These climate data were output from the fully coupled GCM HadCM3L Atmospheric–Ocean General Circulation Model, and kindly made available by A. Farnsworth. The model was trained in areas of Maastrichtian sedimentary outcrop, and projected to the extent of North America to predict the ideal habitat range. This analysis suggests that the ideal habitat range for *Champsosaurus* in Appalachia was restricted further North than NJ, meaning that these vertebrae may represent the southern margin of a potentially large population of neochoristoderes in Appalachia. This makes it unsurprising that neochoristoderes appear to be so rare in the Appalachian fossil record, given that their ideal habitat likely extended further North where latest Cretaceous sediments are not preserved. If accurate, this model suggests that *Champsosaurus* fossils are to be expected in low frequencies in NJ, but further sampling is encouraged to elucidate the range of this taxon in North America.

### Fishes & Chondrichthyans: Evolution & Distribution

#### THE HOLOCEPHALIAN FAUNAS OF THE LATE JURASSIC LITHOGRAPHIC LIMESTONES OF SW GERMANY

Duffin, Christopher J.<sup>1</sup>, Ward, David J.<sup>1</sup>, Lauer, Bruce<sup>2</sup>, Lauer, Rene<sup>2</sup>

<sup>1</sup>Earth Sciences, Natural History Museum, London, U.K.,  
<sup>2</sup>Lauer Foundation for Paleontology, Science and Education, Wheaton, Illinois, U.S.A.

The lithographic limestone succession in SW Germany includes the lagerstätten of Nusplingen (Nusplingen Formation, Ulmense Subzone, upper Kimmeridgian) and the Solnhofen areas (Altmühltal Formation, *Hybonotum* Zone, Tithonian). The holocephalian faunas from these two centres include isolated tooth plates and dorsal fin spines, as well as minimally disarticulated holomorphic specimens showing high fidelity preservation; members of both the Myriacanthiformes and Chimaeriformes are represented. The Solnhofen area has yielded rare examples of the youngest recorded myriacanthoid, *Chimaeropsis paradoxa*, characterised by the presence of tuberculated fin spines, stellate scales in the reduced squamation, a typical myriacanthid crushing dentition and four pairs of tuberculated dermal plates in the head region (LF 2317). At

around 730 mm in length, members of this taxon are much larger than the ‘rhinochimaerid’, *Elasmodectes avitus*, which reached a maximum length of around 500 mm. *Elasmodectes* had a sectorial dentition, a short, straight and unornamented dorsal fin spine, and a diphycercal tail (LF 2322). Callorhynchids are represented by *Ischyodus quenstedti*, which grew up to 1.5 m long and possessed a long, weakly curved and unornamented dorsal fin spine, crushing dentition and a heterocercal tail (LF 1369). Two partial specimens of an un-named callorhynchid, clearly not juveniles of *I. quenstedti*, have been described from Nusplingen (SMNS 80144/22 and 95823/4). Furthermore, rare examples of callorhynchid egg cases have been recorded from the Solnhofen area (NHMUK PX Z.183). The Plattenkalk holocephalian fauna is clearly moderately diverse with representative taxa enjoying a range of feeding strategies.

### Permo-Triassic Tetrapods

#### RECOGNISING JUVENILES: AN ONTOGENETIC STUDY OF THE ENIGMATIC BIARMOUSUCHIA (SYNAPSIDA: THERAPSIDA) USING CT SCANNING.

Duhamel, Alienor<sup>1</sup>, Benoit, Julien<sup>1</sup>, Rubidge, Bruce S.<sup>1</sup>, Day, Michael O.<sup>2</sup>

<sup>1</sup>Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa, <sup>2</sup>Natural History Museum, London, U.K.

Non-mammalian Therapsida is a paraphyletic group of Permian-Jurassic amniotes closely related to mammals and comprises five clades: Biarmosuchia, Dinocephalia, Dicynodontia, Therocephalia, and Cynodontia. The Biarmosuchia is generally considered to be the most basal, and thus an important group when trying to understand the distant origins of the Therapsida. Apart from the Eutheriodontia (Therocephalia, Cynodontia), ontogenetic development of most therapsids is poorly understood. Most biarmosuchian genera are monospecific and are represented by only one cranial specimen, which limits the possibility of ontogenetic studies. Here, for the first time, two new juvenile biarmosuchian skulls are described from the late Permian of South Africa. Using micro-CT tomography these skulls are compared to known juvenile specimens and their corresponding adults. The study demonstrates that certain characters (eg. relatively large orbits, open cranial sutures, and comparatively less well-compartmented braincase and bony labyrinths) are indicative of juvenile biarmosuchians. These juvenile specimens also manifest multiple centres of ossification within the parietal and preparietal bones. Detailed analysis of the upper dentition of the two juvenile specimens reveals several replacement teeth and the presence of a double-

canine, a replacement pattern previously observed in ‘pelycosaurs’ and derived therapsids.

In comparison, a CT study of the holotype of *Lemurosaurus pricei* (BP/1/816), which comprises a small skull believed to represent a juvenile, evidences no sign of juvenility. This suggests that the much larger skull (NMQR 1702) previously referred to *L. pricei*, is not an adult of that species but rather represents a new biarmosuchian taxon.

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### **Colbert Poster Prize/Dinosaur Systematics, Diversity & Ecology**

#### **ONTOGENETIC ANALYSIS OF THE SKULL OF THE EARLY-DIVERGING IGUANODONTIAN *DRYOSAURUS ELDERAE* (DINOSAURIA: ORNITHOPODA) FROM THE UPPER JURASSIC MORRISON FORMATION OF UTAH: NEW INSIGHTS FROM MICROCOMPUTED TOMOGRAPHY**

Dunfee, Daniel R.<sup>1</sup>, Ridgely, Ryan C.<sup>2</sup>, Lamanna, Matthew C.<sup>3</sup>, Witmer, Lawrence<sup>2</sup>

<sup>1</sup>Honors Tutorial College, Geological Sciences, Ohio University, Athens, Ohio, U.S.A., <sup>2</sup>Biomedical Sciences, Ohio University Heritage College of Osteopathic Medicine, Athens, Ohio, U.S.A., <sup>3</sup>Section of Vertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.

New analysis of skulls of the early-diverging iguanodontian ornithopod dinosaur *Dryosaurus elderae* from the Upper Jurassic Morrison Formation of Dinosaur National Monument (Utah) using computed tomography (CT scanning) has yielded results that provide the opportunity to explore ontogenetic changes within the species. The three skulls referred to *D. elderae* differ in size, with that of CM 11340 being about 40% the length of that of CM 3392, such that the former specimen is often regarded as a ‘baby’ and the latter as an adult or subadult; CM 87688, an isolated basicranium, is the largest. Previous analyses pointed to clear signs of juvenility in CM 11340, such as small size, large orbits, short face, and large neurocranium. Our studies confirm those findings, but CT scanning provides new information about internal aspects of cephalic anatomy such as tooth-position counts, scleral rings, brain endocast, and the presence of undescribed bones. These new data provide a more detailed view of the ontogenetic trajectories of morphological characters. CM 11340 and CM 87688 were microCT scanned at 25 µm, whereas CM 3392 was scanned at 300 µm. The CT data were analyzed using Amira-Avizo, using both watershed and manual segmentation. New ontogenetic data include,

when comparing CM 11340 to CM 3392, an increase in maxillary and dentary tooth positions from 12 to 14, a 6% decrease in the ratio of orbit diameter to skull length, and a 13% decrease in the ratio of orbit diameter to humerus length. In addition, analysis of CM 11340 has yielded the previously undescribed right postorbital embedded in matrix as well as the presence of vascular canals on the skull roof. Analysis of the adult CM 3392 confirms previous tooth-position counts, and microCT analysis of CM 11340 provides insight on tooth-position counts unavailable in prior studies. A surprising finding was the presence of a theropod-like caudal tympanic recess in all three specimens. Comparison to a juvenile individual of the Tanzanian dryosaurid *Dysalotosaurus lettowvorbecki* reveals that the juvenile CM 11340 had approximately three more maxillary teeth. The presence of vascular canals on the endocranium roof indicates that the brain entirely filled the neurocranium of juvenile *D. elderae*. Results to date indicate the following ontogenetic changes in *D. elderae*: an increase in the number of tooth positions, a decrease in the relative size of the orbit, and changes in the brain endocast.

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### **Symposium: Paleoneurology**

#### **DEVELOPMENTAL CONSTRAINTS AND FUNCTIONAL INNOVATIONS DURING THE EVOLUTION OF THE SARCOPTERYGIAN HEAD**

Dutel, Hugo<sup>1</sup>, Fabbri, Matteo<sup>3</sup>, Navalón, Guillermo<sup>4</sup>, Porro, Laura B.<sup>5</sup>, Paredes, Daniel S.<sup>3</sup>, Watson, Peter J.<sup>2</sup>, Bhullar, Bhart-Anjan S.<sup>3</sup>, Fagan, Michael<sup>2</sup>, Rayfield, Emily<sup>6</sup>

<sup>1</sup>School of Earth Sciences/Department of Engineering, University of Bristol/University of Hull, Bristol, U.K., <sup>2</sup>Department of Engineering, University of Hull, Hull, U.K., <sup>3</sup>Department of Geology and Geophysics, Yale University, New Haven, Connecticut, U.S.A., <sup>4</sup>Department of Earth Sciences, University of Oxford, Oxford, U.K., <sup>5</sup>Centre for Integrative Anatomy, Cell and Development Biology, University College London, London, U.K., <sup>6</sup>School of Earth Sciences, University of Bristol, Bristol, U.K.

The head is a complex system that underwent dramatic changes during the evolution of sarcopterygians, including tetrapods. Although the phenotypic transformations of the head during sarcopterygian evolution are well-documented in the fossil record, the mechanisms that drive these changes are poorly understood. The brain and other soft tissues play a central role in the formation of the vertebrate head, and in determining its final phenotype in adults.

Understanding the interplay between the brain, the cranium, and other adjacent soft tissues, such as muscles, is therefore critical to shed light on the mechanisms underpinning cranial diversity and interpreting major evolutionary transitions. Developmental data are pivotal to achieve this goal, but the information available for non-tetrapod sarcopterygians have remained scarce. Here, we first present recently published data on the development of the extant coelacanth *Latimeria chalumnae*. In this species, the brain and the surrounding cranial elements become decoupled during development, and changes in the neurocranium are associated with an extreme reduction in the size of the brain relative to the endocranial cavity. We then compare both qualitatively and quantitatively the development of *L. chalumnae* with ontogenetic series of five species spanning the fish-tetrapod transition using volumetric data, 3D geometric morphometrics and phylogenetic comparative methods. These observations allow us to discuss the evolution of the developmental mechanisms underpinning the integration between the brain and neurocranium within a phylogenetic framework. A strong integration between the brain and cranium likely appears to be a derived condition in tetrapods. We finally address how extrinsic factors linked to functional demands might have impacted brain and cranial evolution in sarcopterygians. Using Multibody Dynamics Analysis and Finite Element Analysis, we simulated the feeding mechanics of the skull of *L. chalumnae* and calculated the stress in the cranium and brain caused by the feeding loads. We suggest that the evolution of a functional intracranial joint in coelacanths, and potentially other sarcopterygian fish, might have imposed a major constraint on the allometry of the brain. Our results shed new light on the evolution of the form and function of the head during sarcopterygian evolution and highlight the importance of an integrative, cross-disciplinary approach for our understanding of phenotypic evolution.

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### **Symposium: Paleoneurology**

#### **AN AVIAN CASE STUDY OF INFERRING NEUROANATOMY AND POTENTIAL FUNCTIONAL CAPABILITIES FROM ENDOCAST STRUCTURES**

Early, Catherine M.  
Florida Museum of Natural History, University of Florida,  
Gainesville, Florida, U.S.A.

In the absence of brains, endocasts provide the most direct source of information about neuroanatomy. As a result, paleoneurologists often rely on endocasts and the Principle of Proper Mass to make inferences about behavior and functional capabilities in extinct animals. Inferences are only as strong as the assumptions on which they are based, and a major assumption in studies that infer behavior from endocasts is that endocasts are a faithful representation of the size and shape of brains. This is generally true, especially in highly encephalized clades like mammals and birds. However, unlike in mammals, the number of neuroanatomical traits visible on bird endocasts is limited because avian brain organization generally results in a smooth surface. Still, the Wulst and optic lobe are two discrete endocast structures that do appear consistently on avian brain endocasts. Their underlying brain structures, the hyperpallium and optic tectum, respectively, play important roles in visual pathways of birds. Accordingly, paleontologists have inferred visual capabilities in extinct birds based on the size of their Wulsts and optic lobes. I tested the strength of these inferences by quantifying the relationship between the surface area of the Wulsts and optic lobes and the volume of the hyperpallia and optic tecta. I found a strong, significant relationship between the sizes of the endocast structures and their corresponding brain regions, supporting the use of the relative size of the Wulst and optic lobe to infer certain functional capabilities or behavioral traits. I combined the relationship between the sizes of the endocast structures and brain regions with recently published quantitative methods to predict hyperpallia and optic tecta volumes of a few extinct birds. These methods also allowed me to test if any of the studied extinct birds differed significantly from the rest of our sample in terms of Wulst or optic lobe surface area and hyperpallium or optic tectum volume. My results indicate that none of the studied extinct birds differed significantly from sampled extant birds in terms of Wulst or hyperpallium size. Interestingly, a species of moa (*Dinornis robustus*) had a significantly smaller optic lobe and optic tectum than the rest of the sample. The framework I used could be applied to endocast structures of other highly encephalized groups, as well as in clades where only a few isolated structures are visible on the endocast.

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### **Mesozoic & Early Cenozoic Mammalian Evolution**

#### **A NEW, TINY, LATE CRETACEOUS GYPSONICTOPID (MAMMALIA, EUTHERIA) FROM THE NORTH SLOPE OF ALASKA**

Eberle, Jaelyn J.<sup>1</sup>, Clemens, William A.<sup>2</sup>, Erickson, Gregory M.<sup>3</sup>, Druckenmiller, Patrick S.<sup>4</sup>

<sup>1</sup>Museum of Natural History and Department of Geological Sciences, University of Colorado, Boulder, Colorado, U.S.A., <sup>2</sup>University of California Museum of Paleontology, Berkeley, California, U.S.A., <sup>3</sup>Florida State University, Tallahassee, Florida, U.S.A., <sup>4</sup>University of Alaska Museum, Fairbanks, Alaska, U.S.A.

Terrestrial faunas along the western coast of the Late Cretaceous Western Interior Seaway show latitudinal variation in composition. A new gypsonictopid from the Prince Creek Formation of northern Alaska adds to the evidence for endemism of the Arctic, high paleolatitude (80° to 85° N) fauna that prior studies have suggested based on the dinosaurian fauna and a recently described metatherian. Four species of *Gypsonictops*, *G. illuminatus*, *G. hypoconus*, *G. clemensi*, and *G. lewisi* are recognized from Late Cretaceous localities at lower paleolatitudes. With molars just over half the size of *G. clemensi*, approximately two-thirds the size of *G. illuminatus*, and three-quarters the size of *G. hypoconus* and *G. lewisi*, the Alaskan species is the smallest of any gypsonictopid yet discovered. Upper molars of the Alaskan gypsonictopid differ from those of *G. hypoconus* in having a more lingual paracone and metacone as well as a larger, more labial parastyle. Unworn lower molars of the Alaskan gypsonictopid differ from *G. hypoconus* in that the metaconid is usually taller than the protoconid, and the hypoconulid is slightly closer to the entoconid than to the hypoconid. As in P3s of *G. hypoconus* and *G. illuminatus*, but unlike P3s of *G. lewisi* and *G. clemensi*, the P3 of the Alaskan gypsonictopid bears a metacone. The Alaskan species is the only known gypsonictopid from above the Arctic Circle, and extends the geographic range of the clade by over 2,000 km. Furthermore, the discovery of deciduous premolars of the Alaskan gypsonictopid suggests, not unexpectedly, that this tiny eutherian was a year-round inhabitant on the North Slope of Alaska, as has been hypothesized for the dinosaurs on the basis of perinatal remains. As the first documented eutherian from the Prince Creek Formation, the Alaskan gypsonictopid helps corroborate the existence of a distinctive northern high-latitude vertebrate faunal province during Late Cretaceous time.

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## Mammalian Skeletal Morphology

### SHAPE GRADIENT ACROSS THE LUMBAR VERTEBRAE REFLECTS LOCOMOTOR STYLE IN MAMMALS

Edie, Riley A., Kort, Anne E., Polly, P. David  
Earth and Atmospheric Sciences, Indiana University,  
Linden, Indiana, U.S.A.

The locomotive adaptations that make a mammal a successful hunter are reflected in the morphology of its skeleton, such as cursorial adaptations in the limbs. Although the lumbar section of the vertebral column forms an important part of the locomotor apparatus by contributing dorsiflexion to the stride, its ecomorphology is comparatively less studied than the limbs. Carnivores employ widely disparate methods used in tracking, engaging, and killing their prey. Ambush predators stalk and strike when prey is close, while pursuit predators maintain speed to follow prey over long distances. We hypothesized that pursuit and ambush predators would show shape differences in individual lumbar vertebrae, as well as differences in patterns of shape change across the lumbar column reflective of functional differences. We chose two specimens: an ambush predator, a cougar (*Puma concolor*; WRAZL 0110164), and a pursuit predator, a grey wolf (*Canis lupus*; WRAZL 9910092). We scanned the seven individual lumbar vertebrae from each specimen. 3D landmarking was performed on all 14 scans using Slicer 4.10.2. All landmarks were imported into Mathematica, where we superimposed the data with a Procrustes analysis, performed a principal components analysis (PCA) on the superimposed landmarks, and measured the variance among the lumbar in each specimen. PC1 explained over half of the shape variance and generally separated cranial from caudal lumbar. PC2 explained 22% of the shape variance and differentiated the sets of vertebrae by species. The cougar shows elongate centra and longer processes relative to the wolf. The disparity within each specimen, calculated as a summed variance, was found to be 0.0246 for the cougar and 0.0177 for the wolf, indicating that the cougar possessed more variation in the shape of its lumbar vertebrae. The larger variation within the cougar's lumbar vertebrae may come from increased process length in the posterior vertebrae, which adds leverage for quick movement in jumping or sprinting. Alternatively, the more consistent shape in the wolf vertebrae may limit dorsiflexion and increase efficiency during longer chases. These results show that both individual lumbar shape and shape gradient of lumbar from anterior to posterior have implications for locomotor function. By applying this information to the fossil record, we could interpret the evolution of lumbar and locomotion in mammals.

## Quantitative Methods

### INFLUENCE OF DIFFERENT ACID TREATMENTS ON THE RADIOCARBON CONTENT SPECTRUM

## OF BONE MATERIAL AS DETERMINED BY RPO/ACCELERATOR MASS SPECTROMETRY

Ehon, Ehi  
Imperial College, Lagos, Nigeria

In practice, obtaining radiocarbon ( $^{14}\text{C}$ ) composition of organic matter (OM) in sediments requires first removing inorganic carbon (IC) by acid-treatment. Two common treatments are acid rinsing and fumigation. Resulting  $^{14}\text{C}$  content obtained by different methods can differ, but underlying causes of these differences remain elusive. To assess the influence of different acid-treatments on  $^{14}\text{C}$  content of sedimentary OM, we examine the variability in  $^{14}\text{C}$  content for a range of marine and river sediments. By comparing results for unacidified and acidified sediments [HCl rinsing (RinseHCl) and HCl fumigation (FumeHCl)], we demonstrate that the two acid-treatments can affect  $^{14}\text{C}$  content differentially. Our findings suggest that, for low-carbonate samples, RinseHCl affects the Fm values due to loss of young labile organic carbon (OC). FumeHCl makes the Fm values for labile OC decrease, leaving the residual OC older. High-carbonate samples can lose relatively old organic components during RinseHCl, causing the Fm values of remaining OC to increase. FumeHCl can remove thermally labile, usually young, OC and reduce the Fm values. We suggest three factors should be taken into account when using acid to remove carbonate from sediments: IC abundance, proportions of labile and refractory OC, and environmental matrix.

### Fishes & Chondrichthyans: Evolution & Distribution

#### THE CENOZOIC RECORD OF THE OTODONTID SHARKS (LAMNIFORMES, OTODONTIDAE) IN NEW JERSEY, U.S.A.

Ehret, Dana J., Ballwanz, Steve  
Natural History, New Jersey State Museum, Trenton, New Jersey, U.S.A.

The Otodontidae, or megatoothed sharks, includes some of the largest chondrichthyan species to ever live. Their fossil record extends from the late Cretaceous through the Pliocene, with specimens recovered from all continents. Along the western Atlantic seaboard of the U.S.A., Cenozoic otodontid fossils are well-known to researchers and collectors from sites in Florida, Georgia, South Carolina, North Carolina, Virginia and Maryland. However, little attention has been paid to records farther north. Here we report on the occurrence of the *Otodus*, *Carcharocles* and *Parotodus* from New Jersey. The *Otodus* lineage is well-represented in the fossil record of the state and includes: *Otodus obliquus*, *Otodus aksuaticus*, *Carcharocles auriculatus*, *Carcharocles chubutensis* and

*Carcharocles megalodon* from Paleocene, Eocene and Miocene deposits, respectively. Outcrops in the central and southern portions of the state where specimens have been recovered include the Paleocene Hornerstown and Vincentown formations, early to mid-Eocene Manasquan and Shark River formations and the early Miocene Kirkwood Formation. Otodontid fossils from New Jersey record the evolutionary shift from the smooth-edged *O. obliquus* to the semi-serrated *O. aksuaticus* to the fully serrated *C. auriculatus* across the late-Paleocene through mid-Eocene. Rare *C. megalodon* teeth from New Jersey were recovered *ex situ* and cannot be confidently referred to specific geologic units. The genus *Parotodus* is provisionally referred to the Otodontidae, thus we have included it in this study. *Parotodus benedeni* is uncommon in New Jersey but is present in the Kirkwood Formation and has been recovered at a few localities in central New Jersey. Otodontid specimens from New Jersey add to the fossil record of the family and provide further evidence for the chronospecies-hypothesis for the *Otodus* lineage.

### Dinosaur Systematics, Diversity & Ecology

#### FIRST RECORD OF THE REPETITIVE STRAIN INJURY FIBULAR TENDINITIS IN A DUCKBILLED DINOSAUR

Ekhtiari, Seper<sup>1</sup>, Popovic, Snezana<sup>2</sup>, Nagesan, Ramon<sup>3</sup>, Bertozzo, Filippo<sup>4</sup>, Tanke, Darren H.<sup>5</sup>, Crowther, Mark<sup>2</sup>, Evans, David<sup>6</sup>

<sup>1</sup>Surgery, McMaster University, Hamilton, Ontario, Canada, <sup>2</sup>Pathology and Molecular Medicine, McMaster University, Hamilton, Ontario, Canada, <sup>3</sup>Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan, U.S.A., <sup>4</sup>School of Natural and Built Environment, Queen's University Belfast, Belfast, Northern Ireland, U.K., <sup>5</sup>Royal Tyrrell Museum, Drumheller, Alberta, Canada, <sup>6</sup>Vertebrate Palaeontology, Royal Ontario Museum, Toronto, Ontario, Canada

The fibular (peroneal) muscles form the lateral compartment of the lower leg, passing around the ankle joint and inserting on the foot. In humans, fibular tendinitis is a common pathology, occurring secondarily to trauma, instability, or overuse. Here we describe an unambiguous case of fibularis brevis tendinitis in the distal fibula of an indeterminate hadrosaurid dinosaur from the late Campanian (76–74 Ma) Dinosaur Park Formation of Alberta, Canada.

The specimen described in this report (TMP 1994.172.0114) is the distal third of an adult hadrosaurid fibula from the collection of the Royal Tyrrell Museum, Drumheller, Alberta, Canada. Gross examination of the specimen was performed by vertebrate paleontologists and clinical experts in human pathology. A three-dimensional photogrammetric model of the specimen allowed the

pathology to be easily visualized and inspected by the team. The specimen will also be compared to a human fibula with clinically and radiographically confirmed fibular tendonitis.

Gross examination of the dinosaur specimen reveals an ovoid region of rugose tumor-like bony protuberans approximately 100 mm from the normal, distal end of the bone. The rugose region measures approximately 50×30mm. This area on the lateral side of the fibula is where the origin of *m. fibularis brevis* has been reconstructed in other non-avian dinosaurs based on the extant phylogenetic bracket approach, but typically does not leave a distinct scar in hadrosaurids. Microscopic examination will be performed and is expected to reveal changes which mimic those seen in human calcific tendinitis or fibro-osseous metaplasia within fibrocollagenous tissue related to secondary changes due to injury and degenerative changes within fibroconnective tissue of a tendon or ligaments.

The gross and pathohistologic appearance of the hadrosaurid dinosaur fibula is similar to fibular tendinitis in humans, despite the lack of preserved soft tissue structures in the former. We conclude, to a similar degree of certitude as would be possible in an extant animal, that this dinosaur bone demonstrates fibular tendonitis. Repetitive strain injuries have also been reported in the digits of ceratopsid dinosaurs, but have not yet to our knowledge been reported in duck-billed dinosaurs, and this pathology constrains the origin of the *fibularis brevis* muscle, which typically does not leave a strong scar in dinosaurs.

## Bird Biology & Evolution

### THE OLDEST FOSSIL PELICAN, FROM THE EOCENE OF WADI AL HITAN, EGYPT

El Adli, Joseph J.<sup>1</sup>, Wilson Mantilla, Jeffrey A.<sup>2</sup>, Antar, Mohamed S.<sup>3</sup>, Gingerich, Philip D.<sup>2</sup>

<sup>1</sup>Paleontology, Statistical Research, Inc., Redlands, California, U.S.A., <sup>2</sup>Museum of Paleontology, University of Michigan, Ann Arbor, Michigan, U.S.A., <sup>3</sup>Wadi Al-Hitan World Heritage Site, Egyptian Environmental Affairs Agency, Fayum, Egypt

The known fossil record of pelicans (Pelecanidae) extends to the early Oligocene (Rupelian) at present, based on a single partial skeleton from southeastern France. This specimen, assigned to *Pelecanus* sp., is the only definitive pelecavid described from the Paleogene, highlighting the scarcity of early pelican material. Here we describe a new pelecavid from the Wadi Al-Hitan World Heritage Site of northern Egypt that pushes back the earliest record of pelicans into the late Eocene and provides insight into the morphology of Paleogene pelecavids. This specimen, a nearly complete and well-preserved right tibiotarsus, bears

a striking resemblance to extant *Pelecanus*, though sufficient differences exist to support consideration as a separate taxon. Phylogenetic analysis of 186 taxa (151 ingroup neornithine taxa and 35 outgroup taxa) using 2,954 equally-weighted characters similarly recover a sister-taxon relationship with *Pelecanus*. The Wadi Al-Hitan pelecavid was discovered in a marine sandstone in the upper part of the Birket Qarun Formation on the south side of Garet Gehannam. This sandstone is situated approximately three meters above a prominent marker bed of gray-to-black gypsiferous clay that is interpreted as a maximum marine flooding surface. The Birket Qarun Formation is bracketed by the underlying Gehannam Formation and the overlying Qasr el-Sagha Formation. The Gehannam Formation is a transgressive sequence that follows the global Bartonian-Priabonian low sea stand in magnetochron C17N, while the lower Qasr el-Sagha Formation preserves the subsequent low sea stand in the Wadi Al-Hitan stratigraphic section. With these constraints, the Wadi Al-Hitan pelecavid is reliably placed within magnetochron C16N in the middle to late part of the early Priabonian Stage/Age of the late Eocene, and thus is ca. 36 Ma in age. This result extends the record of pelicans by some 6 million years. The close relationship of *Pelecanus* to *Balaeniceps* and *Scopus*, coupled with molecular phylogenetic data, indicate that *Pelecanus* emerged from Africa or southern Asia. Discovery of the oldest pelican fossil in northern African strata gives further support to this hypothesis. Furthermore, the apparent consignment of the oldest fossil pelecavids, scopids, and balaeniceptids to the African continent, implies that the Pelecanidae + Scopidae + Balaeniceptidae clade also originated in Africa.

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## Cenozoic Herpetology

### NEW RECORDS OF LEGLESS SQUAMATES FROM THE EARLIEST UPPER EOCENE DEPOSITS OF THE FAYUM DEPRESSION, EGYPT

El-Hares, Marwa A.<sup>2</sup>, Zaher, Hussam<sup>6</sup>, EL-Mekkawy, Desouki<sup>2</sup>, El-Sayed, Sanaa<sup>3</sup>, Seiffert, Erik<sup>4</sup>, Antar, Mohamed S.<sup>5</sup>, Sallam, Hesham<sup>1</sup>

<sup>1</sup>School of Sciences and Engineering, American University in Cairo, New Cairo, Egypt, <sup>2</sup>Department of Zoology, Alexandria University, Alexandria, Egypt, <sup>3</sup>Department of Geology, Mansoura University, Mansoura, Egypt, <sup>4</sup>Department of Integrative Anatomical Sciences, University of Southern California, Los Angeles, California, U.S.A., <sup>5</sup>Geology and Paleontology Department, Egyptian Environmental Affairs Agency,

Maadi, Egypt, <sup>6</sup>Museum of Zoology, University of Sao Paulo, Sao Paulo, Brazil

The Eocene epoch was a key period for the diversification of squamates worldwide. However, little is known about their early evolution in Africa due to the scarcity of the fossil record. Some of the most important Eocene vertebrate assemblages in Africa are known from the Fayum Depression of Egypt, but only a few lizards and snakes have been reported from these deposits. Here we report on the first Paleogene record of the clade Amphisbaenia in Egypt, from the earliest late Eocene (~37 Ma) Birket Qarun Locality 2 (BQ-2). It corresponds to a mid-trunk vertebra characterized by a depressed centrum with a flattened base, hemispherical synapophyses, and absence of a neural spine. Additional material from BQ-2 includes seven gracile vertebrae attributed to colubroidean snakes which are characterized by long blade-like neural spines invading the zygosphenal tectum, paradiapophyses distinctly divided into parapophyseal and diapophyseal portions, and a narrow and long centrum with a well-marked subcentral ridge. One trunk vertebra resembles those of early Eocene *Procerophis* from India in being very elongate, with compressed prezygapophyseal buttresses forming a vertical ridge, anteriorly directed prezygapophyseal articular facets, and a slightly depressed cotyle. Unfortunately, the presence of anteriorly directed finger-like prezygapophysial processes, also characteristic of *Procerophis*, cannot be ascertained due to the worn condition of the prezygapophysial tips. However, the strongly anteriorly directed prezygapophysial facets suggest that the prezygapophyses retain anteriorly directed prezygapophysial processes. The remaining colubroidean vertebrae are placed as cf. *Thaumastophis* (early Eocene of India), and are characterized by well-developed prezygapophysial processes that are compressed anteroposteriorly below the articular facets, and the presence of parazygosphenal foramina (though not in all the vertebrae). Similarities in mid-trunk vertebral morphology between cf. *Thaumastophis* and BQ-2 *Renenutet* suggest a close affinity between them. The presence of these two taxa in the Eocene of Egypt adds to the evidence for terrestrial faunal exchange between Asia and North Africa during the early/middle Eocene along the southern margin of the Tethyan Sea.

**Funding Sources** Mansoura University research grant, American University in Cairo Intramural grant, Leakey Foundation.

#### **Fishes & Chondrichthyans: Evolution & Distribution**

#### **DIVERSE MARINE FISH ASSEMBLAGES INHABITED THE PALEOTROPICS DURING THE PALEOCENE-EOCENE THERMAL MAXIMUM**

El-Sayed, Sanaa<sup>4</sup>, Friedman, Matt<sup>2</sup>, Anan, Tarek<sup>4</sup>, Faris, Mahmoud<sup>3</sup>, Sallam, Hesham<sup>1</sup>

<sup>1</sup>School of Sciences and Engineering, American University in Cairo, New Cairo, Egypt, <sup>2</sup>Department of Earth and Environmental Sciences, University of Michigan, Ann Arbor, Michigan, U.S.A., <sup>3</sup>Department of Geology, Tanta University, Tanta, Egypt, <sup>4</sup>Department of Geology, Mansoura University, Mansoura, Egypt

Global temperatures rose 5–10 °C in the early Eocene in an interval known as the Paleocene-Eocene Thermal Maximum (PETM). Different aquatic and terrestrial groups show a range of responses to environmental changes associated with the PETM, but implications for marine fishes are little explored. Here we report a diverse paleotropical fish fauna from the Dababiya Quarry Member (DQM) of the Esna Formation in the Eastern Desert of Egypt with a bearing on this question. Biostratigraphic and lithological correlation with multiple regional sections, including the Paleocene-Eocene GSSP at the nearby Dababiya site, confirm an early Eocene age (~56 Ma) for our new locality of Ras Gharib A. Dating to the PETM with a paleolatitude of ~12 degree North at the time of deposition, the Ras Gharib A fauna provides a window on marine fish diversity in the paleotropics at a time where sea surface temperatures are estimated to have substantially exceeded modern values, and approached lethal thresholds for some modern fish species. The Ras Gharib A assemblage yields an offshore fauna with more than a dozen distinct teleost taxa dominated by percomorphs. The moonfish *Mene* is the most common identifiable percomorph in the assemblage, and is joined by at least nine additional percomorph taxa. Non-percomorphs are typical of marine teleost faunas of early Eocene age, and include clupeomorphs and osteoglossids. The taxonomic composition of the Ras Gharib A fauna is consistent with other PETM or early Eocene assemblages reported from higher-latitude sites. The new Egyptian fauna, in conjunction with a few other faunas of similar age at higher latitude, suggest some consequences of the PETM for marine fishes paralleling those reported in some terrestrial vertebrates. This includes small body sizes and expanded latitudinal ranges during the PETM.

**Funding Sources** Mansoura University research grant, National Geographic Society (NGS) Young Explorer Grant (CP-023ER)-17, Fulbright Grant, Patterson Memorial Grant (SVP).

#### **Romer Prize**

#### **DO BODY SIZE CHANGES IN LOCAL REPTILE ASSEMBLAGES CORRESPOND TO LOCAL OR GLOBAL TEMPERATURES ON DEEP TIME SCALES?**

ElShafie, Sara J.  
Integrative Biology, University of California, Berkeley,  
Berkeley, California, U.S.A.

Conventional wisdom suggests that body size ought to be correlated with environmental parameters in reptiles. But relationships between climate and body size are hard to discern among different groups of extant reptiles. Is there an observable relationship between these variables in deep time? Here I test the hypothesis that body size range in local assemblages of lizards and crocodylians correlates with transitions in local or global environmental temperatures over geologic time scales. I estimated snout-vent length (SVL) for 289 lizards and 234 crocodylians from intermontane basins in the Western Interior of North America spanning time intervals in the Paleogene (66–23 million years ago), including several warming and cooling periods documented from other proxies. My results show that changes in local ambient temperature may drive overall body size changes in lizards, but not in crocodylians, over deep time scales. Large-bodied lizards are restricted to the Eocene in this geo-temporal range. Lizard SVL increased from about 200 mm during the Paleocene to over 750 mm in the early Eocene, then returned to 200 mm by the Oligocene. These body size changes in local lizard assemblages are correlated with changes in local environmental temperatures measured from published terrestrial proxies. These results reflect some recent findings that local temperature may correlate with body mass in extant lizards. In contrast to lizards, the range of maximum crocodylian SVL does not change considerably between the Paleocene and Eocene, oscillating between about 1.5 m to 2.2 m during both epochs. Crocodylian SVL is not correlated with local temperature change but does show weak correlation with global temperature change, in agreement with another recent study of global crocodylians through the Cenozoic. Minimum SVL remains consistent through the Paleogene in both groups (around 60–70 mm in lizards, 150–250 mm in crocodylians). This study adds new evidence to suggest that lizard body size may be more constrained by environmental temperature, whereas crocodylian body size may be more associated with habitat and ecology than with environmental temperature. In both cases, response to these factors seems to depend at least in part on the temporal, geographic, and taxonomic scale in question.

#### **Anatomical & Developmental Explorations of the Mammalian Skull**

#### **ESTIMATING BODY MASS IN EXTINCT THERIAN MAMMALS USING WIDTH OF THE OCCIPITAL CONDYLES**

Engelman, Russell K.

Case Western Reserve University, Chagrin Falls, Ohio,  
U.S.A.

Body mass is a trait of paramount importance to mammalian paleontologists, as it influences numerous parameters of paleoecology and evolutionary history including dietary habits, life history, physiology, and extinction risk. However, estimating body mass has proven difficult in cases where taxa have non-analogous dentitions or postcrania, few or no living relatives, are outside the range of body sizes spanned by living forms, or exhibit proportions unlike any extant mammal (e.g., the disproportionately large heads of ‘creodonts’ and other extinct groups). Body mass has traditionally been estimated by regression equations based on craniodental and long bone measurements, though pitfalls with both methods have been noted in previous studies. Occipital condyle width (OCW) offers a possible alternative to traditional metrics of body mass estimation. Due to the occiput’s role in connecting the cranium and postcranium, OCW is expected to correlate with the size of the postcranium and be highly subject to stabilizing selection. Occipital measurements have been underused in body mass estimation and in most cases have been restricted to intraordinal comparisons. I constructed a database of 22 orders and 348 species of mammals using specimens with recorded weights to investigate the correlation between OCW and body mass across Mammalia. OCW accurately predicts body mass within Theria with a higher degree of accuracy than most previous craniodental regression equations. Taxa that exhibit high error in body mass estimates typically exhibit apomorphic occiput morphologies, such as narrow, ‘pulley-like’ condyles in lagomorphs, allowing them to be identified as unsuitable for OCW-based regression a priori. Phylogenetic signal is low, except for rate shifts related to occiput specialization in several mammalian subclades. Because the relationship between OCW and body mass is consistent across Theria, it is possible to produce phylogenetically bracketed body mass estimates for wholly extinct groups. Several extinct therian mammals for which body mass estimates have been problematic (creodonts, sparassodonts, giant caviomorph rodents) are used as case studies for potential applications of OCW in body mass estimation. Creodont and sparassodont body mass estimates generally agree with previous postcranial-based estimates, whereas body masses (200–400 kg) on the low end of previous studies are supported for the giant caviomorphs *Phoberomys* and *Josephaortigasia*.

#### **Cenozoic Herpetology**

#### **BRAINCASE ANATOMY OF THE PALEOCENE CROCODYLIFORM *RHABDOGNATHUS***

Erb, Arthur  
Stony Brook University, South Setauket, New York,  
U.S.A.

Dyrosaurids, specialized marine relatives of crocodylians, are one of few archosaur lineages to survive the K-Pg extinction and present a unique combination of morphology and ecology absent in living crocodylians. Little is known about their endocranial anatomy, leaving questions about their neurosensory adaptations unaddressed. We CT scanned a well-preserved skull of *Rhabdognathus*, a Paleocene dyrosaurid from Mali. We focused on three specific internal structures: the cranial endocast; inner ear; and paratympanic sinuses. The *Rhabdognathus* endocast showed novel features including a dorsal venous system that appears to communicate with the external skull table, enlarged tympanic bullae that meet at the endocranial midline, and elongate olfactory tracts forming half the total endocast length. The tracts end in paired olfactory bulbs with complex bony projections, a unique morphology perhaps serving to increase surface area for olfaction. *Rhabdognathus* has a novel conformation of its paratympanic system. The anterior and posterior divisions of the lateral Eustachian canal meet outside the skull and a unique duct was discovered connecting the pharynx to the adductor chamber. These findings require a reinterpretation of the associated external foramina in dyrosaurids and potentially their close relatives pholidosaurids. The inner ear exhibits aspects of both *Pelagosaurus* and *Gavialis*. The common crus is spherical, as in *Gavialis*, but significantly expanded. The cochlear duct is shifted anteriorly as in *Gavialis*. The semicircular canals appear pyramidal as in *Pelagosaurus* unlike the spherical shape of crocodylians. This is the first time dyrosaurid braincase and neurosensory features have been examined using CT scans. Our work reveals novel morphologies in the ear, paratympanic sinuses, and olfactory bulb that may relate to dyrosaurid adaptation to a marine habitat.

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### **Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

#### **A MAMMOTH HYBRID FROM IDAHO: TAXONOMIC COMPARISONS AND RADIOCARBON DATING**

Erdman, Jonathan  
Geology, University of Idaho, Moscow, Idaho, U.S.A.

In the late Pleistocene to early Holocene, there were three mammoth species in North America: the Woolly,

Columbian, and the recently discovered hybrid of the two, the Jeffersonian Mammoth. When assigning mammoth species to fossilized specimens, there is uncertainty surrounding mammoth taxonomy when it is based solely on molar measurements, which display a degree of overlap between species. Recent genetic studies also provide insight into mammoth speciation, but a lack of testable genetic material prevents this method from being used on a broader scale. The purpose of this study is to:

(1) Solve the discrepancy of taxonomic assignment applied to mammoths using molar measurements. To do this, digital images and physical specimens of mammoth skulls, mandibles, molars, and tusks were examined and described according to 77 different characteristics from a mammoth specimen at the University of Idaho and published images of skulls associated with the type specimens at the Smithsonian Museum and American Museum of Natural History.

(2) Provide an absolute age of when the University of Idaho mammoth lived using radiometric dating methods. If hybridization did occur, this will provide a minimum age for when interbreeding occurred.

Woolly and Columbian mammoth characteristics were measured off of images in publications from mammoths associated with the type specimen. Jeffersonian Mammoth characteristics were measured on a University of Idaho specimen and other publications of the type specimen. The Woolly Mammoth has a larger skull that can reach up to 1/3 of its total body height. Its occipital condyles are triangular in shape, external nares even with the occipitals. The mandible displays an acute angle between the ramus and corpus, with a wide ascending ramus. An image for the skull of the Columbian Mammoth was not obtained, but the mandible displays a longer corpus and symphysis length compared to the other two taxa, with a wide ramus ascending at 90 degrees and positioned behind the lower molars. The Jeffersonian Mammoth displays characteristics from the other taxa, with an acute mandible similar to the Woolly Mammoth, but more robust condyles and external nares that open above the occiputs more akin to the Columbian. Radiocarbon AMS dating on the University of Idaho mammoth specimen's molar yielded an age of 11,700 +/- 40 years, which is the timeframe for the last glacial retreat in North America and Jeffersonian hybridization observed in the fossil record.

**Funding Sources** At the time of writing, applications for the GSA Research Grant, Paleontological Society Research Grant, Evolving Earth Grant, and Sigma Xi Grant are under review.

### **Dinosaur Systematics, Diversity & Ecology**

#### **CRANIOFACIAL CONSTRAINT AND INNOVATION IN THE HEADS OF SAURISCHIA**

Fabbri, Matteo<sup>1</sup>, Navalón, Guillermo<sup>2</sup>, Paredes, Daniel S.<sup>1</sup>, Mongiardino, Nicolas K.<sup>1</sup>, Vergara, Miccaella E.<sup>1</sup>, Bhullar, Bhart-Anjan S.<sup>1</sup>

<sup>1</sup>Geology & Geophysics, Yale University, New Haven, Connecticut, U.S.A., <sup>2</sup>Earth Sciences, Oxford University, Oxford, U.K.

Although the influence of the brain on the surrounding skull has been well-established, the pattern of formation of cranial elements around this central organ remains poorly understood. We use high-resolution cell-level imaging techniques (synchrotron tomography and confocal microscopy) to show that mesenchymal cells condense early in organogenesis between the regions of the developing brain. It is only after establishment of the facial region that the primordial skull roof begins to form. Birds show a delayed genesis of the cranial roof in comparison to reptiles; we suggest that this owes to positive allometry of the brain in birds in contrast to negative allometry in reptiles. More specifically, we suggest that intraventricular pressure from the bulging avian brain causes a delay of dermal ossification. Various characters of the cranial roof are therefore non-independent, and the evolution of the dorsal dermatocranium is tightly linked to the evolution and development of the brain.

Given the dichotomy in brain and skull development between Crocodylia and Theropoda, we set out to understand neuroanatomical and cranial evolution in archosaurs more broadly. We used microCT scan and shape analyses to quantify changes in these two systems. *Euparkeria*, a pivotal taxon closely related to crown Archosauria, shows the first identifiable instance of an ‘archosaur type’ endocast with considerable remaining cerebral flexure. Major innovation of the brain appears in theropods on the line to birds, with an enlargement of the forebrain and cerebellum and latero-ventralization of the optic lobes. The elaboration of the brain in theropods led to considerable modification of the surrounding bones, especially in the temporal region. In contrast, in sauropodomorph dinosaurs, the temporal region is significantly modified although the brain is not dramatically different from that of other archosaurs. We find that the highly modified sauropod skull is a product of early reshaping of cranial elements, probably in service to feeding morphology. Early sauropodomorphs close to Sauropoda proper acquire these modifications during postnatal ontogeny, whereas sauropods already display them as embryos.

### **Biomechanics & Functional Morphology**

#### **COMPARING 3D SHOULDER MOBILITY AND MUSCLE MOMENT ARMS IN SPRAWLING AND UPRIGHT AMNIOTES**

Fahn-Lai, Philip<sup>1</sup>, Regnault, Sophie<sup>2</sup>, Biewener, Andrew<sup>3</sup>, Pierce, Stephanie E.<sup>2</sup>

<sup>1</sup>Museum of Comparative Zoology, Concord Field Station and Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts, U.S.A.,

<sup>2</sup>Museum of Comparative Zoology and Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts, U.S.A., <sup>3</sup>Concord Field Station and Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts, U.S.A.

The evolution of upright posture was a landmark event in synapsid evolutionary history, paving the way for mammals to exapt their appendicular skeletons and radiate into terrestrial, aquatic, and aerial ecosystems. However, in spite of an excellent fossil record, the lack of unambiguous skeletal correlates for posture has made it exceedingly difficult to pinpoint exactly when in synapsid evolution the transition from a ‘sprawling’ to an ‘upright’ limb posture occurred. Reconstructing muscle moment arms is a commonly-used tool for inferring function and ecology in extinct animals, and provides an appealing avenue for investigating mammalian postural evolution. But any attempt to interpret the synapsid fossil record through moment arms must be grounded in a robust understanding of how joint mobility and pose-varying moment arms interact to produce integrated function – something that has not been extensively studied in non-human amniotes. Here, we used X-ray Reconstruction of Moving Morphology (XROMM) to map out shoulder girdle and forelimb musculoskeletal function in an extant phylogenetic bracket for the synapsid stem: the sprawling Argentine black and white tegu and the upright Virginia opossum. Briefly, we implanted the girdle, limb bones, and key muscles that cross the shoulder joint in cadaveric specimens with radio-opaque markers and manipulated the forelimbs through their full range of motion, taking care to capture interactions between degrees of freedom. The 150,000 frames of biplanar video were digitized via a hybrid workflow utilizing the DeepLabCut machine learning toolkit to determine joint kinematics. Three-dimensional geometric moment arms were calculated with a novel Python tool implemented in Maya, taking the shortest distance between a muscle’s line of action and each of the three orthogonal axes of the shoulder’s coordinate system. With the resulting dataset, we are able to resolve how a given rotation at the shoulder joint impacts moment arms of the muscles spanning it, and how effective those same muscles are at producing torque from a given kinematic pose. We present preliminary results from this analysis, showing mobility envelopes and pose-varying muscle moment arms compared between the tegu and the opossum. In the future, these data will be used to constrain and validate musculoskeletal models spanning synapsid

evolutionary history to fully flesh out the story of mammalian postural evolution.

**Funding Sources Funding information:** NSF DEB-1757749 (S.E.P).

### Mesozoic Herpetology

#### MULTISPECIES LEATHERBACK ASSEMBLAGE FROM THE CHANDLER BRIDGE AND ASHLEY FORMATIONS (OLIGOCENE) OF SOUTH CAROLINA, U.S.A.

Fallon, Bailey, Boessenecker, Robert  
Geology and Environmental Geosciences, College of Charleston, Charleston, South Carolina, U.S.A.

Paleogene dermochelyid species richness far exceeded that of today. Leatherback sea turtles were most diverse in the Paleogene, but declined sharply during the Neogene, and only one species exists today, *Dermochelys coriacea*. Therefore, studying ancient leatherbacks is essential to understanding past richness and why it may have declined over time. We describe the fossil remains of leatherbacks from the lower Oligocene Ashley Formation and upper Oligocene Chandler Bridge Formation of South Carolina, U.S.A. The fossils consist of isolated and some associated carapacial ossicles likely representing four extinct taxa: *Natemys*, *Pseudosphargis*, *Egyptemys*, and *Psephophorus*. Some ossicles are referred to cf. *Natemys* because of their likeness to ossicles that comprise the sunflower pattern specific to this genus. *Pseudosphargis* sp. ossicles are notably large and one shows evidence of ontogenetic fusion of adjacent ossicles. The *Egyptemys* sp. ossicle exhibits a shallow keel that shows no expression on the visceral surface, and the cf. *Psephophorus* ossicles have an internal diploic structure with one exhibiting a dorsal radial pattern. We report three leatherback genera (*Natemys*, *Egyptemys*, *Psephophorus*) from the Chandler Bridge Formation and three (*Natemys*, *Pseudosphargis*, *Psephophorus*) from the Ashley Formation, making this the first multispecies assemblage of leatherback fossils reported to date. Dermochelyid richness gradually declined from its peak in the Paleogene, with the Oligocene representing the last gasp of diverse leatherback assemblages. The ossicles we describe suggest that differences in shell structure may have abetted niche partitioning during the Oligocene, which may have permitted high local leatherback richness.

**Funding Sources** College of Charleston.

### Late Cenozoic Mammalian Macroecology & Macroevolution

#### FIRST OCCURRENCES OF *PALAEOGALE* IN THE PACIFIC NORTHWEST, U.S.A.

Famoso, Nicholas A.<sup>1</sup>, Orcutt, John D.<sup>2</sup>

<sup>1</sup>John Day Fossil Beds National Monument, US National Park Service, Kimberly, Oregon, U.S.A., <sup>2</sup>Department of Biology, Gonzaga University, Spokane, Washington, U.S.A.

The feliform carnivoran *Palaeogale* appeared in the Eocene of North America and had a Holarctic distribution in the Oligocene and early Miocene. Despite its large range, *Palaeogale* has not previously been reported from the Pacific Northwest of North America. We report three new specimens from the John Day Basin of Oregon that fill in this geographic gap. The oldest of these is a largely complete cranium from the Turtle Cove Member of the John Day Formation (Oligocene, 30.0–28.9 Ma). The other two specimens are a left and a right dentary from separate individuals, both recovered from the Kimberly Member (Oligocene, 25.3–23.5 Ma). Because *Palaeogale* species are almost entirely distinguished by their lower dentition, the cranium cannot be identified to species. However, the cranium is the first occurrence of the genus in the Pacific Northwest. The absence of a posterior accessory cusp on the p4 and of lateral expansion of the m1 protoconid allows the dentaries to be assigned to an endemic North American species, *P. dorothisae*. This is not only the first instance of this species in the Pacific Northwest and outside of South Dakota and Nebraska, but also the youngest known occurrence of *P. dorothisae*. We expect that these specimens will inform future analyses of phylogenetics, systematics, morphology, and biogeography in *Palaeogale*.

### Evolution & Biology of Non-Avian Theropods

#### NEW VERTEBRATE LOCALITIES AND BIOSTRATIGRAPHIC INTERPRETATIONS OF THE MESAVERDE FORMATION (CAMPANIAN, LATE CRETACEOUS) IN NORTHWESTERN WYOMING

Farke, Andrew A.<sup>1</sup>, Lettau Stallings, Mason R.<sup>2</sup>, Andrews, Wyatt J.<sup>2</sup>

<sup>1</sup>Raymond M. Alf Museum of Paleontology at The Webb Schools, Claremont, California, U.S.A., <sup>2</sup>The Webb Schools, Claremont, California, U.S.A.

Terrestrial vertebrates from Campanian-aged (83.6–72.1 Ma) rocks in the Western Interior of North America were at least partially partitioned into northern and southern faunal assemblages. The nature of the interface between these assemblages is uncertain, largely due to undersampling in critical locations. The Mesaverde Formation of western Wyoming is thus geographically and

temporally relevant. Depending upon the site, previously reported microvertebrate assemblages from the southern Bighorn and southern Wind River basins have been interpreted as representing freshwater and estuarine environments of mid- to late Campanian ages.

During the summer of 2019, the Raymond M. Alf Museum of Paleontology (RAM) identified new sites in the northwestern Bighorn Basin of Park County, Wyoming, over 75 km distant from previously known localities and thus potentially sampling new depositional environments and temporal windows. One site in particular (RAM V2019026) produced fragmentary hadrosaur postcrania along with a diverse microvertebrate assemblage. Typical Campanian taxa are found here, including testudines, lepisosteids, avialans, tyrannosaurids, and hadrosaurids. A small theropod tooth (RAM 24759) represents the first known occurrence of *Richardoestesia gilmorei* from the Mesaverde Formation of Wyoming. Multiple chondrichthyan taxa are represented, including the ginglymostomatid *Cantioscyllium bighornensis*. The overall assemblage and geology are most consistent with a freshwater environment, rather than an estuarine assemblage like that previously reported from the southeastern Bighorn Basin. Significantly, rhinobatoid teeth from this and another new locality have unornamented enamel, more similar to the condition in *Cristomylus* and *Pseudomyledaphus* than that in *Myledaphus bipartitus*. This suggests on biostratigraphic grounds that the new Mesaverde localities are likely mid-Campanian at youngest, and thus may be penecontemporaneous with the Wahweap (Utah) and lower Judith River (Montana) formations. Future work aims to better constrain correlations across the Mesaverde Formation in Wyoming, and sample additional localities to refine environmental interpretations.

**Funding Sources** David B. Jones Foundation; Augustyn Family Fund; Mary Stuart Rogers Foundation.

### **Symposium: Paleoneurology**

#### **UNRAVELING THE EVOLUTIONARY HISTORY OF THE AVIAN BRAIN THROUGH BEHAVIORAL NEUROIMAGING AND DIFFUSIBLE IODINE-BASED CONTRAST-ENHANCED COMPUTED TOMOGRAPHY**

Ferrer, Elizabeth A.<sup>1</sup>, Salerno, Michael<sup>2</sup>, Wei, Shouyi<sup>2</sup>, Vaska, Paul<sup>2</sup>, Balanoff, Amy<sup>3</sup>

<sup>1</sup>Anatomical Sciences, Stony Brook University Renaissance School of Medicine, Stony Brook, New York, U.S.A., <sup>2</sup>Stony Brook University, Stony Brook, New York, U.S.A., <sup>3</sup>Johns Hopkins, Baltimore, Maryland, U.S.A.

Birds are one of only three vertebrate groups to attain powered flight, and as such we still lack a basic

understanding of the neuroanatomy necessary to support this unusual mode of locomotion in the crown group – let alone in its deep, evolutionary history. Previous work based on endocranial morphology of the stem lineage of birds has hypothesized that specific regions such as the Wulst, which processes both visual and somatosensory information, might be important for the evolution of flight, but there are few quantitative data available to support such hypotheses. This study aims to understand the neurological substrates that are necessary for the evolution of powered flight by determining those regions of the brain that are most utilized in living birds and then analyzing their morphological variation across the avian tree. To do this we use a combination of diffusible iodine-based contrast-enhanced computed tomography and the biodistribution of 18F-Fludeoxyglucose (FDG) with positron emission tomography (PET) in extant birds. 18F-FDG builds in regions of high metabolic activity, which can be used to help identify active nuclei during specific behaviors such as flight. These active nuclei can then be linked to neuroanatomy. Using baseline measures, we found that peak brain uptake of 18F-FDG occurred at around 10 minutes, which was the total time the birds were flown before scanning. For flight measures, birds were prompted to fly between pedestals after injection with 18F-FDG. We found that areas of the brain associated primarily with motor and somatosensory pathways increased significantly in activity during flight, including the cerebellum and somatomotor Wulst. Activation was most highly concentrated within specific cerebellar lobes that have been shown to receive somatosensory information from the wing. We then analyzed the volume and shape of these neuroanatomical areas of increased activity across crown Aves using DiceCT. This ongoing analysis aims to combine these morphological and PET data with endocranial data obtained from stem birds to better understand how these important neuroanatomical regions correlate with other anatomical indicators of powered flight through deep time.

**Funding Sources** National Science Foundation.

### **Preparators**

#### **THE USE OF THE TEAS TRIANGLE TO REMOVE AGED MATERIALS APPLIED TO FOSSILS: AGED HYDROGENATED POLYMER (BLUE-TACK®) ON *HYPsilOPHODON FOXII* IN IGEA (LA RIOJA, SPAIN).**

Ferrer Ventura, Mireia<sup>1</sup>, Torices, Angelica<sup>1</sup>, Mas-Barberà, Xavier<sup>2</sup>, San Juan Palacios, Raúl<sup>1</sup>, Navarro-Lorbés, Pablo<sup>1</sup>  
<sup>1</sup>Human Science Department, University of La Rioja, Logroño, La Rioja, Spain, <sup>2</sup>Department of Conservation and Restoration of Cultural Heritage, Polytechnic University of Valencia, Valencia, Valencia, Spain

Igea, a locality of La Rioja (Spain), contains fossil remains attributed to *Hypsilophodon foxii*. These remains were found, prepared, and put on display in 1994. The specimen was adhered to methacrylate sheets using a hydrogenated polymer (synthetic rubber) commonly known as Blue-Tack and displayed in a glass case.

Due to the need for further studies on the fossils, it was necessary to extract the specimen from the showcase and remove the aged Blue-Tack. Blue-Tack is composed of a hydrogenated polymer (synthetic rubber), which contains a particulate-shaped mineral filler, mixed with a blue pigment and a mineral oil, which is not specified, but presumably a paraffin, naphthenes, or aromatic hydrocarbons. The product also indicates that under optimal conditions of preservation (temperature, humidity, and low light incidence), it can last up to 4 years.

Knowing the physical-chemical characteristics, we can place the Blue-Tack inside the Teas Triangle. In this way, we can superimpose two Teas Triangles (solvents and product) with the information of the organic solvents, and thus be able to determine which mixture of organic solvents is better and safer for the removal of the material. The organic solvents selected for the solubility tests are acetone and white spirit, given the nonpolar nature of the material we want to dissolve.

Finally, solubility tests are carried out by different applications of the solvents separately and together in the selected quantity, by swab in three methods: applied, rolled, and rubbed. Thanks to these tests and the comparison between the swabs, we can determine how solvents work on the material. With this comparison, we can see how the removal of both solvents works without having to use the rolled and rubbed swab, and the fossil suffers less mechanical stress. Therefore, the use of the Teas Triangle for the removal of applied materials can determine the necessary quantity of solvent and mode of removal to safely restore fossils for research.

## Bird Biology & Evolution

### LATE CRETACEOUS NEORNITHINE FROM EUROPE ILLUMINATES CROWN BIRD ORIGINS

Field, Daniel J.<sup>1</sup>, Benito, Juan<sup>1</sup>, Chen, Albert<sup>1</sup>, Jagt, John W.M.<sup>2</sup>, Ksepka, Daniel T.<sup>3</sup>

<sup>1</sup>Department of Earth Sciences, University of Cambridge, Cambridge, U.K., <sup>2</sup>Natuurhistorisch Museum Maastricht, Maastricht, Netherlands, <sup>3</sup>Bruce Museum, Greenwich, Connecticut, U.S.A.

Our understanding of the earliest stages of crown bird evolution is hindered by an exceedingly sparse Mesozoic fossil record. The most ancient phylogenetic divergences among crown birds are known to have occurred in the

Cretaceous, but stem lineage representatives of the deepest crown bird subclades – Palaeognathae (ostriches and kin), Galloanserae (landfowl and waterfowl), and Neoaves (all other extant birds) – are entirely unknown from the Mesozoic. As a result, key questions related to ancestral crown bird ecology, biogeography, and divergence times remain unanswered. Here, we report a new Mesozoic fossil that occupies a position close to the last common ancestor of Galloanserae, filling a key phylogenetic gap early in crown bird evolutionary history. *Asteriornis maastrichtensis*, gen. et sp. nov., from the Maastrichtian of Belgium, is represented by a nearly complete, three-dimensionally preserved skull and associated postcranial elements. The fossil represents one of the only well-supported crown birds from the Mesozoic Era, and is the first Mesozoic crown bird with well represented cranial remains. *A. maastrichtensis* exhibits a heretofore undocumented combination of galliform (landfowl)-like and anseriform (waterfowl)-like features, and, along with a previously reported *Ichthyornis*-like taxon from the same locality, provides the first direct evidence of co-occurring crown birds and avialan stem birds. Its occurrence in the northern hemisphere challenges biogeographic hypotheses of a Gondwanan origin of crown birds, and its relatively small size and possible littoral ecology may corroborate recently proposed ecological filters influencing crown bird persistence through the end-Cretaceous mass extinction.

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## Fishes & Chondrichthyans: Evolution & Distribution

### THE DEVONIAN LOST WORLD: THE FIRST ACTINOPTERYGIAN OCCURRENCE FROM THE MALVINOKAFFRIC REALM

Figueroa, Rodrigo T., Friedman, Matt  
Earth and Environmental Sciences, University of Michigan, Ann Arbor, Michigan, U.S.A.

The early record of osteichthyans is geographically sparse and taxonomically imbalanced. Well-studied late Silurian and Early Devonian assemblages derive from localities at tropical and subtropical paleolatitudes. These faunas contain a diversity of sarcopterygians, but vanishingly few actinopterygians. Contemporaneous vertebrate faunas from higher paleolatitudes are poorly known, but invertebrate fossils from near the Early Devonian South Pole are highly distinctive and define the Malvinokaffric biogeographic realm. Jawed vertebrates from the Malvinokaffric realm are rare, represented only by placoderms and total-group chondrichthyans. Here we report the first definitive osteichthyan from a high-latitude locality within the Malvinokaffric realm: a large (9 cm)

dentary from the Pragian-Eifelian of the Paraná Basin, Brazil. Preserved as a natural mold, the specimen bears pronounced conical teeth organized as labial and lingual rows, vermiform ornamentation on its external surface, and reflexed symphysis. Several features indicate an actinopterygian affinity for the specimen, including presence of the mandibular canal through the dentary, absence of a facet for the tooth whorl, the organization of the teeth, and the geometry of the dorsal lamina to which the teeth attach. Among actinopterygians, the Brazilian specimen does not show a close anatomical correspondence to known Early or Middle Devonian genera, but instead shares large size, distinctive ornamentation, and an enlarged symphysis with the Late Devonian *Tegeolepis*. The presence of an actinopterygian crownward of *Meemania* and *Cheirolepis* in the Early Devonian of Brazil suggests that early diversification of ray-finned fishes may have taken place in undersampled regions. This discovery highlights the potential importance of fossils of the poorly known vertebrate record of the Malvinokaffric realm for establishing the timing of events in early actinopterygian evolution.

**Funding Sources** College of LSA and Department of Earth and Environmental Sciences, University of Michigan.

### Dinosaur Systematics, Diversity & Ecology

#### PROLONGED TOOTH FORMATION TIME IN THE CRETACEOUS BRACHIOSAURID SAUROPOD DINOSAUR *ABYDOSAURUS MCINTOSHI*

Finch, Stephen<sup>1</sup>, Wilson Mantilla, Jeffrey A.<sup>2</sup>, Britt, Brooks B.<sup>3</sup>, D'Emic, Michael<sup>1</sup>

<sup>1</sup>Adelphi University, Garden City, New York, U.S.A.,

<sup>2</sup>University of Michigan, Ann Arbor, Michigan, U.S.A.,

<sup>3</sup>Brigham Young University, Provo, Utah, U.S.A.

Tooth formation time and replacement rate are important components of feeding ecology in non-mammalian vertebrates and can be calculated in extinct species by counting incremental lines of von Ebner deposited daily in tooth dentine. Dinosaurs have a broad range of tooth replacement rates, consistent with the great dental diversity within the clade. Sauropod skull morphology is conservative relative to other herbivorous dinosaur clades, but both tooth slenderness and replacement rate vary substantially. Several sauropod lineages independently evolved narrow-crowned teeth and high tooth replacement rates. To examine the potential relationship of these two factors in more detail, we estimated tooth formation times in the moderately slender-toothed brachiosaurid *Abydosaurus mcintoshi* from the Early Cretaceous (Albian)

Cedar Mountain Formation of Dinosaur National Monument, U.S.A. Based on histological data, we estimate that *Abydosaurus* had unusually slow tooth formation times (~18 months), compared to teeth of similar apicobasal length in *Diplodocus* (~5 months), and *Camarasaurus* (~7 months). This prolonged tooth formation time relative to other sauropods stems from unusually thin daily increments in *Abydosaurus*, which are only one-half to two-thirds the thickness of daily increments found in nearly any of the approximately two dozen dinosaurs and crocodylians that have been sampled. Computed tomography of *Abydosaurus* jaws indicates that teeth in each alveolus differ substantially in size, as in *Brachiosaurus*, but contrast with diplodocoids and titanosaurs, wherein successive teeth in each alveolus are similar in size. The extended tooth formation times and the large size discrepancy between successive teeth within an alveolus suggest slow tooth replacement rates in *Abydosaurus*, in keeping with published estimates from the brachiosaurids *Giraffatitan* and *Brachiosaurus*. Together, these data suggest that brachiosaurids evolved the slowest tooth replacement rates within Neosauropoda.

### Holocene & Pleistocene Mammalian Macroecology & Faunal Studies

#### ANTHROPOGENIC AND NON-ANTHROPOGENIC CONTRIBUTIONS TO END-PLEISTOCENE MEGAFAUNAL EXTINCTIONS IN THE AMERICAN WEST

Finkelman, Leonard<sup>1</sup>, Davis, Edward B.<sup>2</sup>, Boyd, Bronwyn<sup>1</sup>, Hart, Ashley<sup>1</sup>, Johnson, Colleen<sup>1</sup>

<sup>1</sup>Philosophy, Linfield College, McMinnville, Oregon, U.S.A., <sup>2</sup>Earth Sciences, University of Oregon, Eugene, Oregon, U.S.A.

The cause of widespread extinctions of mammalian megafauna at the end of the Pleistocene epoch remains undetermined. In North America, approximately 60 such species disappeared in a window between 13 and 11 ka that is coincident both with large-scale climate changes and with human arrival on the continent, and so both factors remain candidate explanations for megafaunal extinctions. Analytical methods for distinguishing causal contributions to faunal extinctions may help to resolve the debate. Here I give one such analysis for 13 extinct megafaunal taxa from the American west. I have compiled a comprehensive chronology of fossil occurrences for these taxa and used the Gaussian-resampled, inverse-weighted method to infer 95% confidence intervals for the true extinction date of each taxon; these inferences were then compared with human occupation, temperature, and palynological data from different sites west of the North American continental divide. My results suggest that human activity, climate shifts, and vegetation change all made distinct

contributions to megafaunal extinctions in the American west. When compared against the pattern of extinctions in the region, these results imply that later megafaunal extinctions were a consequence of an ecological state shift triggered by initial human-driven extinctions of megafaunal predators and ecosystem engineers.

**Funding Sources** Linfield College.

### **Evolution & Biology of Non-Avian Theropods**

#### **ON THE SIGNIFICANCE OF THE FIRST NON-DENTAL REMAINS OF A DROMAEOSAURIDAE (DINOSAURIA: THEROPODA) FROM ARCTIC ALASKA**

Fiorillo, Anthony R.<sup>1</sup>, Chiarenza, Alessandro<sup>1</sup>, Tykoski, Ronald<sup>1</sup>, McCarthy, Paul J.<sup>2</sup>, Flaig, Peter<sup>3</sup>

<sup>1</sup>Paleontology, Perot Museum of Nature and Science, Dallas, Texas, U.S.A., <sup>2</sup>Department of Geosciences, University of Alaska, Fairbanks, Alaska, U.S.A., <sup>3</sup>Bureau of Economic Geology, University of Texas, Austin, Texas, U.S.A.

Compared to the more complete osteological record of herbivorous dinosaurs from the Prince Creek Formation of northern Alaska, the theropod record has provided fewer skeletal remains. While most of the theropod material from this unit comprises isolated teeth, the only non-dental remains known can be attributed to the troodontid *Troodon* and the tyrannosaurid *Nanuqsaurus*. The presence of the Dromaeosauridae has thus far been limited to isolated teeth. Here we describe a symphyseal portion of a dentary with two ziphodont teeth of diminutive size. Based on tooth crown and denticle morphology, the position of the Meckelian groove, parodontal plates, and a principal component analysis comparing the osteological observations of this specimen with comparison of other theropod taxa from the latest Cretaceous Western Interior Basin of North America, we attribute this partial dentary to a saurornitholestine dromaeosaurid. The fibrous bone surface, small size, and higher number of mesial denticles compared to distal ones point to a juvenile status for this individual. This is the first confirmed non-dental fossil specimen from a member of Dromaeosauridae in the Arctic. The specimen described here is particularly important because it represents a very young individual. As there is a decided preference for modern mammalian long-distance migrations to occur among large-bodied herbivores rather than carnivores, we infer that the *Pedimys* point dromaeosaurid implies a perennial residency of this dromaeosaur clade (Saurornitholestinae) in the Arctic, based on the decided preference for long-distance migration to occur among modern terrestrial herbivorous mammals rather than carnivores. To sum, this specimen expands on the role of Beringia as a dispersal route for this clade between Asia and North America. Just

as importantly, the specimen adds to a growing body of data that suggests that Cretaceous Arctic dinosaurs of Alaska did not undergo long-distance migration, but rather they were year round residents of these paleopolar latitudes. While we take a conservative approach and do not advocate for a new taxon based on this specimen, specimens from future collecting may support establishment of a new dromaeosaurid taxon in the Early to early Late Maastrichtian of Arctic Alaska.

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### **Evolution & Biology of Non-Avian Theropods**

#### **THE OLDEST DINOSAUR FROM THE NORTHERN HEMISPHERE AND THE ORIGINS OF THEROPODA**

Fitch, Adam J.<sup>1</sup>, Lovelace, David M.<sup>2</sup>, Stocker, Michelle R.<sup>1</sup>

<sup>1</sup>Department of Geosciences, Virginia Tech, Blacksburg, Virginia, U.S.A., <sup>2</sup>University of Wisconsin Geology Museum, Madison, Wisconsin, U.S.A.

The earliest divergences among dinosaurs are well-established to have occurred by ~235 Ma because of a well-documented early dinosaur record across Carnian-aged strata of formerly Gondwanan continents (Africa, South America, and India). However, dinosaur fossils of equivalent age are absent from North America and Eurasia, and Carnian-aged taxa from Gondwana are either members of Sauropodomorpha or lack obvious affinities within Dinosauria. Here we present a new taxon of theropod dinosaur represented by a partial associated postcranium as the first dinosaur from the Popo Agie Formation (Triassic, Carnian) of Wyoming. We coded this specimen into the 2019 matrix by Marsh and colleagues of early dinosaur relationships. It shares the following combination of character states with Dinosauria: surface ventral to the proximal head of the femur possesses a concave emargination, the proximal articular facet for the fibula on the astragalus occupies less than one-third of the transverse width, and the possession of a marked rimmed and elliptical fossa posterior to the anterior ascending process of the astragalus (the latter feature of which is notably absent in neotheropods, but present among early-diverging sauropodomorphs, herrerasaurids, *Eodromaeus*, and non-neotheropod theropods). Furthermore, the new taxon is recovered as sister to Neotheropoda based on the coossification of the astragalus and calcaneum and the transverse compression of the calcaneum such that the posterior projection and the medial process of the calcaneum are reduced. It is distinguishable from *Lepidus praecisio*, the previous oldest North American theropod, in

the possession of a greater anteroposterior width in the medial than the lateral astragalus, of a subrounded distal articular surface of the astragalus (rather than the distinct ‘roller joint’ of *Lepidus*), and of a fossa on the lateral surface of the calcaneum. The presence of a mosaic of anatomical features found in early-diverging dinosaurs and in later Neotheropoda demonstrates that this new taxon fills a critical phylogenetic gap in the evolution of theropod dinosaurs and supports the early and rapid diversification of dinosaurs in the Carnian. Its presence in Carnian-aged strata of North America also represents the oldest dinosaur occurrence from the Northern Hemisphere, challenging the hypothesis for a Gondwanan origin of dinosaurs and demonstrating the wide geographic spread of neotheropods by the earliest Late Triassic.

### **Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

#### **IDENTIFICATION OF THE PLEISTOCENE FAUNA FROM MCFADDEN BEACH, TX**

Flores, Deanna<sup>1</sup>, Godwin, William<sup>1</sup>, Bell, Christopher J.<sup>2</sup>, Lewis, Patrick J.<sup>1</sup>

<sup>1</sup>Biological Sciences, Sam Houston State University, Huntsville, Texas, U.S.A., <sup>2</sup>Geosciences, University of Texas at Austin, Austin, Texas, U.S.A.

McFaddin Beach (MB) is an archeological and paleontological locality (41JF50) extending approximately 20 miles along the eastern coastline of Jefferson County, Texas. It is well known for lithics attributed to several Paleoindian groups. Fossils recovered indicate a Rancholabrean age due to the presence of taxa such as *Bison* spp. and *Canis dirus*. The MB material is scattered into many small collections throughout Texas. Only the Lamar University collection has been studied, in an unpublished thesis written in 1975. The focus of our current study is to reassess all accessible MB collections, specifically those from Lamar University, Sam Houston State University, vertebrate paleontology collections at The University of Texas at Austin, and the Proctor Museum. Preliminary analysis suggests that these collections contains many taxa common through the Pleistocene, such as Equidae, Camelidae, Proboscidea, and Folivora. Common taxa include *Holmesina*, *Bison antiquus*, *Canis dirus*, and *Mammut americanum*. Some uncommon taxa also are present, including Tapiridae, *Tremarctos*, and *Castoroides*. The identification of fossil material belonging to *Trichechus manatus bakerorum*, the first ever recorded in the Pleistocene of Texas, further distinguishes the MB locality from other nearby localities of similar age. A more comprehensive understanding of taxa present in the MB fauna will provide a clearer picture of the paleoenvironment and faunal diversity of the region.

Because of its location, study of the MB fauna may also refine our understanding of the Great American Biotic Interchange.

### **Permo-Triassic Tetrapods**

#### **NEW INFORMATION ON THE LATE TRIASSIC REPTILE *SCLEROMOCHLUS TAYLORI* FROM $\mu$ CT DATA**

Foffa, Davide<sup>1</sup>, Barrett, Paul M.<sup>2</sup>, Butler, Richard J.<sup>3</sup>, Nesbitt, Sterling J.<sup>4</sup>, Walsh, Stig<sup>1</sup>, Brusatte, Stephen<sup>5</sup>, Fraser, Nicholas<sup>1</sup>

<sup>1</sup>Natural Sciences, National Museums Scotland, Edinburgh, U.K., <sup>2</sup>Natural History Museums, London, London, U.K., <sup>3</sup>University of Birmingham, Birmingham, U.K., <sup>4</sup>Virginia Tech, Blacksburg, Virginia, U.S.A., <sup>5</sup>University of Edinburgh, Edinburgh, U.K.

The herpetofauna of the Lossiemouth Sandstone Formation (Late Triassic) of Elgin (Moray, Scotland) includes several close relatives of key groups such as dinosaurs, pterosaurs, crocodylians and lepidosaurs, although the affinities of some taxa within this assemblage are contentious. The specimens of this assemblage are notoriously challenging to study because of their preservation as voids in sandstone. Historically, the ‘Elgin reptiles’ have been studied primarily using physical molds, which only provide incomplete, and potentially distorted information, an issue that particularly affects small-bodied taxa. Here we use microcomputed tomographic ( $\mu$ CT) techniques as an alternative method to study these important specimens, and access hidden parts of their skeletons.

*Scleromochlus taylori* is one of the most controversial taxa within the assemblage. It is an enigmatic, small-bodied, bipedal reptile that was long hypothesised to be closely related to dinosaurs and pterosaurs, and is represented by several specimens of varying completeness. It was recently reinterpreted as a quadrupedal ‘hopper’, positioned phylogenetically either within doswelliid archosauriforms, or outside of the Archosauria + Erythrosuchidae clade. Neither of these interpretations has been universally accepted, and other aspects of the biology of *Scleromochlus* are also contentious.

Here we analyse the first  $\mu$ CT scan data collected for *Scleromochlus*, using all available specimens, and show that historic molding incompletely captured its anatomy. We access and describe previously inaccessible (and thus unaltered) portions of its skeleton including a complete, as well as new details of already described regions. Overall, we clarify previous ambiguous features such as vertebral count, dorsal rib length and curvature, and reveal new details from the neck, tail, girdles, fore and hindlimb (particularly manus, femur and pes). We use this information, alongside that from multiple generations of

molds, to shed light on some of the most controversial aspects of its anatomy, phylogenetic relationships, taphonomy, and ecology.

**Funding Sources** DF: Science Fellowship - Royal Commission for the Exhibition of 1851

### **Biomechanics & Functional Morphology**

#### **TERRESTRIAL POSTURE AND ITS CONTROLS ON SECONDARILY AQUATIC AMNIOTE EVOLUTION: FORELIMB CHANGES IN LAND-TO-SEA LINEAGES**

Formoso, Kiersten K.

Earth Sciences, University of Southern California, Los Angeles, California, U.S.A.

Secondarily aquatic amniotes are excellent models for understanding the functional evolution of major transitions because these lineages underwent immense morphological changes when recolonizing aquatic environments. Except for sea snakes, all aquatic amniotes descended from terrestrial ancestors with limb driven locomotion that had either an upright or sprawling posture and evolved one or a combination of axial or limb-based aquatic locomotion. The adaptive predisposition of clades to undergo secondary aquatic transitions is of great interest to evolutionary biologists, but there have been few studies based on the controls of posture, which is a key functional feature that separates clades of aquatic amniotes at the onset of their transitions, despite eventual convergence in aquatic morphology. To study how posture affects secondarily aquatic transitions, taxa from four clades of aquatic amniote lineages (and a semi-aquatic outgroup [O] for each) were ranked from low to high degree of aquatic adaptation. These clades include two with ancestrally upright posture, and axial and limb-driven locomotion respectively (1. Cetaceans: *Hippopotamus* [O], *Maiacetus*, *Orcinus*; 2. Pinnipeds: *Lontra* [O], *Enaliarctos*, *Zalophus*) and two with ancestrally sprawling posture, with respective swimming styles (3. Mosasaurs: *Amblyrhynchus* [O], *Portunatasaurus*, *Platecarpus*; 4. Sauropterygians: *Placodus* [O], *Ceresiosaurus*, *Dolichorhynchops*). During forward motion in the water column, the forelimbs are an important source of drag. In amniotes with limited swimming adaptations the forelimbs are either folded out of the way when swimming (as in sprawling axial swimmers like lizards), or directly used in swimming as paddles (as in upright mammals). Geometric morphometrics of the pectoral girdle, humerus, ulna, radius, and manus are being used for analysis in corresponding NMDS morphospaces to test the hypothesis that ancestrally sprawling aquatic clades with axial locomotion (e.g., mosasaurs) have more morphological conservation in the proximal forelimb elements between early semi-aquatic forms and highly aquatic forms, than

ancestrally upright aquatic clades with axial locomotion (e.g., cetaceans). This would suggest that sprawling amniotes require fewer functional steps when evolving axial aquatic locomotion, and that an upright posture, though resulting in numerous aquatic amniotes, confers an evolutionary hurdle in achieving axial aquatic locomotion.

**Funding Sources** NSF Graduate Research Fellowship grant DGE-1418060, Evolving Earth Foundation.

### **Biomechanics & Functional Morphology**

#### **THE ROLE OF SYMPHYSEAL TISSUES AND SUTURES ON MANDIBLE FUNCTION IN ARCHOSAURS**

Fortner, John D.<sup>1</sup>, Wilken, Alec<sup>1</sup>, Cost, Ian<sup>2</sup>, Sellers, Kaleb<sup>1</sup>, Middleton, Kevin<sup>1</sup>, Holliday, Casey<sup>1</sup>

<sup>1</sup>Pathology & Anatomical Sciences, University of Missouri, Columbia, Missouri, U.S.A., <sup>2</sup>Albright College, Reading, Pennsylvania, U.S.A.

The mandible is a biomechanically important structure wherein forces are transferred to and from the organism during biting behaviors. Because reptile mandibles are composed of numerous bones and joints, they have evolved diverse adaptations to the competing pressures of mandibular development and function. Sauropsids including archosaurs generally possess unfused dentary symphyses and prominent intramandibular joints (IMJs) whose roles in mediating mandibular forces are not yet fully appreciated. Moreover, archosaurs variably possess laterally-wrapping pterygoideus, depressor mandibulae and intramandibularis jaw muscles whose roles in mandibular mechanics remain unclear. Theropods dinosaurs are an ecologically diverse archosaur clade with great diversity in mandibular shape and many taxa have been described as possessing forms of mandibular kinesis. This however presents a biomechanical paradox for stiff-skulled, osteophagous theropods like *Tyrannosaurus rex* that must use its jaw muscles to both produce extreme bite forces and mediate flexibility of the dentary about the IMJ. We examine the role of symphyseal tissue, intramandibular joints and jaw muscle loads in *Varanus*, *Alligator*, and *Struthio* mandibles in order to bracket inferences of structure and function in non-avian dinosaurs such as *T. rex*. We used anatomical techniques, contrast imaging, and computational modeling to test how the mandibles of extant sauropsid species and *T. rex* perform under differing hypothesized soft tissue properties and loads. Because the osteological correlates of m. pterygoideus ventralis in non-avian dinosaurs are poorly defined we built different finite element models with differing hypotheses of muscle attachments. Our results found that long axis rotation and medial bending about the IMJ induced by a laterally-wrapping m. pterygoideus ventralis inserting onto the mandibular shelf, and medially-inserting m. adductor

mandibulae externus medialis, is best reduced by a dorsomedial orientation of m. intramandibularis that is contiguous with m. pseudotemporalis superficialis. These results also suggest m. intramandibularis prevents lateral bending and long axis rotation of the mandible of theropods with prominent IMJs, and that the developmentally primitive IMJ may present biomechanical problems for archosaurs and other non-mammalian tetrapods.

**Funding Sources** NSF IOS 1457319 and NSF EAR 1631684.

### **Anatomical & Developmental Explorations of the Mammalian Skull**

#### **CT-INFORMED CRANIAL ANATOMY OF *PALAEOLAGUS HAYDENI* (MAMMALIA, LAGOMORPHA) AND ITS BEARING ON THE RECONSTRUCTION OF BASAL LAGOMORPH MORPHOTYPE**

Fostowicz-Frelik, Lucja, Wolniewicz, Andrzej S.  
Institute of Paleobiology, Polish Academy of Sciences,  
Warsaw, Poland

Lagomorpha are a globally distributed clade of herbivorous mammals comprising two extant families representing two markedly different body plans: the long-eared and long-limbed Leporidae (hares and rabbits) and the short-eared and short-limbed Ochotonidae (pikas). The two lagomorph lineages likely diverged in the latest Eocene, but it is unclear whether the last common ancestor of crown lagomorphs was more leporid- or ochotonid-like in morphology. *Palaeolagus* from the Eocene–Oligocene of western North America is of particular importance for addressing this controversy. Although *Palaeolagus* was historically regarded as an early-diverging leporid, recent phylogenetic analyses have recovered it as a stem lagomorph outside the leporid-ochotonid split. *Palaeolagus* is represented by numerous, well-preserved skulls and skeletons, but several details of its cranial anatomy, particularly those of the base of the skull and the braincase, remain unknown. Here, we present new data on the cranial anatomy of *Palaeolagus haydeni*, the type species for the genus, based on micro-computed tomography (micro-CT). Our results enable us to visualise the cranial anatomy of this species in unprecedented detail and allow for determining, for the first time, the states of several morphological characters associated with the passage of nerves and blood vessels in the skull. Our micro-CT data allow us to confirm the presence of the alisphenoid canal in the anterior wall of the pterygoid fossa (present in both leporids and ochotonids), the craniopharyngeal canal in the basisphenoid (present in leporids, but absent in ochotonids), a single hypoglossal foramen in the

exoccipital (present in ochotonids, whereas two foramina perforate each exoccipital in leporids), a well delineated pterygoid fovea on the medial surface of the mandibular ramus (present in leporids, with the exception of *Brachylagus*, and absent in ochotonids) and others. Our anatomical observations have the potential to provide data important for modeling the character states present in the hypothetical last common ancestor of ochotonids and leporids. They will also be of great importance in phylogenetic studies focusing on resolving the relationships at the base of Lagomorpha in particular, and Glires in general.

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### **Quantitative Methods**

#### **TESTING RODENT DENTAL ECOMETRICS AS PREDICTORS OF CLIMATE AND BIOME**

Fox, David L.<sup>1</sup>, Keller, Jonathan S.<sup>2</sup>, Birlenbach, David<sup>1</sup>, McNulty, Kieran P.<sup>3</sup>

<sup>1</sup>Department of Earth & Environmental Sciences, University of Minnesota, Minneapolis, Minnesota, U.S.A.,

<sup>2</sup>Department of Biology, University of New Mexico, Albuquerque, New Mexico, U.S.A., <sup>3</sup>Department of Anthropology, University of Minnesota, Minneapolis, Minnesota, U.S.A.

The ecological structure of modern North American rodent faunas is closely related to continental-scale environmental gradients based on multivariate comparisons of the frequency of species in dietary and body size categories in 100 km<sup>2</sup> equal area grid cells with climatic conditions and physiography in each cell. Diet category and body size of rodents can be predicted with >90% accuracy using a suite of 36 published and novel 3D dental ecometric traits measured from mCT scans of lower tooth rows of 149 extant species of North American rodents across the crown group. Here we explore the potential for these ecometric traits to estimate climate and biome quantitatively for fossil rodent assemblages. Species richness in 2,020 equal area grid cells with >50% land ranges from 3–53, but species sampling for traits is incomplete and the number of species in grid cells with trait data ranges from 2–43. We sampled a subset of 730 grid cells representing six biomes that have ≥10 total rodent species and lack ecometrics for ≤3 species (70.0–96.3% complete). In each grid cell, we calculated the mean species value of each trait and summarized the trait data for all species with PCA and calculated mean species scores on each of the first three PC axes in grid cells. The relationships of traits to environment were assessed by non-parametric correlations (Spearman's  $\rho$ ) with annual and seasonal measures of temperature, moisture, and

energy (e.g., MAT, MAP, PET, etc.), summaries of eight climate variables by PC scores, elevation, relief, and biome type in each grid cell. Most comparisons are significant even for weak correlations, but some traits have consistently weak correlations and seem relatively insensitive to environment. The relationships between traits and environmental variables have various forms, but many are strongly linear. Of the 468 correlations of mean traits and PC scores with environmental variables and PC scores, 26.7% have Spearman's  $\rho$  better than ( $\pm$ ) 0.50, and 8.3% better than ( $\pm$ ) 0.75. Precipitation variables, elevation, and relief have the weakest correlations with traits and the most that are not significant; temperature variables have moderate to strong correlations (as strong as  $\rho = -0.89$ ) with a majority of traits. Correlations with biome type are mostly significant but weak to only moderately strong. These results indicate that dental ecometric traits can be used to estimate aspects of past environments from fossil rodent teeth.

### Romer Prize

#### COMMUNITY ECOLOGY AND STABLE ISOTOPE ECOLOGY OF SMALL MAMMAL FOSSILS REFLECT REGIONAL CLIMATE CHANGE PATTERNS AT RANCHO LA BREA, LOS ANGELES, CALIFORNIA, U.S.A.

Fox, Nathaniel  
Environmental Systems Graduate Group, University of California, Merced, California, U.S.A.

The extent of environmental change during the late Quaternary in the region around the Rancho La Brea (RLB) tar pits in Los Angeles, California has long been debated. Some studies suggest that environments were relatively stable over the last 50,000 years while others suggest that local climates mirrored regional patterns of both long-term and abrupt warming and cooling. To investigate this, I examine small mammal fossils from several RLB deposits and evaluate changes in community composition, as well as the diet and size of a subset of taxa, through time. Such responses are good proxies for characterizing environmental change because small mammals are sensitive to local perturbations due to their small home ranges and limited mobility. Community changes are described as changes in mean community trait values and compared with  $\delta^{18}\text{O}$  climate data from the Santa Barbara Basin. Diet is evaluated via  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  stable isotope analysis of fossil collagen, and intraspecific size is quantified from morphometric measurements of several taxa and their extant representatives. If past environments of Los Angeles were similar through time, I hypothesize that no relationship occurs between regional climate and small mammal community traits. Further, I expect no

correlation between intraspecific diet/size and climate if local conditions remained stable. Results of community and intraspecific analyses show conspicuous faunal-climate relationships. At coarse temporal scales (i.e., with deposit specific time-averaged data), community traits and regional climate are concordant, such that deposits recording overall cooler time periods have cooler-adapted and less diverse faunas and deposits recording warmer time periods have warmer-adapted and more diverse faunas overall. At higher temporal resolutions (i.e., by examining directly-dated specimens), climatically facilitated trait changes are evident. For example, rabbit (*Sylvilagus* spp.) and squirrel (*Otospermophilus beecheyi*) dietary carbon ( $\delta^{13}\text{C}$ ) strongly track decadal scale  $\delta^{18}\text{O}$  oscillations from ~50,000 to ~2,500 calibrated years before present. Overall, community-averaged – and intraspecific – trait changes indicate that climatically driven shifts in the local environment likely occurred across the last glacial transition. These findings help contextualize the paleobiology and climate responses of other RLB biota and emphasize the utility of small mammals for tracking environments at various spatial and temporal scales.

**Funding Sources** National Science Foundation (EAR-1623852); Paleontological Society (N. Gary Lane Award); American Society of Mammologists (Grant-in-Aid of Research).

### Preparators

#### EFFECTS OF CONSOLIDANTS (PVAC, PARALOID, BUTVAR, CELLULOSE NITRATE, CYCLODODECANE) ON BONE COLLAGEN AND BIOAPATITE COMPOSITION – CONSIDERATIONS FOR FUTURE CHEMICAL ANALYSES

France, Christine<sup>1</sup>, Kaczowski, Rebecca A.<sup>1</sup>, Kavich, Gwenaelle M.<sup>1</sup>, Giaccari, Jennifer A.<sup>2</sup>

<sup>1</sup>Smithsonian Museum Conservation Institute, Suitland, Maryland, U.S.A., <sup>2</sup>Freer Gallery of Art, Smithsonian National Museum of Asian Art, Washington, District of Columbia, U.S.A.

Consolidation is a critical step in preserving valuable specimens in museum collections. Common consolidants such as polyvinyl acetate (PVAc), polyvinyl butyral resins (Butvar), methyl methacrylate resins (Acryloid/Paraloid), and cellulose nitrate resins (Ambroid, Celluloid, Duco Cement) have been used for decades to stabilize fragile bone material. Temporary consolidants that readily sublimate also have been explored, such as cyclododecane (CDD). However, advances in chemical analyses of paleontological bone require pristine specimens unaltered by addition of secondary consolidants. We examined the effects of PVAc, Butvar B-98, Paraloid B-72, Duco

cement, and CDD on the chemical composition of a modern whale rib and modern seal femur. Various solvents and drying methods were examined to determine the efficacy of different removal processes. Stable isotopes of carbon, nitrogen, and oxygen were used to monitor changes in the collagen and bioapatite. Results show that all consolidants can be successfully removed using appropriate solvents (acetone, ethanol, or Cyclosol C-53) and low heat ( $\leq 80^{\circ}\text{C}$ ). Collagen carbon and nitrogen isotope values, bioapatite phosphate oxygen isotope values, and bioapatite carbonate carbon isotope values were unaltered by application and removal of all consolidants. Bioapatite carbonate oxygen isotope values were altered during application of PVAc, Butvar B-98, Paraloid B-72, and cellulose nitrate in an unpredictable manner. The CDD had no effect on bioapatite carbonate oxygen isotope values. These results bode well for chemical analyses involving the organic protein in the bone, such as stable isotopes, C-14 dating, and proteomics. However, the labile ionic groups in bone mineral apparently are susceptible to alteration and exchange during consolidant treatment. This study highlights the need for limited exposure to consolidants, as well as thorough treatment documentation, for bone specimens where future chemical analyses of the bioapatite mineral may be desired. Furthermore, the results support the use of non-polar sublimating consolidants like CDD as a viable alternative for temporary consolidation to avoid chemical alteration.

**Funding Sources** This work was supported by Smithsonian Museum Conservation Institute federal and trust funds.

## Mesozoic Herpetology

### A NEW ASSOCIATED SKELETON OF THE RARE SPHENODONTIAN *EILENODON ROBUSTUS* FROM THE UPPER JURASSIC MORRISON FORMATION OF UTAH

Frederickson, Joseph A.<sup>1</sup>, Davis, Brian<sup>2</sup>, Cifelli, Richard<sup>3</sup>  
<sup>1</sup>Weis Earth Science Museum, UWO Fox Cities Campus, Menasha, Wisconsin, U.S.A., <sup>2</sup>Department of Anatomical Sciences and Neurobiology, University of Louisville, Louisville, Kentucky, U.S.A., <sup>3</sup>Vertebrate Paleontology, Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma, U.S.A.

*Eilenodon robustus* is a relatively large and possibly herbivorous sphenodontian from the Upper Jurassic of Colorado and Utah. Though known from multiple sites, described specimens of *E. robustus* are largely limited to isolated remains of tooth-bearing elements. Here we describe a new specimen represented by a partial skull and associated postcranial elements from eastern Grand

County, Utah. This specimen is identified as *E. robustus* based on its relatively large size and distinctive dentition, with labiolingually expanded teeth bearing a wear facet on both the lateral and occlusal crown faces. Skull elements identified so far include a complete right maxilla, complete left and partial right palatine, basioccipital, and nearly complete right and partial left lower jaw. The postcranial skeleton is represented by partial left and right scapula and coracoid, complete left and proximal right humerus, left radius, left ulna, right femur, right tibia, as well as multiple vertebrae, metapodials, and ribs. The lower jaw is 6 cm long, comparing favorably in size and morphology with other specimens of *E. robustus*. Unlike another referred specimen, the maxilla does not possess a dramatic medial curve and is similar in shape to that of the closely related *Priosphenodon avelasi* from the Late Cretaceous of Argentina. The forelimb (humerus + ulna = 8.4 cm) of this specimen is 73% the length of the hindlimb (femur + tibia length = 11.5 cm), a ratio that is intermediate among other Mesozoic species, and indicates that despite the dental modifications and a general increased robustness, *Eilenodon* had skeletal proportions that do not wildly depart from the general sphenodontian body plan. Further, multiple unguals have been recovered with the specimen giving insight into the ecology of this creature. The unguals are sharp with an average ( $n = 3$ ) outer curvature of  $86^{\circ}$ , which is similar to the angle seen in ground-dwelling lizards and birds. Future study of this new specimen will drastically improve our understanding of the morphology and ecology of these enigmatic Mesozoic lepidosaurs.

**Funding Sources** Canyonlands Natural History Association, Discovery Pool Grant #16-03-BLM.

## Taphonomy & Stratigraphy

### MAMMAL-BEARING REGURGITALITES POTENTIALLY ATTRIBUTABLE TO *TROODON FORMOSUS* AT THE EGG MOUNTAIN LOCALITY, UPPER CRETACEOUS TWO MEDICINE FORMATION, MONTANA, U.S.A.

Freimuth, William J.<sup>1</sup>, Varricchio, David<sup>1</sup>, Brannick, Alexandria L.<sup>2</sup>, Weaver, Lucas N.<sup>2</sup>, Wilson, Gregory P.<sup>2</sup>  
<sup>1</sup>Department of Earth Sciences, Montana State University, Bozeman, Montana, U.S.A., <sup>2</sup>Department of Biology, University of Washington, Seattle, Washington, U.S.A.

Though rare, fossil gastric pellets (regurgitalites) have distinct taphonomic characteristics and allow for inferences of trophic interactions and behavioral ecology. When a specific predator can be identified, regurgitalites offer rare insight into dietary processes, physiology, and the evolution of predatory behaviors in deep time. In more recent deposits, the taphonomic features of small mammal skeletal remains, including element relative abundance,

characteristic breakage patterns, and digestive corrosion, reflect broad predator groups and can be used to assess paleoecology. We use these guidelines to evaluate the taphonomy of three unusual multi-individual aggregates of mammal skeletons from paleosol deposits at Egg Mountain, a dinosaur nesting locality from the Campanian (~75.5 Ma) of the Two Medicine Formation, Montana, U.S.A. Two amalgams are composed of three and eleven individuals preserved within <100 cm<sup>2</sup> and <300 cm<sup>2</sup>, respectively, primarily of the marsupialiform *Alphadon halleyi*. High proportions of paired crania and indigestible tooth-bearing elements, prevalent disarticulation, extensive breakage, periosteal corrosion, and the absence of a phosphatic ground mass are indicative of regurgitalites and align with features of prey in gastric pellets of modern diurnal raptors. These are the first known mammal-bearing regurgitalites from the Mesozoic. A third aggregate consists of two individual multituberculates characterized by high breakage of crania, greater representation of articulated postcrania, and a distinct absence of corrosion and other traces attributable to feeding; these features are suggestive of a non-predatory origin. The discrepancy of taphonomic features may suggest ecological or behavioral separation between the two mammalian taxa at the locality. The available evidence suggests the non-avian theropod *Troodon formosus* is the predator responsible for the regurgitalites, corroborating previous inferences of a small prey diet and potentially indicating a nocturnal feeding interaction. The parallels between prey in regurgitalites here and those in diurnal raptor pellets suggest manipulation of prey during feeding, a behavior previously inferred for other deinonychosaurs. The ability to egest pellets in a large-bodied non-volant troodontid supports previous hypotheses that avian-style pellet egestion may have evolved to enhance digestive efficiency and accommodate increased physiological processes in groups leading to modern birds.

**Funding Sources** Work was funded by the National Science Foundation (EAR) grant nos. 0847777 to DJV and 1325674 to DJV and GPW.

### **Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

#### **MINIMAL MESO-CARNIVORE RELEASE WITHIN THE FELID GUILD FOLLOWING THE PLEISTOCENE MEGAFUNAL EXTINCTION**

Freymueller, Nicholas<sup>1</sup>, Myers, Corinne<sup>2</sup>, Pardi, Melissa I.<sup>3</sup>, Smith, Felisa A.<sup>1</sup>

<sup>1</sup>Biology, University of New Mexico, Albuquerque, New Mexico, U.S.A., <sup>2</sup>Earth & Planetary Sciences, University of New Mexico, Albuquerque, New Mexico, U.S.A., <sup>3</sup>Research and Collections Center, Illinois State Museum, Springfield, Illinois, U.S.A.

Meso-carnivore release occurs when large predators are removed from an ecosystem and smaller carnivores begin to fill-in vacant eco-space. The Pleistocene Megafaunal Extinction (PME; ~13,000 years ago) exemplifies a recent broad-scale wipeout of the most massive carnivores such as the saber-toothed cats *Smilodon fatalis* and *Homotherium serum*, the American lion (*Panthera atrox*), and the American cheetah-like cat (*Miracinonyx trumani*). However, it is unclear if smaller surviving felids such as the jaguar (*Panthera onca*), mountain lion (*Puma concolor*), bobcat (*Lynx rufus*), and lynx (*Lynx canadensis*) began to infill the ecological vacuum caused by the extinction of the megafaunal felids. Here, we apply a dual-pronged approach of species distribution modeling (SDM) and ecological niche modeling (ENM) to test this meso-carnivore release question in the Americas, hypothesizing that surviving felids ought to have shown increased niche- and geographic-overlap patterns with the extinct megafelids post-PME. We additionally introduce methodological modifications to more accurately model species realized niches in environmental space; this aligns ENM analyses with best-practices for sister analyses like SDM. We demonstrate that surviving felids did not meaningfully exhibit meso-carnivore release post-PME. We additionally show that felid niches have been primarily structured by climate over the past 30,000 years, and that the small amount of meso-carnivore release post-PME is primarily attributed to this. Our results address how to independently parse out how climatic and biotic changes may structure ecosystems when those processes occur simultaneously, and additionally highlight the irreplaceable uniqueness of megafauna in the Earth system.

**Funding Sources** Funding was provided via a Grant-In-Aid-Of-Research (\$1500) from the American Society of Mammalogists.

### **Mesozoic & Early Cenozoic Mammalian Evolution**

#### **TESTING THE UTILITY OF EXTANT DIDELPHID MARSUPIALS AS MODERN ANALOGS FOR DENTAL FUNCTION IN EARLY TRIBOSPHERIC MAMMALS USING OCCLUSAL FINGERPRINT ANALYSIS**

Fulghum, Henry Z.<sup>1</sup>, Grossnickle, David<sup>1</sup>, Schultz, Julia A.<sup>2</sup>, Jäger, Kai R.<sup>2</sup>, Wilson, Gregory P.<sup>1</sup>

<sup>1</sup>Department of Biology, University of Washington, Seattle, Washington, U.S.A., <sup>2</sup>Abteilung Paläontologie, Universität Bonn, Bonn, Germany

The evolutionary development of the tribosphenic molar is considered a landmark event in mammalian history. The versatile and highly efficient combination of shearing, crushing, and grinding action permitted by this structure is the foundation from which all therian dentitions have evolved. Due to the retention of primitive tribosphenic

features among didelphid marsupials, studies often consider the dentition of extant didelphids to be an appropriate analog for early tribosphenic dentitions. However, comparative functional analyses of the dentitions of these groups are limited, and thus the degree to which we can use extant didelphids to infer the molar adaptations in early tribosphenic taxa remains unclear. Here we investigate the use of extant didelphid dentitions as a modern analog for early tribosphenic dentitions. First, we assess what variation exists between the occlusal patterns of two extant didelphids, *Monodelphis domestica* and *Didelphis virginiana*, using Occlusal Fingerprint Analysis (OFA). Micro-computed tomography scans were used to generate 3D polygonal surface models of associated upper and lower molars from these taxa. Wear facets were then used to infer the pathway of teeth during mastication cycles. Chewing animations and surface contact readings of *Monodelphis* and *Didelphis* are markedly similar and demonstrate a pattern consistent with that of Phase I and Phase II occlusion. This pattern comprises an upward shear as the talonid basin approaches the protocone, culminating with the crushing action of centric occlusion (Phase I). Phase I appears to be longer in *Monodelphis* due to the taller postvallid. This is followed by a brief grind and downward shear of the hypoconid against the lingual surface of the protocone as the jaw descends and the molars diverge (Phase II). Second, we compare the occlusal patterns of *Monodelphis* and *Didelphis* to the Late Cretaceous stem marsupial *Alphadon halleyi*, which is often considered close to the ancestry of marsupials. Patterns observed in *Alphadon* reveal an extended Phase I shear similar to *Monodelphis*, followed by a relatively long Phase II. These preliminary results demonstrate the retention of Phase I and II occlusal patterns but imply distinct functional differences between the dentitions of these groups. This study suggests that the use of extant didelphid dentitions as a modern analog for those of early tribosphenic taxa should remain limited to broad comparisons of molar adaptations.

### **Anatomical & Developmental Explorations of the Mammalian Skull**

#### **A BAYESIAN MULTILEVEL APPROACH TO THE CALCULATION OF ENCEPHALIZATION QUOTIENTS**

Fulwood, Ethan  
Neuroscience, Washington University in St. Louis School of Medicine, St. Louis, Missouri, U.S.A.

Biologists, anthropologists, and paleontologists have long been interested in comparing vertebrate brain sizes. Differences in brain size appear to reflect variation in behavioral complexity and trends in brain size increase

over time are a common observation among fossil clades. However, brain size is also closely related to body size. This fact appears to require some correction to arrive at a biologically meaningful metric of relative brain size. Encephalization quotients (EQ) represent one common method for arriving at this correction using the residual difference between each observed brain size value and the predicted values from a regression against body size. Researchers have taken varying approaches to determining the slope of this regression equation, often reflecting the taxonomic inclusiveness of the sample used to fit the line of subtraction. Bayesian multilevel approaches are well-suited to address both uncertainty in the calculation of regression slopes and taxonomic clustering in the underlying data. Here, body and brain size data from a wide range of extant and fossil mammals are taken from the published literature and used to demonstrate a Bayesian multilevel implementation of encephalization quotients (bEQ). Models were constructed to allow nested clustering at the ordinal, subordinal, and family levels and model fits compared using the pareto smoothed leave-one-out information criterion. The most highly parameterized model (incorporating family as well as subordinal and ordinal clustering) was preferred and used to calculate bEQ. Values are largely consistent with earlier EQ calculations, but allow point estimates to be replaced by probability density intervals calculated using the posterior distributions of slopes, intercepts, and the intercept offsets characteristic of each mammalian order. These density intervals reveal considerable overlap between the most encephalized non-human primate *Pan troglodytes* and the most encephalized cetacean species and confirm a general pattern of higher brain size in recent members of the most highly encephalized orders.

### **Evolution & Biology of Non-Avian Theropods**

#### **BABY TYRANNOSAUR BONES FROM THE LATE CRETACEOUS OF WESTERN NORTH AMERICA**

Funston, Gregory F.<sup>1</sup>, Powers, Mark J.<sup>2</sup>, Whitebone, Stephanie A.<sup>3</sup>, Brusatte, Stephen<sup>1</sup>, Scannella, John<sup>4</sup>, Horner, John R.<sup>5</sup>, Currie, Philip J.<sup>2</sup>

<sup>1</sup>School of GeoSciences, University of Edinburgh, Edinburgh, Scotland, U.K., <sup>2</sup>Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada, <sup>3</sup>University of Calgary, Calgary, Alberta, Canada, <sup>4</sup>Museum of the Rockies, Bozeman, Montana, U.S.A., <sup>5</sup>Chapman University, Orange, California, U.S.A.

Tyrannosaurs were the apex predators of Late Cretaceous Laurasia, and were among the largest terrestrial predators ever. Their status as dominant carnivores has garnered considerable interest since their discovery, both in the popular and scientific realms. As a result, they are well

studied and much is known of their anatomy, diversity, growth, and evolution. Recent discoveries have further elucidated the origin of their distinctive body plans, sensory apparatus, and large body size. In contrast, little is known of the earliest stages of tyrannosaur development. Eggs and embryos remain elusive, and juvenile specimens – although known – are rare. Perinatal tyrannosaur bones from the Campanian–Maastrichtian of western North America provide the first window into this critical period of the life of a tyrannosaur. A tiny dentary, measuring just twenty-nine millimetres long, from the Two Medicine Formation of Montana already exhibits distinctive tyrannosaurine characters, and reveals the earliest stages of tooth development. Perinatal teeth, a possible premaxilla, and an embryonic ungual from the Horseshoe Canyon Formation of Alberta likewise show that the hallmark characters that distinguish tyrannosaurs from other theropods were present early in life. Together, these specimens roughly constrain the size and morphology of tyrannosaur embryos. Sedimentary and taphonomic similarities in the sites that produced the material provide clues to the nesting habits of tyrannosaurs, and may help to refine the search image in the continued quest to discover baby tyrannosaurs.

**Funding Sources** Royal Society Natural Sciences and Engineering Research Council of Canada.

### **Taphonomy & Stratigraphy**

#### **CHEW ON THIS: EXPANDING DIAGNOSTIC CRITERIA OF UNGULATE-GNAWED BONES**

Gaetano, Madison<sup>1</sup>, Miller, Joshua H.<sup>1</sup>, Wald, Eric J.<sup>3</sup>, Druckenmiller, Patrick S.<sup>2</sup>

<sup>1</sup>Geology, University of Cincinnati, Cincinnati, Ohio, U.S.A., <sup>2</sup>University of Alaska Museum of the North, University of Alaska Fairbanks, Fairbanks, Alaska, U.S.A., <sup>3</sup>National Park Service, Fairbanks, Alaska, U.S.A.

Bone gnawing by carnivores, rodents, and ungulates records otherwise unattainable aspects of species-interactions and dietary ecology. However, interpreting these data requires confident identification of the bone modifying agent. Ungulates consume bone in response to dietary deficiencies in critical minerals such as phosphorus and calcium. Identifying ungulate bone gnawing, therefore, facilitates comparisons of dietary pressures through time and across spacio-environmental gradients. Unfortunately, ungulate gnawing has historically been attributed to carnivores or humans. While our capacity to recognize bones modified by ungulate gnawing has improved, few traces are widely recognized as diagnostic. Utilizing an ecosystem where ungulates (caribou; *Rangifer tarandus*) are the dominant bone modifier, we document a spectrum of ungulate bone gnawing categories and intensities, and

evaluate the potential of these patterns to broadly inform paleoecological and taphonomic assessments. In 2018, all encountered caribou antlers and bones were collected during 15 standardized bone surveys of openly vegetated tundra habitats on the Arctic National Wildlife Refuge, Alaska. Collection efforts resulted in 562 antlers. Each antler was visually inspected for gnawing and other modifications. We used a 3x macroscope to investigate finer-scaled modifications. We then compared observed gnawing traces to diagnostic criteria associated with carnivores (wolf, bear, fox). Rodent gnawing is visually distinctive and does not necessitate formal comparison. We identified 21 distinct modification types, including pits, punctures, furrows, scores, and fractures. We attributed 13 of these to caribou gnawing. Approximately 96% of Arctic Refuge antlers record modification, yet only 70% of modified antlers exhibit previously described ungulate gnawing criteria, including shallow, overlapping scores and 'forked' tines. Importantly, we find that these features arise late in the gnawing process. Thus, commonly employed criteria fail to identify antlers with lower degrees of gnawing, which includes roughly a third of ungulate-gnawed antlers. Preliminary comparisons between caribou and carnivore punctures indicate morphological distinctions resulting from differences in tooth cusp shape. Incorporating bone punctures as diagnostic classes of ungulate gnawing permits a more complete assessment of their dietary needs; expanding the ecological and behavioral data available from fossil records.

### **Dinosaur Systematics, Diversity & Ecology**

#### **EVIDENCE OF SCALE DIVERSITY IN THE LATE JURASSIC SAUROPOD *DIPLODOCUS* SP. FROM THE MOTHER'S DAY QUARRY, MONTANA**

Gallagher, Tess E.<sup>1</sup>, Poole, Jason<sup>2</sup>, Schein, Jason<sup>2</sup>

<sup>1</sup>Union college, Schenectady, New York, U.S.A., <sup>2</sup>Bighorn Basin Paleontological Institute, Philadelphia, Pennsylvania, U.S.A.

The life appearance of dinosaurs is a hotly debated topic in the world of paleontology, especially when it comes to dinosaur integument. In the case of sauropods, however, the topic is harder to properly discuss due to the limited amount of fossilized skin impressions that have been discovered. So far sauropod integument fossils include titanosaur fetuses from Patagonia, diplodocid dorsal spines, foot impressions, and other isolated skin impressions found in association with sauropod fossil remains. Several prominent skin impressions have been found at the Mother's Day Quarry, located in the Bighorn Basin, Montana. These discoveries may bring up new important information about diplodocids, specifically *Diplodocus* sp. Here we describe a newly uncovered skin

impression that gives evidence of scale diversity in the *Diplodocus* genus. The scales themselves represent tubercles and represent various shapes including: rectangular, oval, polygonal, and circular shaped scales. The tubercles themselves are small in size, the biggest of which only reach about 1cm in length. Considering how diverse the scale orientation is in such a small area of skin, it is possible that these impressions may represent a transition on the body from one region to another; perhaps from the abdomen to dorsal side, or abdomen to neck. Based on analysis of extant integument and scale orientation of crocodylians and other reptiles, it is possible to hypothesize on the location of the impressions relative to the body as well as the size and age of the individual.

### **Taphonomy & Stratigraphy**

#### **SOFT TISSUE AND CELLULAR PRESERVATION IN PALEOGENE VERTEBRATE FOSSILS OF THE NEBRASKA AND SOUTH DAKOTA BADLANDS**

Gallucci, John

Earth and Environmental Science, Temple University, Philadelphia, Pennsylvania, U.S.A.

Multiple studies have identified soft tissue and cellular structures in fossil bone, such as osteocytes, blood vessels, and fibrous/proteinaceous matrix, which closely resemble those of extant vertebrates. However, controls on soft tissue preservation in vertebrate fossils (e.g., paleoclimate, depositional environment, diagenetic history) remain poorly understood. Strata of the Eocene–Oligocene White River Group (WRG) and Oligocene Arikaree Group (AG) of the northern Great Plains provide a perfect setting for evaluating these potential influences across the Eocene–Oligocene Transition (EOT), ~37–30 mya. I herein present the results of demineralization assays and geochemical tests on vertebrate fossils from the WRG and AG to explore potential geologic and paleoenvironmental controls on soft tissue preservation in vertebrate fossils. The specimens used in this study were collected from the WRG of northwest Nebraska and WRG and the AG of southwest South Dakota, and include postcranial fragments of mammals (various taxa) and reptiles (tortoises) from both the late Eocene (Chadron Formation) and Oligocene (Brule and Sharps Fms). Fossils were excavated from a variety of host rock types, including siltstones, mudstones, and sandstones representing fluvial and aeolian depositional environments. Associated paleosols suggest neutral to alkaline, oxidizing conditions. Demineralization was conducted in 0.5 M EDTA at pH 8.0 for four to six weeks, with exchanges of fresh EDTA performed every 48 hrs. Resulting demineralization products were loaded onto standard glass slides, cover-slipped, and imaged by optical microscopy. Many potential endogenous microstructures

were identified, including numerous osteocytes and vessel fragments, with each fossil sample preserving organic microstructures regardless of age, depositional environment, taxon, or bone crystallinity. Trends identified in trace element analyses obtained via Laser Ablation Inductively Coupled Mass Spectrometry (LA-ICP-MS) included higher rare earth element (REE) concentrations and relatively flat REE patterns in cortical bone, with slight, positive cerium anomalies, denoting moderate variations in the chemical alterations experienced by the fossils in their respective diagenetic microenvironments. Estimated REE diffusion periods varied from tens of thousands to millions of years, and suggest a possible connection between longer diffusion periods and cellular degradation.

**Funding Sources** National Park Service.

### **Dinosaur Systematics, Diversity & Ecology**

#### **DESCRIPTION AND FUNCTIONAL ANATOMY OF THE QUADRATE OF THE DICRAEOSAURID SAUROPOD *BAJADASAURUS PRONUSPINAX* FROM THE LOWERMOST CRETACEOUS OF PATAGONIA**

Garderes, Juan P.<sup>1</sup>, Gallina, Pablo A.<sup>1</sup>, Whitlock, John A.<sup>2</sup>, Toledo, Néstor<sup>3</sup>

<sup>1</sup>Área de Paleontología, Fundación Félix de Azara, Ciudad Autónoma de Buenos Aires, Argentina, <sup>2</sup>Department of Science and Mathematics, Mount Aloysius College, Cresson, Pennsylvania, U.S.A., <sup>3</sup>Unidades de Investigación Anexo Museo, FCNyM-UNLP, La Plata, Buenos Aires, Argentina

The quadrate is an element with outsized importance to sauropod paleobiology. As in most nonmammalian amniotes, it links skull and mandible (quadrate-articular joint: QAJ), as well as chondrocranium and dermatocranium. The QAJ is the only kinetic arthrosis in the sauropod skull. Adductor musculature crossing this joint puts distinctive stresses on it. In particular, the angulation of these stresses change greatly between the different clades of Neosauropoda: diplodocoids, with their ventrally rotated facial skeleton, would have experienced mAMP-related stresses on the quadrate that are much more aligned with the long axis of the element than would have been present in macronarians. Likely as a result of the combination of differential stresses, the anatomy of the quadrate is often quite distinctive, making it both phylogenetically and functionally important.

Here, we describe the quadrates of the Early Cretaceous *Bajadasaurus pronuspinax* Gallina, Apesteguía, Canale & Haluza (Dicraeosauridae: Diplodocoidea). As in other diplodocoid sauropods, this element presents as a triradiate element with posterodorsally oriented main axis, a

posterior shallow fossa and a subtriangular shaped articular surface. Both quadrates of *Bajadasaurus pronuspinax* are nearly completely preserved. The squamosal capitulum is long, with a triangular section, and presents an elongated articulation surface for the squamosal, more than four times higher than wide, differentiating from the ‘swelling’ morphology observed in *Suuwassea* Harris. This capitulum presents a deep posterolateral fossa, with a thick lateral margin. The mandibular capitulum, which presents a triangular shaped articular surface, is connected with the body of the quadrate without a distinctive neck, conversely with the condition observed in *Suuwassea*. This condition results in the expansion of the attachment surface for the muscle adductor mandibulae posterior (mAMP), despite the lacking of an osteological correlate, as inferred in other dinosaurs. The pterygoid process is short and thins anteriorly. It presents a slight anteromedial concavity, with an overall sigmoid morphology in ventral view. None of the quadrates preserved the medial surface completely. The traits observed in the quadrates of *Bajadasaurus* could imply a shifting in the angle of the mAMP regarding the other adductor muscles and QAJ, resulting in differences in feeding biomechanics compared with other diplodocoid dinosaurs.

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### **Taphonomy & Stratigraphy**

### **DINOSAURS IN DISGUISE: SUBSTRATE FLOW ACCOUNTS FOR UNUSUAL EARLY JURASSIC TRACKS**

Gatesy, Stephen M., Turner, Morgan T.  
Brown University, Providence, Rhode Island, U.S.A.

The classic Early Jurassic ichnofauna of the Connecticut Valley (MA and CT, U.S.A.) encompasses substantial track disparity. Most thick-toed (‘pachydactylous’) tracks are now attributed to dinosaurian trackmakers. However, many thin-toed (‘leptodactylous’) tracks have unusual proportions not seen in the pedal skeletons of either extinct or extant species. Edward Hitchcock’s hundreds of leptodactylous specimens are now recognized as penetrative tracks, formed by animals sinking into soft substrates. During or soon after the foot passed down through multiple layers, the cavities produced by the toes and metatarsus collapsed into narrow furrows. Might the movement of sediment around and over the penetrating foot have affected more than just the width of the remaining impressions?

We experimentally explored the impact of sediment flow on track shape using physical models. 3-D printed tridactyl feet were mounted horizontally on a linear actuator and plunged vertically into two semi-liquid muds (NC red clay and a mixture of glass bubbles and ball clay). A uniform

grid was imprinted on the sediment surface prior to indentation. We analyzed videos to quantitatively compare model and track proportions, as well as to follow grid deformation throughout descent. As predicted, the impact of sediment flow was strongly foot shape-dependent. Models with extremely thin toes produced tracks with similar proportions. However, in models with larger toe diameters and/or smaller interdigital angles, flow between digits II–IV was relatively restricted. Preferential flow of sediment around the sides of the models shifted the track hypex forward, thereby shortening digital impression lengths while increasing interdigital impression angles and metatarsus impression length.

A realistically modelled theropod foot produced tracks closely resembling some unusual CV specimens. Mud flowed more easily around the lateral and medial sides of the foot than between the well-padded, closely apposed toes. The broad metatarsus caused the subduction of substantial material, often completely obliterating the hallux impression. Our experiments dramatically highlight the imprudence of trying to identify track-makers by Cinderella-style matching of foot and leptodactylous track proportions. These results, although restricted to observations at the air-substrate interface, have implications for tracks sampled from deeper horizons, as well as for the reconstruction of motion from penetrative tracks.

**Funding Sources** US National Science Foundation (EAR-1452119); SICB Grants-in-Aid of Research.

### **Anatomical & Developmental Explorations of the Mammalian Skull**

### **OSTEOLOGICAL ANOMALIES IN THE NARIAL ANATOMY OF THE EXTANT TWO-TOED SLOTH *CHOLOEPUS* AND THE HOMOLOGY OF THE INTERNARIAL BAR IN SOME FOSSIL SLOTHS**

Gaudin, Timothy J.<sup>1</sup>, Smith, Kaitlyn<sup>1</sup>, Wible, John R.<sup>2</sup>  
<sup>1</sup>Biology, Geology & Environmental Science, University of Tennessee at Chattanooga, Chattanooga, Tennessee, U.S.A., <sup>2</sup>Section of Mammals, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.

We have uncovered several specimens of the extant two-toed sloth (*Choloepus hoffmanni* and *C. didactylus*) that exhibit unusual osteological features in and around the opening for the external nares. These features include the presence of a median, unpaired internasal bone separated by a posterior suture from the paired nasal bones; a thick, ossified or calcified nasal septum perforated by a large, membrane covered fenestra; and, an ossified or calcified processus lateralis ventralis of the nasal capsule, bearing on its anterodorsal surface a small, rectangular ‘septomaxilla.’ The last element, which we also observed in an adult specimen of the pygmy anteater *Cyclopes*, has heretofore

only been recorded among pilosan xenarthrans in embryonic specimens of *Choloepus* and *Tamandua*. The ossified or calcified nasal septum in *Choloepus* extends from the undersurface of the nasal/internasal to the dorsal surface of the premaxilla, and with its fenestra, greatly resembles the internarial bar of some extinct sloths. Full or partial internarial bars (the latter including only the ventral portion) have been recorded in the extinct mylodontids *Myiodon* and *Scelidotherium*, as well as in the megatheriid *Megatherium*. It has never been clear whether these internarial bars represented an extension of the nasal and/or premaxillae bones or an anterior ossification of the nasal septum. However, the morphology in our extant *Choloepus* specimens, combined with the frequent presence of a partially ossified nasal septum in these three extinct sloth taxa, even in those individuals lacking an internarial bar, suggest that the internarial bar likely derives from the nasal septum.

**Funding Sources** This work was funded in part by a National Science Foundation grant (DEB: 1654949) to JRW.

### **Paleozoic Tetrapods & Lissamphibians**

#### **NEUROCRANIAL ONTOGENY IN EARLY PERMIAN DISSORPHOIDS: SURPRISING OSSIFICATIONS AND SURPRISING IMMATURITY**

Gee, Bryan M.<sup>1</sup>, Bevitt, Joseph<sup>2</sup>, Reisz, Robert<sup>1</sup>

<sup>1</sup>Department of Biology, University of Toronto - Mississauga, Mississauga, Ontario, Canada, <sup>2</sup>Australian Centre for Neutron Scattering, Australian Nuclear Science and Technology Organisation, Lucas Heights, New South Wales, Australia

Dissorophoids are a diverse clade of temnospondyls that have long been of interest for their putative relationship to crown lissamphibians and for their remarkable diversity in Permo-Carboniferous terrestrial environments. To date, most of the work on dissorophids has been restricted to examinations of externally exposed cranial anatomy. Advances in the capability and accessibility of scanning methodologies for paleontology have led to a proliferation of tomographic studies that examine historically inaccessible internal regions and that use these novel data to inform comparative anatomy and phylogenetic analyses. However, temnospondyls remain undersampled relative to other Paleozoic clades in this regard. Here we utilize neutron tomography to analyze the internal anatomy of the olsoniform dissorophoids *Cacops* and *Acheloma* across partial ontogenetic ranges. We identify a similar pattern of neurocranial development in *Cacops* to that previously reported for *Acheloma*, indicating conservatism among olsoniforms. In turn, the adult condition of *Acheloma* exhibits numerous similarities to the adult condition

reported for other Paleozoic taxa such as *Eryops* and *Edops*, such as co-ossification of the otic capsules and an anteroposteriorly extensive sphenethmoid. These broader similarities indicate a conserved ontogenetic trajectory among Paleozoic temnospondyls in general. Conservatism of the ontogenetic trajectories at both scales provides compelling evidence that even large specimens of *Cacops* are still distinctly immature and probably reached much larger body sizes than is presently suggested by the fossil record. Using the same neurocranial markers of relative ontogeny, this hypothesis of a record comprised largely of immature individuals can also be extended to most other olsoniforms. Lastly, our study reveals the presence of a distinct cryptic ossification of the synotic tectum in both clades, highlighting the need for additional exploration of temnospondyl neurocrania to determine the variability and distribution of synotic tectum ossifications in temnospondyls, which have long been of controversial identity and homology and which are important for further resolution of early tetrapod relationships.

**Funding Sources** Australian Nuclear Science & Technology Organisation Proposal Grant 6332 & 6333; Natural Sciences & Engineering Research Council of Canada Discovery Grant to RRR.

### **Symposium: Paleoneurology**

#### **EXTENDING THE ENDOCAST PARADIGM: STANDARD AND CONTRAST-ENHANCED COMPUTED TOMOGRAPHY UNITE PALEONTOLOGICAL AND NEONTOLOGICAL NEUROIMAGING**

Gignac, Paul<sup>1</sup>, Beyl, Alexander R.<sup>2</sup>, Gold, Maria Eugenia L.<sup>3</sup>, Gray, Jaimi<sup>1</sup>, Morhardt, Ashley C.<sup>4</sup>, Stout, Randy<sup>5</sup>, Vazquez-Sanroman, Dolores<sup>1</sup>, Watanabe, Akinobu<sup>5</sup>, Wilson, Manon<sup>6</sup>, Kley, Nathan J.<sup>2</sup>

<sup>1</sup>Anatomy and Biology, Oklahoma State University Center for Health Sciences, Tulsa, Oklahoma, U.S.A., <sup>2</sup>Stony Brook University, Stony Brook, New York, U.S.A., <sup>3</sup>Suffolk University, Boston, Massachusetts, U.S.A., <sup>4</sup>Washington University at St. Louis, St. Louis, Missouri, U.S.A., <sup>5</sup>New York Institute of Technology, Old Westbury, New York, U.S.A., <sup>6</sup>MicroCT Consortium for Research and Outreach (MICRO), Fayetteville, Arkansas, U.S.A.

Computed tomography (CT) has fundamentally reshaped vertebrate paleontology by enabling the virtual sharing, three-dimensional (3D) printing, and internal examination of fossilized forms. A hallmark aspect of this revolution has been the ability to generate digital models of the endocranial cavity (endocasts), which have greatly expanded the inference and study of neuroanatomical variation in deep time. Endocasts represent an essential data source for probing neuroanatomical diversity and

function because they act as a size and shape proxy for the brain, cranial nerves, inner-ear structures, superficial intracranial arteries, and dural venous sinuses within the braincase. Fossilized vertebrates are, therefore, an indispensable window into the historical pace and trait sequence of neurological transformations. Chronicling this diversity is critical for analogizing the extant and extinct neuromorphologies that permit paleontologists to infer behavioral shifts, recognize altered ecological breadth, and interrogate major evolutionary innovations. In this study we illustrate how diffusible iodine-based contrast-enhanced CT (diceCT) links paleontological and neontological neuroimaging domains through use of extant exemplars. DiceCT simultaneously visualizes the skull, white- and gray-matter structures of the brain, undisturbed pathways of cranial and peripheral nerves, and the organ systems they innervate. We compare diceCT with other neontological brain-imaging tools (e.g., histology, light-sheet microscopy, magnetic resonance imaging, positron emission tomography) and discuss how they can be conceptually and analytically integrated with endocasts in novel ways. We exemplify this by demonstrating for the first time that diceCT staining is non-abrasive to neurons and glia, allowing us to reliably undertake standard and immunofluorescent histological imaging of post-diceCT brains in chicken and rat models. These advances validate an endocast-diceCT-neuron bridge, permitting 3D size and shape variation of endocasts to be spatially correlated with soft-tissue characters at increasingly smaller scales of organization from braincases to cells (e.g., lineage-specific brain region hypertrophies). The multi-scale nature of these data and their ready applicability to non-model neuroanatomical systems will enable previously intractable explorations of extant neuromorphologies necessary to inform expanded interpretations of nervous system diversity in the fossil record.

**Funding Sources** National Science Foundation; American Association for Anatomy; JB Johnston Club for Evolutionary Neuroscience.

### **Dinosaur Systematics, Diversity & Ecology**

#### **SYNCHROTRON MICROCT COMPARISON OF HUMERI IN *TRICERATOPS* AND EXTANT-MODEL *BISON* CONSISTENT WITH INFLATIONARY EARLY GROWTH IN CERATOPSID DINOSAURS**

Gilbert, Meagan M.<sup>1</sup>, Snively, Eric<sup>2</sup>, Woodward, Holly<sup>2</sup>, Cooper, David M.<sup>3</sup>, Scannella, John<sup>4</sup>, Tokaryk, Tim T.<sup>5</sup>

<sup>1</sup>Saskatchewan Geological Survey, La Ronge, Saskatchewan, Canada, <sup>2</sup>College of Osteopathic Medicine, Oklahoma State University, Tulsa, Oklahoma, U.S.A.,

<sup>3</sup>Anatomy Physiology and Pharmacology, University of Saskatchewan, Saskatoon, Saskatchewan, Canada,

<sup>4</sup>Museum of the Rockies, Bozeman, Montana, U.S.A.,

<sup>5</sup>University of Regina, Regina, Saskatchewan, Canada

Bones of extant mammalian artiodactyls and extinct dinosaurs, such as ceratopsians, record evidence of rapid growth as demonstrated by highly vascular histology, and permit age calibration through lines of arrested growth. Synchrotron phase-contrast microCT can augment data from histology of single thin sections, enabling 3D reconstruction of canal networks. To initiate and anchor synchrotron-scanned growth series for ornithischians and large artiodactyls, we scanned humeri of a small juvenile *Triceratops* (21 cm; Frenchman Formation, Royal Saskatchewan Museum P2691.1) as well as subadult and adult *Bison*, and produced 3D reconstructions of vascular canal morphology and density. Histological sections from other *Triceratops* and mammal specimens provided a reference standard for evaluating information content of 2D CT sections.

Midshaft regions of the *Bison* and *Triceratops* humeri were scanned on the Biomedical Imaging and Therapy beam line of the Canadian Light Source synchrotron, at 120-600 ms exposure times and energy of 80 kVp. Precessed rotation captured interpretable data outside the reconstructed transverse field of view. Canal networks were reconstructed in Amira, with color coding for canal diameter differentiating primary osteons and remodeling canals.

For all three specimens, phase contrast imaging at 9.2 μm pixel size reveals details such as inferred osteon cement lines that are visible in histological preparations, but impossible to resolve with attenuation-based CT. Osteocyte lacunae were not evident at this resolution.

The *Triceratops* specimen showed no regions of arrested growth, and extraordinarily dense networks of primary osteons with primarily proximodistal orientation. Canals of more deep-to-superficial orientation mark entheses at the deltopectoral crest. Otherwise, the *Triceratops* displayed little evidence of remodeling from Basic Multicellular Units except adjacent to the medullary cavity. In contrast, the *Bison* specimens possessed much sparser canal networks and greater numbers of larger-diameter remodeling canals consistent with adult status.

The 3D results are concordant with known fibrolamellar histology that demonstrates rapid growth in dinosaurs, including ceratopsians. In concert with histological sectioning, our synchrotron protocols for large bones will facilitate expanded, granular growth series for further quantification of growth in dinosaurs and mammals.

### **Anatomical & Developmental Explorations of the Mammalian Skull**

#### **PHYLOGENETIC RELATIONSHIPS BETWEEN CRANIAL AND INNER EAR MORPHOLOGIES OF ODONTOCETES**

Glass, Abigail M.<sup>1</sup>, Uhen, Mark D.<sup>1</sup>, Racicot, Rachel A.<sup>2</sup>, Ekdale, Eric<sup>3</sup>

<sup>1</sup>Atmospheric, Oceanic and Earth Sciences, George Mason University, Fairfax, Virginia, U.S.A., <sup>2</sup>Senckenberg Museum of Natural History, Frankfurt, Germany, <sup>3</sup>Evolutionary Biology, San Diego State University, San Diego, California, U.S.A.

Echolocation in toothed whales (Odontoceti) is a highly specialized adaptation for feeding and communication that evolved at the Eocene/Oligocene boundary. Previous studies show that measurements of bony labyrinths of the inner ear show interspecific differences in hearing frequency ranges and habitat preferences of odontocetes. Craniofacial features such as cranial asymmetry, posterior migration of the maxilla, downturned rostrum, and the presence of air sac fossae have also been used as characteristics of echolocation. Odontocetes use echolocation to assist in a variety of methods to capture prey such as suction and raptorial feeding. These feeding behaviors have been hypothesized to relate to cranial morphological features such as longirostry (long rostrum) and brevisrostry (short rostrum). It is important to understand how the evolution of these structures relate to habitat, behavior, and feeding preferences. In order to determine if there is a relationship between inner ear morphology and feeding behavior, we look for phylogenetic patterns between measurements of the inner ear and compare them to feeding regimes and their associated cranial morphological features. In this study we use existing measurement data from endocasts, generated by CT scanning technology, of the inner ear labyrinths of extinct and extant odontocetes along with existing data of rostral proportion index measurements. We also compare these measurements to cranial morphological features of echolocation. We compare these characters on a composite phylogenetic tree generated in Mesquite. We have found associations between inner ear measurements on the tree such as extension of the secondary spiral lamina and decreased number of cochlear turns that agree with previous studies. Pending further studies, we hope to find a stronger correlation between feeding adaptations, cranial morphology and inner ear morphology. Understanding how these characteristics evolved together is an important part of understanding the evolution of odontocetes and how they behave today.

## Marine Mammals

### **CARCHAROCLES-BITTEN SPERM WHALE TOOTH FROM THE COASTAL EASTERN U.S.A.**

Godfrey, Stephen J., Nance, John, Riker, Norm  
Paleontology, Calvert Marine Museum, Solomons,  
Maryland, U.S.A.

We report on a single sperm whale (Physeteridae) tooth from the Neogene of the PCS Phosphate Mine (formerly known as the Lee Creek Mine) (Aurora, North Carolina) that was bitten either by the extinct mega-tooth shark *Carcharocles chubutensis* or *Carcharocles megalodon*. The tooth shows three gouges, one of which also preserves raking marks, made as the serrations on the *Carcharocles* tooth struck and cut into its surface. This tooth preserves the first evidence in the fossil record of trophic interaction between two marine macro-predators.

**Funding Sources** The citizens of Calvert County, the Calvert County Board of County Commissioners, and the Clarissa and Lincoln Dryden Endowment for Paleontology.

## Macroecology & Macroevolution

### **THE INFLUENCE OF ECOLOGICAL TRANSITIONS ON DIFFERENT SKELETAL REGIONS OF CROCODYLIFORMS**

Godoy, Pedro L.<sup>1</sup>, Montefeltro, Felipe C.<sup>2</sup>, Bronzati, Mario<sup>3</sup>, Larsson, Hans<sup>4</sup>, Butler, Richard J.<sup>5</sup>, Turner, Alan H.<sup>1</sup>

<sup>1</sup>Department of Anatomical Sciences, Stony Brook University, Stony Brook, New York, U.S.A., <sup>2</sup>Departamento de Biologia e Zootecnia, Universidade Estadual Paulista (FEIS), Ilha Solteira, SP, Brazil, <sup>3</sup>Departamento de Biologia, Universidade de São Paulo (FFCLRP), Ribeirão Preto, SP, Brazil, <sup>4</sup>Redpath Museum, McGill University, Montreal, Quebec, Canada, <sup>5</sup>School of Geography, Earth and Environmental Sciences, University of Birmingham, Birmingham, U.K.

Aspects of crocodylomorph morphology are known to reflect species ecology. For example, ecological transitions between distinct crocodylomorph lifestyles (e.g., terrestrial, freshwater and marine) are associated with changes in overall cranial shape and inner ear morphology. Whether such relationships exist for the postcranium remains untested. To investigate this, we estimated morphological disparity from discrete characters, following Principal Coordinate Analysis of two of the most comprehensive phylogenetic data matrices to date. We performed our analyses with either complete datasets (using all characters) or subsets of cranial-only and postcranial-only characters. We have interpreted the results with caution, given that the vast majority of characters (>80% in both datasets) are based on cranial features. First, we estimated disparity for different lifestyles categories, which show that terrestrial crocodylomorphs exhibit relatively higher disparity, independently of the dataset and type character used. Nevertheless, morphospace occupation of different ecologies show relatively more

overlap when only postcranial characters are considered, suggesting that most of the morphological variation seen in the postcranium is not necessarily associated with changes in lifestyle (or, alternatively, that this variation has yet to be incorporated into data matrices). We then estimated evolutionary rates and found that postcranial characters rates are not significantly different from those of cranial characters. This indicates that, even represented by fewer characters, the postcranial characters subset is still able to provide informative results. Finally, to test if distinct modes of evolution drove the variation observed in these two skeletal regions, we fitted different evolutionary models to our data, including two uniform models (single-regime BM and OU models) and a multi-regime OU model, with shifts associated with ecological transitions. Although a multi-regime OU model offered the best solution for both cranial and postcranial character subsets, the difference between uniform and multi-regime models was significantly higher in the cranial subset. Combined, these results provide evidence that crocodylomorph cranial morphology was more prone to modifications from ecological transitions than the postcranium, possibly because some modifications associated with these transitions, such as feeding strategies, are closely linked to craniomandibular features.

**Funding Sources** Funding provided by Universitas 21, CAPES (CAPES 3581/14/4) and National Science Foundation (NSF DEB 1754596).

## Marine Mammals

### A NEW PROTOCETID WHALE (CETACEA, ARCHAEOCETI) FROM THE MIDDLE EOCENE OF THE FAYUM DEPRESSION IN EGYPT SHEDS NEW LIGHT ON RAPTORIAL FEEDING ECOLOGY IN ANCIENT WHALES

Gohar, Abdullah<sup>1</sup>, Antar, Mohamed S.<sup>2</sup>, Boessenecker, Robert<sup>3</sup>, El-Sayed, Sanaa<sup>1</sup>, Sallam, Hesham<sup>1</sup>

<sup>1</sup>Mansoura University Vertebrate Paleontology center, Mansoura University, Mansoura, Dakahlia, Egypt, <sup>2</sup>Nature conservation sector, Egyptian Environmental Affairs Agency (EEAA), Cairo, Cairo, Egypt, <sup>3</sup>Department of Geology and Environmental Geosciences, College of Charleston, Charleston, South Carolina, U.S.A.

Over 10 million years, whales transformed from hoofed, deer-like, herbivorous terrestrial mammals into fully aquatic carnivorous cetaceans. Protocetidae are Eocene archaeocetes representing a unique semiaquatic phase in that dramatic evolution. Three protocetid genera have been described from Egypt, including *Protocetus* (the first discovered), *Aegyptocetus*, and *Aegicetus*, which represents the latest surviving protocetid ever. Here, we describe a new protocetid skeleton (MUV 500) from the middle to late Lutetian age of the Midawara Formation in

the Fayum Depression of Egypt. MUV 500 is an associated partial skeleton of an individual represented by skull, mandibles, two vertebrae, including the fifth cervical and the sixth thoracic vertebrae, and rib fragments. MUV 500 is a protocetid whale based on the presence of the upper third molar, identifiable trigonid and talonid on the molars, and the absence of distinct accessory denticles on preserved postcanine teeth. Nevertheless, it also retains unique features, including large, elongated temporal fossae, anteriorly placed pterygoids, elongated parietals, an unfused mandibular symphysis that terminates at the level of P3 (51% of total preserved dentary length, longer than most other protocetids), and an enlarged i3 (rather than i2 as in other protocetids). Dimensions of the skull and the mandibles of MUV 500 indicate a medium to large adult protocetid, with the body estimated to be about 3 meters long. The presence of a large coronoid process typically occurs in species where the temporalis is much larger, and this is consistent with the anteroposteriorly longer temporal muscle fossa and anteriorly shifted orbit. The enlargement of the temporal fossae suggests a larger cross-section of the temporalis muscle, in turn suggesting a more powerful bite force associated with a raptorial feeding style. This powerful bite perhaps made it a successful apex predator in its region. The scarcity of limbs and postcrania may relate to disarticulation caused by shark scavenging; shark bite marks are preserved on the ribs. In addition to being the earliest record of protocetid whales from the Fayum Depression in Egypt, this skeleton is the first evidence of a middle Eocene protocetid from Fayum, since the only named protocetid from Fayum, *Aegicetus*, was recorded from the Priabonian strata. Recovery of such protocetid specimens contributes to a better understanding of the feeding ecology in the protocetid archaeocetes.

**Funding Sources** This work was funded by the Mansoura University Vertebrate Paleontology center (MUV) and Egyptian Environmental Affairs Agency (EEAA).

## Symposium: Paleoneurology

### BRAIN REORGANIZATION AT THE ORIGIN OF CROWN BIRDS

Gold, Maria Eugenia L.<sup>1</sup>, Smaers, Jeroen B.<sup>2</sup>, Norell, Mark<sup>3</sup>, Balanoff, Amy<sup>4</sup>

<sup>1</sup>Biology, Suffolk University, Boston, Massachusetts, U.S.A., <sup>2</sup>Anthropology, Stone Brook University, Stony Brook, New York, U.S.A., <sup>3</sup>Paleontology, American Museum of Natural History, New York, New York, U.S.A., <sup>4</sup>Psychological and Brain Sciences, Johns Hopkins University, Baltimore, Maryland, U.S.A.

Evolutionary acquisitions of new behaviors are thought to be accompanied by changes in the brain. The development of powered flight, for example, may have been preceded

by an outward expansion in the telencephalon. Previous studies have explored how brain volumes have shifted over the evolutionary history of Theropoda, and found that the large brains of crown group birds evolved before the advent of powered flight. Changes in brain shape, however, are only starting to be explored. To understand how the volumetric changes in the avian brain correlate to changes in brain shape, we collected three-dimensional landmark coordinates capturing the endocast shape of 49 crown group and extinct avians and non-avian theropods. The data were Procrustes aligned, then partitioned into the telencephalon, optic lobe, and cerebellum. These data were analyzed together to represent whole brain, and separately to represent different units. We used the R packages ‘Surface’ and ‘MVMorph’ to statistically analyze the fit of different evolutionary models on the shape data. Overall, the results show that crown group birds belong to a fundamentally different brain shape regime than non-avian dinosaurs. *Archaeopteryx* either placed with the non-avian dinosaurs (for the optic lobe and cerebellum), or with crown group birds (telencephalon and whole brain analysis). This suggests a modular pattern of evolution with the telencephalon changing in shape earlier than the optic lobe or cerebellum. Functional studies suggest the telencephalon may play a critical role in flight as a short-term conflict alert system, in which the anterior Wulst and entopallium work together to process visual information coming rapidly during flight, without additional processing from the optic lobe. Here, we see that role emerging in non-avian theropods that were probably capable of some volant behavior – requiring a different internal organization, and therefore shape, of the telencephalon. Even though prior studies found no increase in brain size at the origin of powered flight, a change in brain shape, as quantified here, suggests the differentiation of internal brain regions necessary for flight was well underway in the earliest avians.

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## Permo-Triassic Tetrapods

### CLAW & ORDER: SPECIAL VICTIMS UNIT – UNDERSTANDING DREPANOSAUFOMORPH DIVERSITY WITHIN THE SONSELA MEMBER OF THE CHINLE FORMATION AT PETRIFIED FOREST NATIONAL PARK

Goncalves, Gabriel, Sidor, Christian A.

University of Washington, Seattle, Washington, U.S.A.

Drepanosauromorpha is an extinct group of basal diapsid reptiles known from the Middle to Late Triassic (237–212 MA). The clade currently includes eight genera (*Ancistronychus*, *Avicranium*, *Dolabrosaurus*, *Drepanosaurus*, *Hypuronector*, *Kyrgyzsaurus*, *Megalancosaurus*, and *Vallesaurus*) that are known from

fossils collected in Europe (Italy, U.K.), North America (Arizona, New Mexico, New Jersey), and Asia (Kyrgyzstan). In 2019, a new drepanosauromorph from Petrified Forest National Park (PEFO), *Ancistronychus paradoxus*, was described based on a set of second manual ungual phalanges. Here, we describe another possible drepanosauromorph species from the same locality, also based on a three-dimensionally preserved ungual phalanx of the second digit of the manus. One characteristic that the new morphotype shares with *Drepanosaurus* and *Ancistronychus* is the large size of the ungual relative to its proximal articular surface (as a measure of the penultimate element). Looking at a ratio of claw length to cotyle width, measured as the proximal end of the claw to the distal edge of the apex of the phalanx compared to the transverse width of the proximal articular cotyle, the new specimen has a ratio of 2.97 : 1.05, whereas the corresponding measurements from the Hayden Quarry *Drepanosaurus* is 2.16 : 0.85 and from the holotype of *Ancistronychus paradoxus* is 2.18 : 0.74. When looking at other claws, the fourth manual ungual from the holotype of *Drepanosaurus unguicaudatus* is 1.67 : 0.36. In addition, the new morphotype shares the following characteristics found in *Drepanosaurus*: the presence of a morphologically similar flexor tubercle and distal apex. However, this specimen differs significantly from all known *Drepanosaurus* and *Ancistronychus* specimens in the presence of a somewhat transversely narrow second manual ungual phalanx and; a ventrally directed cotyle that is line with the tubercle along the ventral surface. If the new morphotype is found to represent a new taxon, this suggests that multiple drepanosauromorph taxa coexisted during Sonsele Member-times. Future work identifying and describing additional material of drepanosauromorphs within the Chinle can help paint a clearer understanding the ecological significance of these unusual unguals as well niche partitioning within the small reptile community.

## Mesozoic & Early Cenozoic Mammalian Evolution

### DIETARY RECONSTRUCTION AND PALEOECOLOGY OF EOCENE LOPHIALETIDAE (MAMMALIA, TAPIROIDEA) FROM THE ERLIAN BASIN OF CHINA: EVIDENCE FROM DENTAL MICROWEAR

Gong, Yanxin, Wang, Yuanqing, Mao, Fangyuan, Bai, Bin, Li, Qian, Wang, Haibing

IVPP, Chinese Academy of Sciences, Beijing, China

*Schlosseria magister*, *Breviodon? minutus*, and *Lophialetes expeditus* are dominant species in the family of Lophialetidae, an extinct group of tapiroids widely distributed in the Eocene sediments of Asia. In this study, we provide insight into the paleodiet and paleoecology of these Eocene lophialetids via microwear analysis of fossil teeth (N = 132) from Huheboerhe area, Erlian Basin,

China. The results suggest that *L. expeditus* was likely a mixed feeder consuming substantial grit and a small amount of fruit during feeding, while *Breviodon? minutus* was a browser with fruit and/or seeds incorporated into its dietary regime. The dietary preference of *S. magister* shifted toward more abrasive diets over time (from browsers to mixed feeders). This dietary shift is probably correlated to the decreasing trend in global temperatures following the Early Eocene Climatic Optimum, which likely led to the changes of terrestrial vegetation and environment in the Huheboerhe area during that time interval. Based on the microwear analysis and other evidence (mesowear, stable carbon isotope, and the fossil record), the landscape of the early–middle Eocene Erlian Basin was probably becoming more arid and/or open over time and a mixed habitat, which included forest, woodland and shrubland, was most likely present in the middle Eocene Erlian Basin.

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### Dinosaur Systematics, Diversity & Ecology

#### A TITANOSAURIAN SAUROPOD FROM THE CAMPANIAN QUSEIR FORMATION OF THE KHARGA OASIS, EGYPT, SUPPORTS AFRO-EURASIAN DINOSAUR FAUNAL CONNECTIVITY DURING THE LATE CRETACEOUS

Gorscak, Eric<sup>1</sup>, Lamanna, Matthew C.<sup>2</sup>, Díez Díaz, Veronica<sup>3</sup>, Schwarz, Daniela<sup>3</sup>, Salem, Belal S.<sup>4</sup>, Abu El-Kheir, Gebely<sup>5</sup>, Sallam, Hesham<sup>6</sup>

<sup>1</sup>Midwestern University, Downers Grove, Illinois, U.S.A., <sup>2</sup>Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A., <sup>3</sup>Museum für Naturkunde, Berlin, Germany, <sup>4</sup>Benha University, Benha, Egypt, <sup>5</sup>Al Wadi Al Gadid University, Kharga, Egypt, <sup>6</sup>Mansoura University, Mansoura, Egypt

Recent discoveries have begun to elucidate the affinities of the Upper Cretaceous nonmarine vertebrate faunas of continental Africa, reinvigorating exploration into this critical gap in understanding of Mesozoic paleobiogeography and evolutionary history. For example, titanosaurian sauropod dinosaurs from Egypt (*Mansourasaurus* from the Campanian Quseir Formation) and Tanzania (*Rukwatitan* and *Shingopana* from the Namba Member of the Galula Formation) offer nascent support for the hypothesis that Late Cretaceous faunas from northern Africa had closer relationships to those from Eurasia than to those from southern Africa or other Gondwanan regions.

Here we present an associated postcranial skeleton of a medium-sized titanosaur from the Quseir Formation of the Kharga Oasis, Egyptian Western Desert (MB.R.Vb-621–640). Discovered in 1977, the specimen has been repeatedly mentioned in the literature but has never been the subject of a formally published description. The skeleton consists of five somphospondylous dorsal vertebrae and 12 girdle and limb elements; unfortunately, however, it has undergone considerable taphonomic distortion, rendering many bones incomplete and/or compressed and leaving many anatomical interpretations wanting. Furthermore, the comparatively well-preserved left tibia mentioned in previous reports is currently missing.

Preliminary phylogenetic analysis of MB.R.Vb-621–640 using tip-dating Bayesian methods suggests close affinities with *Mansourasaurus* and Late Cretaceous Eurasian titanosaurians. Support for this placement includes the absence of a postzygodiapophyseal lamina in middle and posterior dorsal vertebrae. Although MB.R.Vb-621–640 has only limited skeletal overlap with other Quseir Formation titanosaur specimens, it differs from *Mansourasaurus* in having a fully enclosed coracoid foramen, proportionally more gracile limbs, and a mediolateral groove on metatarsal I, the latter of which may be autapomorphic. MB.R.Vb-621–640 also differs from another, more recently collected titanosaur skeleton from the Kharga Oasis in having a proportionally slenderer tibia, but resembles this specimen in that the posterior dorsals of the latter also lack a postzygodiapophyseal lamina, suggesting that it too may have affinity with European and Asian taxa. As such, the growing collection of titanosaurian fossils from the Campanian of Egypt supports hypotheses of connectivity between northern African and Eurasian dinosaur faunas during the Late Cretaceous.

### Anatomical & Developmental Explorations of the Mammalian Skull

#### DEVELOPMENTAL CONSTRAINTS, ECOLOGICAL SPECIALIZATION, AND THE EVOLUTION OF THE MAMMAL SKULL AND MANDIBLE

Goswami, Anjali, Fabre, Anne-Claire, Dowling, Carys, Noirault, Eve

Life Sciences, The Natural History Museum, London, U.K. The differing reproductive strategies of the three mammalian groups (Monotremata, Marsupalia, and Placentalia) have been hypothesized to have shaped their morphological evolution. For example, in contrast to placentals, marsupial newborns have some parts of their body that are developed earlier (such as the forelimb and head system) in comparison to others as they need to crawl into the pouch to continue developing. Whereas monotremes lay eggs and are the least speciose mammalian

clade with the lowest rate of reproduction. As such, the morphological and taxonomic diversification of each group may be the result of the different functional constraints imposed by these different developmental strategies. Here, we study the impact of reproductive mode on the evolution of morphofunctional diversity in mammals over time. To do so, we used high-density geometric morphometric approaches to characterize cranial shape for 408 species (208 extant and 112 extinct eutherians, 70 extant and 15 extinct metatherians, and three extant monotremes), spanning the full phylogenetic, developmental, and functional diversity in mammals. A total of 74 landmarks, 77 curves, and 522 surface sliding semilandmarks were used to define 17 cranial regions. We further quantified mandible shape for 184 species (63 extant and 62 fossil eutherians, 53 extant and 3 extinct metatherians, and three extant monotremes) with 20 landmarks, 12 curves, and 60 surface sliding semilandmarks. Each cranial element was analyzed separately in order to test for differences in shape, phylogenetic signal, morphological disparity, and rate of evolution depending on reproductive mode and functional diversity. There is substantial phylogenetic signal in cranial shape ( $K_{mult}$  ranging from 0.79 to 1.36) across mammals, but also extensive convergence across major clades, with both diet and habitat significantly associated with aspects of cranial shape. Dasyuromorphian and South American marsupials overlap entirely in shape, falling intermediate between the other Australian marsupials in cranial morphospace. PC1 in marsupials captures variation in rostral length, this aspect of shape defines PC2 in placentals, with placental PC1 driven by nasal retraction, which takes its most extreme form in whales. The anterior facial bones (premaxilla, maxilla, and nasal) show the highest variation, in contrast to most other tetrapod clades, but marsupials show much less disparity in these regions relative to placentals.

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## **Fishes & Chondrichthyans: Evolution & Distribution**

### **A MALVINOKAFFRIC HOLOCEPHALAN FROM THE EARLY DEVONIAN OF THE FALKLAND ISLANDS (ISLAS MALVINAS)**

Gottfried, Michael D.<sup>1</sup>, Jerve, Anna<sup>2</sup>, Bremer, Oskar<sup>2</sup>, Roberts, Eric<sup>3</sup>, Dirks, Paul<sup>3</sup>, Ostrowski, Summer<sup>4</sup>

<sup>1</sup>Earth and Environmental Sciences and Museum, Michigan State University, East Lansing, Michigan, U.S.A., <sup>2</sup>Uppsala University, Uppsala, Sweden, <sup>3</sup>James Cook University, Townsville, Queensland, Australia, <sup>4</sup>University of Wisconsin Parkside, Parkside, Wisconsin, U.S.A.

Recent field research on the Falkland Islands (Islas Malvinas) has resulted in the recovery of a holocephalan indet. toothplate from the Lower Devonian Fox Bay Formation on Pebble Island. This new find adds to the sparse previous record of Devonian fishes known from the islands (*Machaeracanthus* and ischnacanthid acanthodian elements and an arthrodire plate). The holocephalan specimen covers the internal surface of a relatively thin and rounded nodule that is roughly triangular in outline and measures 8 cm across its broadest part. Preservation of the toothplate is imperfect and discontinuous due to weathering on some areas of the exposed surface, but in places where it is well-preserved along the edges there are dentine tubules that open via closely spaced pores on the oral surface, an arrangement that is characteristic of holocephalans. The oral surface of the specimen bears two prominent apically rounded raised areas, similar to what has been noted on some other early holocephalans.

The Fox Bay Formation on the Falklands, including the exposure on Pebble Island where the specimen was recovered, preserves a variety of Early Devonian invertebrates (trilobites, brachiopods, gastropods, orthocone cephalopods, conulariids, and echinoderms). A Pragian age within the Devonian is supported by the presence in the Fox Bay Formation of the chitinozoan *Ramochitina magnifica* which is considered to be a Pragian indicator in Bolivia and Brazil. Previous very early holocephalan records include *Melanodus* from the Middle Devonian (Givetian) of France, and (possibly) *Stensioella* from the late Early Devonian (Emsian) of Germany (but note that *Stensioella* is considered to be a placoderm by some authors). The Pragian-age Falklands specimen therefore putatively represents the earliest occurrence to date of a holocephalan. It further indicates that holocephalans were present in the biogeographically distinctive Early to Middle Devonian Malvinokaffric cold-water marine realm that extended across parts of the Southern Hemisphere, including Bolivia, Brazil and South Africa, which share endemic trilobites and brachiopods. Non-holocephalan chondrichthyans were already known from the Malvinokaffric, notably *Pucapampella*, and holocephalans can now be added to this early chapter in the history of chondrichthyans.

**Funding Sources** National Geographic Society Committee for Research and Exploration,

## **Marine Mammals**

### **LONGIROSTRINE NEARLY HOMODONT DOLPHIN FROM THE LATE OLIGOCENE OF SOUTH CAROLINA: THE ORIGIN OF EURHINODELPHINIDAE AND AFFINITIES OF 'PHOCA' MODESTA AND 'PHOCA' DEBILIS**

Grantham, Suzanne, Boessenecker, Robert

Geology and Environmental Geosciences, College of Charleston, Woodruff, South Carolina, U.S.A.

Eurhinodelphinidae is an extinct family of marine dolphin from the early to mid-Miocene, well represented in eastern North America and Europe. A newly discovered skeleton from an unusual unlithified sandy facies of the upper Oligocene (24.7–23.5 Ma) Chandler Bridge Formation of South Carolina, CCNHM 5852 includes a fragmentary skull, well preserved tympanoperiotics and mandible, partial dentition, and partial vertebral column. Eurhinodelphinid features preserved in CCNHM 5852 include a thickened post-glenoid process, a shortened zygomatic process, short exposure of the frontals at the vertex, anteriorly excavated and constricted involucrum, a long median furrow on the bulla, a deep anterior bullar facet, an elongate posterior process of the periotic, a bulbous lateral tuberosity of the periotic, a ventrolaterally recurved posterior process of the periotic, and a sharp posterodorsal ridge of the periotic. The specimen also compares favorably with members of the *Chilcacetus* clade, including anterodorsally oriented nasals and an unfused mandibular symphysis. Owing to the nearly identical morphology of the periotic and bulla with *Xiphiacetus*, however, we provisionally identify CCNHM 5852 as an early and plesiomorphic eurhinodelphinid. CCNHM 5852 interestingly includes a heterodont dentition, marked polydonta (mandibular tooth count = 30; all single rooted), with unicuspid conical anterior teeth and molariform multicuspedate teeth with spatulate crowns; 2–4 distal accessory cusps are present on these molariform teeth, and an irregular lingual cingulum with cuspules. These molariform teeth are identical to teeth of '*Phoca modesta*' and '*Phoca debilis*' from the poorly defined 'Ashley Phosphate Beds' of Charleston, taxa named by Leidy and based on isolated teeth. These teeth have been considered to represent seals or heterodont dolphins. These teeth are likely congeneric or conspecific with CCNHM 5852, demonstrating that these specimens are the molariform teeth of a longirostrine eurhinodelphinid-like odontocete with vestigial heterodonty and well-developed polydonta. This specimen appears to pull the Eurhinodelphinidae back into the Oligocene, and placement of Eurhinodelphinidae within many cladistic analyses highlights the possibility of multiple origins of homodonty within crown Odontoceti.

#### **Mammalian Skeletal Morphology**

#### **FOSSIL SLOTH CLAW CURVATURE AND BONY CORE TO SHEATH RATIOS PREDISPOSED A SUSPENSORY LIFESTYLE**

Grass, Andy

Anatomy, A.T. Still University School of Osteopathic Medicine in Arizona, Mesa, Arizona, U.S.A.

There are several things about sloths that make them an interesting and unique group of animals to study, as well as making them a rising star in the public eye. The two features that are the most distinctive of modern sloths are their primarily suspensory lifestyle, and their characteristically prominent and curved claws. Extinct sloths also had impressive claws, though they were far more robust. Indeed, large claws are a feature common throughout the clade Xenarthra. Armadillos and anteaters use them to great effect digging and burrowing, and it has been hypothesized that enigmatic caves in North and South America with large scratch marks on the walls were in fact carved out by giant ground sloths. As for the suspensory lifestyle of modern sloths, the evolution of this unusual mode of locomotion is still somewhat of a mystery, as we still have no fossils of suspensory sloths. Complicating matters even more is the recent upheaval of sloth phylogenetics. Regardless, it still seems as if the suspensory lifestyle is a result of convergent evolution between *Choloepus* and *Bradypus*, and not inherited from a common ancestor.

One explanation put forth to explain this convergent evolution is the digging behavior present in other Xenarthrans. The muscles necessary for these behaviors, and possibly present in the ancestral Xenarthran, are the same muscles used to maintain the suspensory position, and can be easily co-opted for such use. Studies already done on fossil sloth claws have shown support for digging in some giant ground sloths, but the shapes have not been directly compared to modern sloths. This study aims to see if a similar explanation of co-option can be posited for the claws in modern sloths. CT data from modern sloths and a selection of fossil sloth claw specimens that still retain the keratinous sheath were analyzed through a combination of linear lengths and angles, and geometric morphometrics. Ground sloths and modern sloths both possessed similar relationships between the bony core and the keratinous sheath. There was some differentiation between the two groups in the GM data, but this can be possibly attributed to the large difference in robustness between them. The similar shapes and curves between the two groups supports the idea that, along with their musculature, the claws of Xenarthrans were already well suited to be used in suspensory behavior, and took little modification to achieve this unique lifestyle.

#### **Symposium: Dietary Reconstruction**

#### **TRACE METAL COMPOSITIONS IN FORMING TEETH REFLECT BOTH MINERALIZATION AND DIET**

Green, Daniel R.<sup>1</sup>, Smith, Tanya M.<sup>2</sup>, Arora, Manish<sup>3</sup>, Austin, Christine<sup>3</sup>

<sup>1</sup>Human Evolutionary Biology, Harvard University, Cambridge, Massachusetts, U.S.A., <sup>2</sup>Australian Research Centre for Human Evolution, Griffith University, Brisbane, Queensland, Australia, <sup>3</sup>Department of Environmental Medicine and Public Health, Icahn School of Medicine at Mount Sinai, New York, New York, U.S.A.

Trace metals are measured in teeth to provide inferences about diet, behavior, and environment coincident with the timing of tooth formation. However, questions remain about how enamel mineralization itself influences trace metal composition, and may therefore influence reconstructions of organismal biology. To resolve this problem, we measure trace metal compositions in relatively immature and more mature tooth molar germs in two distantly related mammals, macaques ( $n = 2$ ) and sheep ( $n = 2$ ). We demonstrate that trace metals appear to exhibit transient increases in concentrations in either secretion or maturation in both taxa. The pattern of trace metal concentration variation during mineralization is perhaps clearest for magnesium, an indicator of trophic position, which shows a burst of high concentration in superficial enamel early in the maturation phase of all teeth. In fully mature enamel, this transient high concentration is no longer visible. Strontium, whose isotopes serve as a proxy for migration patterns, appears to show highest concentrations in secretory enamel. In mature enamel, strontium concentration bands appear to reflect primary dietary or environmental signals, instead of subsequent mineralization. Our data show that barium, a proxy for nursing behavior, shows high concentrations in the secretory phase of formation. By contrast, manganese data demonstrate a pattern that appears more linked to tooth crown position than to the formation process itself. Toxic at high doses, manganese concentrations appear highest in superficial enamel, indicating that estimates of toxic exposure must take the location of enamel sampling into account. These data provide a promising demonstration of the impact of mineralization stage upon metal concentrations in teeth.

To further explore potential molecular mechanisms that underlie our observations, we query a proteomic database with proteins previously observed in different phases of mineralizing enamel. We find that proteins known to bind magnesium are located in maturation enamel, suggesting that increased protein expression by ameloblasts and abundance in enamel may contribute to our observations of high magnesium in maturing enamel. Altogether, our results demonstrate that certain metals may preferentially reflect mineralization processes in immature teeth, and suggest important molecular mechanisms for further study.

**Funding Sources** Harvard University.

**Colbert Poster Prize/Biomechanics & Functional Morphology**

## APPLYING 2D AND 3D IMAGING TECHNIQUES TO EVALUATE BITE FORCE IN MODERN AND EARLY PALEOCENE MAMMALS

Green, Mariah A.<sup>3</sup>, Fischenich, Kristine<sup>1</sup>, Eberle, Jaelyn J.<sup>3</sup>, Lyson, Tyler R.<sup>2</sup>

<sup>1</sup>Department of Mechanical Engineering, University of Colorado Boulder, Boulder, Colorado, U.S.A., <sup>2</sup>Department of Earth Sciences, Denver Museum of Nature & Science, Denver, Colorado, U.S.A., <sup>3</sup>University of Colorado Museum of Natural History, University of Colorado Boulder, Boulder, Colorado, U.S.A.

Bite force is a measure that biologists and paleontologists use to better understand ecological specializations of extant and extinct mammals. Extant mammals with higher bite forces typically have a carnivorous or a hard object diet and mammals with lower bite forces typically have an herbivorous or soft object diet. The dry skull method is a nondestructive technique that estimates bite force in the absence of soft tissues such as the masticatory muscles on the skull and is particularly useful for evaluating extinct mammalian taxa where soft tissue is not preserved. Here, we apply the dry skull method using 2D and 3D imaging techniques to assess the most appropriate method in acquiring bite force in extant mammals where bite force has been directly measured, including *Vulpes vulpes macroura* (red fox), *Lynx rufus pallescens* (bobcat), *Canis latrans* (coyote), and *Canis lupus tundrae* (wolf). The two techniques produced similar results (~3% difference). We applied these same techniques to the crania of two early Paleocene (Puercan) mammals: *Eoconodon coryphaeus* ('Triisodontidae') and the peripitychid *Carsiptychus coarctatus* recently recovered from the Denver Formation in the Denver Basin, Colorado. We estimate the cross-sectional area of the masseter and temporalis muscles and lever arms using images of the skulls in dorsal, ventral, and lateral orientations. Using the 2D and 3D techniques we determined the bite force of *E. coryphaeus* to be 868 newtons (N) and 922 N, respectively, and *C. coarctatus* to be 188 N when measured in 2D. The bite force of *E. coryphaeus* is significantly higher than a modern wolf (334–342 N in 3D and 2D, respectively) and other extant mammals included in this study. Typically, in extant mammals, a high bite force correlates with a carnivore/predatory niche, which suggests *E. coryphaeus* may have filled a similar niche during the early Paleocene. In addition, the disparate degrees of bite force between *E. coryphaeus* and *C. coarctatus* suggests these large-bodied mammals occupied different dietary niches. Implementing 2D and 3D imaging techniques to estimate bite force provides clues on how extinct mammals may have filled paleoecological niches.

**Funding Sources** This research was funded by the University of Colorado Museum of Natural History Museum Student Research Award Program.

## Education & Outreach

### **“HOW DO YOU KNOW WHERE TO DIG?”: USING A STUDENT-DRIVEN EXPERIENTIAL LEARNING ACTIVITY TO TEACH HYPOTHESIS-BASED FIELDWORK IN A LARGE GENERAL EDUCATION UNIVERSITY COURSE**

Griffin, Christopher, Stocker, Michelle R.  
Virginia Tech, Blacksburg, Virginia, U.S.A.

Experiential learning relies on learner activity and increased responsibility, accountability, and autonomy on the part of the student. This pedagogical style has been shown to provide an effective means of increasing both the quality and duration of information retention in the student. However, experiential learning is seen as easiest to implement in smaller, upper-level classes. Large general education classes (>100 students), in which student interest and background knowledge can vary wildly, make these techniques difficult to incorporate successfully. We developed an hour-long in-class activity to impart hypothesis-driven investigative techniques in the context of paleontological fieldwork for a general education Age of Dinosaurs course. We placed students into ‘research teams’ of paleontologists seeking funding to find a new locality containing early dinosaurs (Carnian stage, ~230 Ma) based on real fieldwork. Each group received information sheets regarding taxa (including index taxa) and rock formations from the Permian–Jurassic, a map of Pangaea, and a description of its paleoclimate. Students also were given questions to guide them through proper reasoning to pick one of the given formations as the most appropriate for their expedition: the rock unit likely to contain fossils and the age, paleoclimate, and paleobiogeography of the earliest known dinosaurs. We acted as facilitators, answering questions and providing clarification but not lecturing, allowing students to sort out ambiguities or disagreements among themselves. In doing this, the students built hypotheses of taxon occurrence, distribution, and paleoenvironment to raise the best possible case for an expedition locality. At the end of the class period we revealed the correct locality and what the students ‘found’ there (given that the project was based on recent excavations), and student investment/excitement was clear during the reveal. This activity incorporated the inferential reasoning of biochronology, the interpretation of paleoecology, and building testable, evidence-based hypotheses regarding historical science in an active, collaborative learning experience rather than passive lecture. Our project can easily be adapted to other field-

based questions or to a digital-only course and provides a way to engage students of diverse backgrounds and abilities in experiential, problem-based learning in a large course without requiring inaccessible travel to field sites.

## Romer Prize

### **‘RECAPITULATION’ OF ANCESTRAL STATES ACROSS THE EARLY ONTOGENY IN THE AVIAN PELVIS IS DRIVEN BY PERSISTENT MODULARITY IN THE ARCHOSAURIAN HINDLIMB**

Griffin, Christopher  
Virginia Tech, Blacksburg, Virginia, U.S.A.

Paleobiology is crucial to unravelling the interplay between developmental processes and the evolution of vertebrate form because ancestral states can only be directly observed through the fossil record. Terminal addition, wherein ancestral states shift to derived states during development (i.e., ‘recapitulation’), is thought to stem from constraints to early development – this remains controversial and is rarely thought to be a source of morphological novelty for deeper (i.e., ‘class’-level) divergences. Living birds (Aves), with an incredible diversity and a highly derived bauplan, represent one such major divergence. Although some avian anatomical regions possess derived morphologies throughout prehatching ontogeny (e.g., the skull), whether this is uniform across all regions is unclear. To test for terminal addition in the development of the distinctive avian pelvis, I integrated a novel embryological imaging technique (modified CLARITY protocol) to record the morphogenesis of avian pelvic tissues in three dimensions at early embryonic stages, allowing direct comparison with the fossil record. The stepwise evolution of the avian pelvis is well-constrained by an excellent fossil record, allowing the progressive sequence of ancestral states to be observed across the avian stem. I found that many ancestral dinosaurian features (e.g., forward-facing pubis, short ilium, pubic ‘boot’) are present early in avian morphogenesis, which only transitions to derived form later in prenatal ontogeny, with the sequence of transition mirroring phylogeny. I integrated this developmental data with the fossil record by creating a dataset of 3D meshes of avian embryonic cartilage created through confocal microscopy and computed tomographic scans of fossilized pelvises across the avian stem. Using 3D geometric morphometrics, I quantitatively demonstrate that avian pelvic ontogeny parallels the theropod-to-avian transition and provide evidence for statistically significant evolutionary modules within the pelvis using covariance ratios of landmarks ( $p < 0.05$ ). Comparisons of covariances reveals that paravian pelvises possess the same modular relationships as early theropods and earlier archosaurs, and

the avian pelvis is the result of these same covarying proportions under a different locomotory strategy. Instead of developmental constraints, terminal addition in avian ontogeny may stem from these conserved modular relationships persisting across millions of years of evolution.

**Funding Sources** NSF GRFP.

## Preparators

### PREPARATION AND RECONSTRUCTION OF THE TEETH OF *ADALATHERIUM HUI*, A GONDWANATHERIAN MAMMAL FROM THE UPPER CRETACEOUS MAEVARANO FORMATION OF MADAGASCAR

Groenke, Joseph R.<sup>1</sup>, Krause, David W.<sup>2</sup>, Hoffmann, Simone<sup>3</sup>

<sup>1</sup>Department of Biomedical Sciences, Ohio University, La Crosse, Wisconsin, U.S.A., <sup>2</sup>Department of Earth Sciences, Denver Museum of Nature and Science, Denver, Colorado, U.S.A., <sup>3</sup>College of Osteopathic Medicine, New York Institute of Technology, Old Westbury, New York, U.S.A.

We describe details of the mechanical and digital preparation of the dentition of the holotype of *Adalatherium hui* (UA 9030), a virtually complete skeleton of a gondwanatherian mammal from the Upper Cretaceous Maevarano Formation of Madagascar. While remarkably complete, taphonomic processes (likely including infiltration of modern roots and swelling clay minerals at and just below the erosional surface) resulted in the destruction of most of the braincase and degradation of other posterior portions of the skull. Mechanical preparation with insect pins and carbide needles revealed that distal aspects of the postcanine dentition in particular were affected, with shattered enamel fragments displaced to varying degrees from their condition prior to death and burial. Because most fragments (sub-mm in size) were realistically too challenging to mechanically repair, and out of concern that disarticulation of fragments would result in important loss of information related to in-situ positions, we digitally separated and reconstructed these fragments. Segmentations of individual teeth were first performed, followed by sub-segmentation into between 2 and 220 fragments depending on the condition of the tooth. These fragments were then reconstructed digitally, with an intermediary step of rapid prototyping at enlarged scale to inform the second round of changes. All fragment position changes from in-situ to idealized, as-in-life reconstructions were recorded for repeatability. Changes between in-situ and in-life position were animated in a 'rocker' style to qualitatively depict patterns of displacement relative to an 'anchor' fragment. Challenges that arose were due to degrees of freedom for fragments capable of passing

through one another, number of fragments, scale of fragments, and displacement. To ground-truth results, we scaled up and rapid prototyped fragments critical to the digital reconstructions, and used fragment maps and animations to create physical reconstructions with the help of researchers and volunteers. These models will be used in ongoing research into the occlusion and function of these extraordinary teeth, which are unlike those of any mammaliaform yet known.

**Funding Sources** National Science Foundation EAR-1528273, EAR-1664432.

## Quantitative Methods

### THE DOS AND DON'TS OF DATING: COMPARING DIFFERENT TIP-DATING METHODS TO ESTIMATE NEOSUCHIAN DIVERGENCE TIMES

Groh, Sebastian S.<sup>1</sup>, Upchurch, Paul<sup>1</sup>, Day, Julia<sup>1</sup>, Barrett, Paul M.<sup>2</sup>

<sup>1</sup>University College London, Harrow, U.K., <sup>2</sup>Natural History Museum London, London, U.K.

The accurate time-scaling of phylogenetic trees is an important basis for subsequent evolutionary studies, such as inferring trait evolution or performing biogeographic analyses. Recently, a number of advances have been made that enable tip-dating of trees based on morphological character data. Four main methods are currently used: cal3, Extended Hedman, the Fossilised Birth-Death model (FBD), and Ghost-Lineage-Analysis (GLA). However, thus far there has been no direct comparison of all four methods and their sensitivity to changes in topology. In this study, we applied all four dating approaches to a set of newly constructed phylogenies for the crocodylomorph clade Neosuchia.

All four methods show sensitivity to taxonomic coverage and changes in topology, with Extended Hedman and GLA emerging as the most vulnerable. In addition, Extended Hedman displays large standard deviations on estimated node ages. Cal3 and FBD were found to be the most suitable methods for time-scaling fossil-only trees. It is important, however, to aim for good taxonomic coverage (in particular the inclusion of the oldest taxa within each clade of interest) and possess a good understanding of the phylogenetic history of the examined group, independent of which method is used.

The application of cal3 and FBD to the neosuchian tree confirms that all major all neosuchian lineages were present and distinct by the Early Jurassic. All of its extant clades (Crocodyloidea, Gavialoidea, and Alligatoroidea, including Caimaninae) had diverged before the K/Pg boundary. Our results support two different evolutionary scenarios around the K/Pg event: 1) a slow, gradual evolution of several smaller neosuchian lineages (Diplocynodontinae, Tomistominae, Crocodylinae)

starting in the Late Cretaceous (FBD); or 2) a diversification burst during the early Paleogene with rapid evolution of the aforementioned clades (ca13). We can reject any hypotheses that place the origin of Caimaninae after the K/Pg boundary, as well as those postulating a much later evolution of clades such as Crocodylinae and Diplocynodontinae.

**Funding Sources** Financial support for this study was provided by the London NERC DTP (NE/L002485/1) and the UCL Bogue Fellowship.

## Mammalian Skeletal Morphology

### SKELTAL ADAPTATIONS IN EXTANT AND FOSSIL GLIDING MAMMALS EXEMPLIFY MANY-TO-ONE MAPPING OF FORM TO FUNCTION, NOT CONVERGENCE

Grossnickle, David<sup>1</sup>, Chen, Meng<sup>4</sup>, Wauer, James<sup>3</sup>, Pevsner, Spencer K.<sup>5</sup>, Weaver, Lucas N.<sup>1</sup>, Meng, Qing-Jin<sup>2</sup>, Liu, Di<sup>2</sup>, Zhang, Yu-Guang<sup>2</sup>, Luo, Zhe-Xi<sup>3</sup>

<sup>1</sup>University of Washington, Seattle, Washington, U.S.A., <sup>2</sup>Beijing Museum of Natural History, Beijing, China, <sup>3</sup>The University of Chicago, Chicago, Illinois, U.S.A., <sup>4</sup>Nanjing Institute of Geology and Palaeontology, Nanjing, China, <sup>5</sup>University of Bristol, Bristol, U.K.

Ecology and biomechanics play central roles in the generation of phenotypic diversity. When unrelated taxa invade a similar ecological niche, biomechanical demands can be a driving mechanism for similar morphological transformations (adaptive convergence). Alternatively, there may be multiple biomechanical solutions to the same functional requirement (many-to-one mapping of form to function). Identifying and examining these distinct evolutionary scenarios help to elucidate the key drivers of phenotypic change. In mammals, gliding locomotion is often presented as a classic case of convergent evolution because it has arisen independently in numerous clades, including six extant lineages and several fossil lineages, each possessing patagia ('wing' membranes) that generate lift during gliding. We test whether the skeletal morphologies of the gliding mammal clades demonstrate convergence by applying phylogenetic comparative methods to skeletal measurements. Analyses include examining evolutionary trajectories in phylomorphospace and fitting evolutionary models to the morphometric data to test for selection toward specific adaptive peaks in a fitness landscape. We find that gliders consistently evolve longer, more gracile limbs than arborealists, likely to increase patagial surface area. However, gliding mammals do not converge on a single glider morphotype. Instead, skeletal morphology varies considerably among gliders, and it is influenced by factors such as body size and attachment location of patagia on the forelimb. Thus, the disparate skeletal morphologies of gliding mammals

exemplify many-to-one mapping of form to function. This conclusion is further demonstrated by fossil haramiyidans (mammaliaforms) from the Mesozoic Era, which are posited to be gliders based on preserved patagia. Multivariate analyses demonstrate that these taxa possess suites of characters that are distinct from those of extant gliders. Thus, gliding adaptations have evolved iteratively in stem and crown mammals, with each clade possessing a unique skeletal morphology.

**Funding Sources** National Science Foundation Postdoctoral Research Fellowship.

## Marine Mammals

### NEW KENTRIODONTIDS (CETACEA, ODONTOCETI) FROM THE MIDDLE MIOCENE OF THE WESTERN NORTH PACIFIC AND A REVISION OF KENTRIODONTID PHYLOGENY

Guo, Zixuan<sup>1</sup>, Kohno, Naoki<sup>2</sup>

<sup>1</sup>School of Life and Environmental Science, University of Tsukuba, Tsukuba, Japan, <sup>2</sup>National Museum of Nature and Science / University of Tsukuba, Tokyo / Tsukuba, Japan

The kentriodontids are small to medium-sized extinct dolphins known throughout the world from the early to late Miocene. Because of the symmetrical arrangements of their cranial bones, which differs from the asymmetrical arrangements of most of the crown odontocetes (toothed whales), kentriodontids are thought to be a stem group among the Delphinida, including the crown delphinoids. In early studies, the kentriodontids were generally recognized as a monophyletic group (Kentriodontidae). However, recent studies show that they may be paraphyletic or polyphyletic.

Recently, two well-preserved fossil kentriodontid-like dolphin crania were recovered from the early middle Miocene (ca. 16–15 Ma) of northern Honshu, Japan. The first specimen consisted of a braincase with right tympanoperiotics, fragments of left and right mandibles, a partial atlas, and one tooth. The second specimen consisted of a nearly complete cranium without tympanoperiotics and teeth. Both specimens have a low and flat cranial vertex and symmetrical and knob-like posterior ends of the premaxillae, which are connected to the symmetrical nasals. All these characters are identical to most kentriodontids. However, these two specimens also have some different character combinations, thus they can be classified as two different species within the kentriodontids.

We performed a phylogenetic analysis to locate the new specimens among the kentriodontids, based on a data matrix combined from previous studies. It consisted of 104 taxa, including almost all of the kentriodontids, and 398

morphological characters, with a tree constraint based on molecular evidence from extant taxa of cetartiodactyls. Results of the analysis indicate that both of the two new specimens are included in the kentriodontids with the type species of the genus *Kentriodon* as the closest taxa. All the known kentriodontids were recognized as monophyletic and positioned as a sister group to the crown Delphinoidea. Our analysis showed that 11 synapomorphies supported the monophyly of the Kentriodontidae. Almost half of the synapomorphies for the node including the Inioidea, Kentriodontidae, and Delphinoidea (s.l.) are those from the tympanoperiotics. This suggests that their hearing capabilities (e.g., high-frequency hearing) laid the foundation for the diversification of their echolocation abilities. At this point, this dynamic renewal might also have been a driver for the diversification of the kentriodontids.

### **Biomechanics & Functional Morphology**

#### **PTEROSAUR SOFT TISSUES REVEALED BY LASER-STIMULATED FLUORESCENCE ENABLE IN-DEPTH ANALYSIS OF WATER LAUNCH PERFORMANCE**

Habib, Michael B.<sup>1</sup>, Pittman, Michael<sup>2</sup>, Kaye, Thomas G.<sup>3</sup>  
<sup>1</sup>Dinosaur Institute, Natural History Museum of Los Angeles County, Valencia, California, U.S.A., <sup>2</sup>Earth Sciences, University of Hong Kong, Hong Kong, Hong Kong, <sup>3</sup>Foundation for Scientific Advancement, Sierra Vista, Arizona, U.S.A.

Water launch capacity has been previously suggested for some marine pterosaurs based on osteological grounds, but robust estimates of specimen-specific performance are difficult without robust estimates of wing area and potential hindfoot webbing. Here, we provide the first estimates of pterosaur water launch performance that take into account preserved soft tissue anatomy. The aurorazhdarhid pterosaur specimen MB.R.3531 from the Upper Jurassic Solnhofen Limestone was imaged using Laser-Stimulated Fluorescence, revealing significant soft tissue preservation. These soft tissues are among the best-preserved of any known Jurassic pterosaur, including for the first time, a complete actinofibrillar complex, an undistorted actinopatagium with the retrophalangeal connective tissue wedge and entire trailing edge, and webbed feet. These physically validated soft tissues formed the basis for analyzing water launch capability in MB.R.3531. We modeled the water launch as quadrupedal and broadly similar to modern ‘puddle jumping’ anseriform birds that use a combination of their webbed feet and partially folded wings to push against the water surface during takeoff. Under this model, both hind limb and forelimb contact areas are critical. Under conservative

assumptions regarding power and range of motion, we predict that MB.R.3531 was capable of rapid takeoff from the water surface. Our model predicts that water launch performance in pterosaurs was particularly sensitive to three factors: available propulsive contact area, forelimb extension range, and extension power about the shoulder. MB.R.3531 possessed both osteological and soft tissue features that significantly enhanced these performance characteristics (including, but not limited to, expanded internal rotator/extensor attachments on the proximal humerus, extended humeral length, chordwise distal actinofibril orientation, and webbed pes). These features would have limited impact on flight performance. We therefore interpret them as likely water takeoff specializations. The osteological specializations in MB.R.3531 are subtle, which may be related to its small size. Larger marine pterosaurs appear to exaggerate these characteristics, which matches expectations from scaling. We show that soft tissue data can be used to help validate the dynamic feasibility of water launch in pterosaurs, suggesting it was a regular part of foraging behavior in some taxa.

### **Quantitative Methods**

#### **THE EFFECT OF REGIONAL PATCHINESS ON THE EVOLUTION OF SIMULATED PHYLOGENIES**

Halliday, Thomas J.<sup>1</sup>, Garwood, Russell<sup>2</sup>  
<sup>1</sup>Earth Sciences, University of Birmingham, Enfield, U.K., <sup>2</sup>Earth and Environmental Sciences, University of Manchester, Manchester, U.K.

There are many types of bias that impact the interpretation of the fossil record. Differences arising from geographic factors, variations in deposition, taphonomy, time-averaging, and the accessibility and area of fossiliferous rock, are non-random and patchy across the Earth’s surface for any given time interval. Biological patchiness enhances this; species distributions are related to ancestral range and environmental factors. While geographic factors are often accounted for in richness studies, their effect on phylogenetic inference is unknown.

Taxa diversifying in unsampled regions whose descendants are later sampled may present problems for inferring tree topology and divergence dates. A clade dispersing from an unsampled region to a sampled region appears in the record like a clade undergoing a rapid adaptive radiation. Here, we investigate the extent to which geographic patchiness in preservation affects accurate reconstruction of evolutionary history.

Using a recently-published agent-based evolutionary model, TREvoSim, we simulated the simultaneous evolution of two communities of constant and equal size. Each community comprised binary genomes, each

representing an individual. In each iteration, mutations were introduced during reproduction, and the fitness of each individual assessed against changing environmental masks, determining the likelihood of reproducing. Dispersal occurred at a symmetric low-level probability. We tested the impact of extreme environmental perturbations and increases in dispersal probability, among other scenarios, and sampled the record to generate a fossil record of the simulation.

For each simulation, the resultant character-taxon matrices were degraded, removing the record of one community, and considering different levels of character and taxon preservation quality. Topology and divergence dates were inferred using Bayesian methods, and compared with the true tree.

Our results demonstrate little effect of taxon or character completeness on phylogenetic accuracy or precision except where character completeness was very low. Increases in dispersal probability had little effect on accuracy but reduced precision, and caused a greater reduction in richness for post-perturbation communities. Notably, for taxa that dispersed together, divergence dates from the virtual fossil record were too young, with intriguing implications for the interactions between the geology and biology that generate our data as paleontologists.

**Funding Sources** Leverhulme Trust Early Career Fellowship to TJDH.

### Symposium: Paleoneurology

#### ENDOCRANIAL MORPHOLOGY OF THE NEOCERATOPSIAN DINOSAUR *LEPTOCERATOPS GRACILIS* FROM THE LATE CRETACEOUS HELL CREEK FORMATION, MONTANA, U.S.A.

Han, Jingyi<sup>2</sup>, Morhardt, Ashley C.<sup>3</sup>, Farke, Andrew A.<sup>1</sup>

<sup>1</sup>Raymond M. Alf Museum of Paleontology at The Webb Schools, Claremont, California, U.S.A., <sup>2</sup>The Webb Schools, Claremont, California, U.S.A., <sup>3</sup>Department of Neuroscience, Washington University School of Medicine in St. Louis, St. Louis, Missouri, U.S.A.

The endocranial anatomy of ceratopsian dinosaurs is increasingly well sampled, with physical and digital endocasts described for the basal ceratopsian *Psittacosaurus*, the basal neoceratopsian *Auroraceratops*, the coronosaur *Protoceratops*, and several ceratopsids (e.g., *Triceratops*). However, leptoceratopsids represent a particularly vexing gap in this sample, occupying a phylogenetic position intermediate between *Auroraceratops* and *Protoceratops*. Here, we describe the first endocast from the leptoceratopsid *Leptoceratops gracilis*, based on a referred partial disarticulated skull (UWGM 200, deposited at the University of Wisconsin Geological Museum) from the late Maastrichtian-aged Hell

Creek Formation of Montana, U.S.A. Disarticulated braincase elements were CT scanned individually and then aligned to a scan of an assembled cast. The resulting data were segmented and visualized in 3D Slicer to construct a digital endocast for this study. Major structures recovered on the endocast include complete or partial impressions for the olfactory bulbs(?) and tracts, cerebral hemispheres, pituitary gland, carotid arteries, various cranial nerves, inner ear, hindbrain, and intracranial veins.

The digital endocast for UWGM 200 has a volume of approximately 83 cm<sup>3</sup>, not including most neurovascular canals or olfactory bulbs. The postcerebral region is relatively straight along its dorsal edge when viewed laterally, more similar to the condition in *Protoceratops* and ceratopsids than to the extremely flexed condition of *Auroraceratops* and *Psittacosaurus*. The olfactory region is angled at approximately 120° relative to the rest of the endocast, more similar to the angle seen in *Protoceratops*, and contrasting with the relatively linear alignment seen in *Auroraceratops* and *Psittacosaurus*. The similarities between the endocasts of *Protoceratops* and *Leptoceratops* may reflect a combination of phylogenetic proximity as well as roughly similar endocast sizes.

**Funding Sources** Department of Neuroscience at Washington University School of Medicine; David B. Jones Foundation; Augustyn Family Fund; Mary Stuart Rogers Foundation.

### Late Cenozoic Mammalian Macroecology & Macroevolution

#### TESTING THE TECTONIC CONTROLS ON PRESERVATION AND MAMMAL SPECIES RICHNESS IN A MIOCENE BASIN FROM SOUTHERN CALIFORNIA

Hardy, Fabian

Earth and Environmental Sciences, University of Michigan, Ann Arbor, Michigan, U.S.A.

The complex topography and excellent fossil record of the Mojave region make it an ideal location for testing hypotheses about the influence of the physical environment on mammals. By placing a well-resolved biochronologic record against the timing of major tectonic or climatic intervals, it is possible to evaluate relationships between landscape development and changes in faunal composition. We examined the fossil record of large mammals in the Dove Spring Formation (12.5–8.0 Ma) in southern California's El Paso Basin to generate a sequence of first and last occurrences within 0.5 Myr time intervals. We focused on four ungulate families (Antilocapridae, Camelidae, Equidae, and Merycoidodontidae) due to their abundant specimens in the section. We found that

antilocaprids and oreodonts occur in most intervals, while camelids and equids are more restricted. Six species of equids occur near the base of the section and persist in the basin until approximately 9.5 Ma, when all perissodactyls disappear from the basin record. Three species of camelids occur only between 11.5 and 9.5 Ma. The majority of ungulate species extirpate or become locally extinct by 9.0 Ma. Peaks in locality frequency and species richness occur between 10.5 and 9.5 Ma, which suggests that the most favorable preservation conditions occurred during this interval.

Beginning near 10.0 Ma, the El Paso Basin was rotated and translated nearly 64 km westward along the Garlock fault, followed by extension and increased subsidence initiating near 9.0 Ma. A sustained low sediment accumulation rate is associated with this interval, suggesting an increase in basin area. Barriers to dispersal were likely removed and habitat availability increased for ungulates. The tectonic episodes did not have an apparent influence on preservation conditions in the basin, as the majority of the section consists of taphonomically similar sedimentary facies. We present a test of alternative hypotheses for the relationships between tectonic change, preservation rate, and species richness.

**Funding Sources** University of Michigan Rackham Graduate School, University of Michigan Department of Earth and Environmental Sciences.

### **Colbert Poster Prize/Mesozoic & Early Cenozoic Mammals**

#### **MASTICATORY MECHANICS IN *PELIGROTHERIUM*, AN OMNIVOROUS NON-TRIBOSPHENIC MAMMAL FROM SOUTH AMERICA SHOWING CONVERGENCE TO MODERN THERIANS**

Harper, Tony<sup>1</sup>, Rougier, Guillermo W.<sup>2</sup>

<sup>1</sup>Cogstone Resource Management, Palm Desert, California, U.S.A., <sup>2</sup>Anatomical Sciences and Neurobiology, University of Louisville, Louisville, Kentucky, U.S.A.

Studies of masticatory motor patterns seen in generalized and derived therian mammals suggest that adaptations for elaborate, medio-laterally extensive, chewing have evolved independently in both marsupials and placentals. While such in vivo recordings are unavailable for fossil mammals, we present biomechanical evidence for another convergent attainment of accentuated 'Phase 2' mediolateral mastication in the Early Paleocene meridiolestidan mammal *Peligrotherium tropicalis* (a non-therian mammal). We contrasted the distribution of estimated bite-force and joint-reaction-force magnitudes between the reconstructed skull of *Peligrotherium* and a variety of extant marsupials and placentals. This was

accomplished using a 3-dimensional extension of the classical bifurcated mandibular leverage analysis over a dense sample of vertices on digitized surfaces of the lower postcanine tooth-row. The analysis suggests that *Peligrotherium* lacks the ability to conserve high bite-force magnitudes at far anterior tooth positions and at high gape, unlike in modern carnivorans and the generalized therian *Didelphis*. At low gape, the relative geometric advantage of Triplet-2 versus Triplet-1 jaw adductor muscles also show general similarity to omnivorous/herbivorous placentals. The Phase-2, low-gape, adapted geometry of the masticatory apparatus of *Peligrotherium* suggests that the complex, bunodont dentition of this taxon was not adapted for extreme durophagy; and that the Mesozoic trend of increasing body size and dental complexity seen in most members of the meridiolestidan lineage allowed *Peligrotherium* to become one of the earliest large-bodied omnivores within the 'Age of Mammals'.

### **Symposium: Dietary Reconstruction**

#### **VERTEBRATE MOBILITY WITHIN STRONTIUM ISOSCAPES: A FRAMEWORK FOR ACCURATE, INFORMATIVE, AND VISUAL MAPPING**

Harrington, Matthew, Widga, Chris  
Center of Excellence in Paleontology, East Tennessee State University, Wheaton, Illinois, U.S.A.

The presence of <sup>87</sup>Sr/<sup>86</sup>Sr in vertebrate bones and teeth provides unique opportunities to identify potential origins and migratory pathways across landscapes. <sup>87</sup>Sr/<sup>86</sup>Sr in vertebrate tissues often represents averaged behavioral information at lifetime, annual, or seasonal scales. Typically, values are mapped onto regional or local strontium isoscapes to qualitatively determine an optimal visual match. Currently, there is no quantitative approach to mapping results in a way that clearly integrates information about the source animal's home range, life history, geographic barriers, or degree of time averaging. As strontium isotope analyses become more commonplace, replicable guidelines for accurate mapping and visualization of results is essential. We create an analytical framework for analyzing and interpreting vertebrate mobility based on biological, ecological, and geological phenomena. Vertebrate mobility can be categorized by geographic scale: (1) local (<5 mi<sup>2</sup>), (2) sub-regional (<25 mi<sup>2</sup>), (3) regional (<50 mi<sup>2</sup>), (4) super-regional (<100 mi<sup>2</sup>), and (5) continental (>100 mi<sup>2</sup>). Life expectancy is paired with this classification scheme as a longer life expectancy is predicted to increase the overall mobility potential. Geographical barriers for each species are identified and removed from the isoscape to avoid over-predicting potential mobility. An understanding of rate of mobility for the study specimen is applied to expand or limit the predicted isoscape regions. This framework promotes a

streamlined approach to mapping vertebrate movements in time and space. To create a standardized, replicable process, we also explore methods to visualize vertebrate movements over time on single or multiple maps. With different vertebrates possessing vastly different movement behaviors, visualizations of target specimens require varying methods of display. We provide recommendations for visualizing a single lifetime average, chronological annual averages, and chronological seasonal averages over a determined landscape. The move towards a standardized approach to mapping vertebrate mobility through  $^{87}\text{Sr}/^{86}\text{Sr}$  analysis will aid in the comparison of results between various species over similar landscapes. This process creates a more accessible and interpretable way to understand extinct and extant vertebrate mobility.

### **Colbert Poster Prize/Biomechanics & Functional Morphology**

#### **MANUS BIOMECHANICS OF A GIANT MASTODON FROM THE GRAY FOSSIL SITE SUGGESTS THE ABILITY TO TRAVERSE UNEVEN TERRAIN IN A KARSTIC AND MOUNTAINOUS REFUGIUM**

Hart, Brenna  
Anatomy and Cell Biology, Oklahoma State University,  
Tulsa, Oklahoma, U.S.A.

The largest terrestrial animals have adapted to supporting their body mass by walking on graviportal limbs. In sauropods and proboscideans, graviportal limbs are typically constrained to several structural features: columnar articulation, digitigrade stance with near vertically oriented metapodials, cushioned by fat pads, tightly and circularly arranged carpals and tarsals, and a greatly reduced distal phalangeal size. Variances in these characters can be adaptive for specific graviportal animals that faced challenges with their habitats, such as terrain navigation and the pursuit for food. A striking manual adaptation is present in the manus of a giant mastodon from the Gray Fossil Site (GFS; Gray, Tennessee, U.S.A.).

GFS is a sinkhole-based, fossil-bearing deposit located in the Appalachians representing a C3 forest refugium present during the spread of the Miocene C4 dominant grasslands at the Hemphillian and Blancan transition 4.5 to 4.9 Ma. The discovery of a nearly complete, giant, and undescribed mastodon highlights variation in manus morphology and biomechanics in Proboscidea. The GFS mastodon had a highly splayed manus, unappressed first and second metacarpals, tripartite terminal phalanges, and a first digit that is oriented approximately  $45^\circ$  from the rest of the manus and is in full contact with the ground surface. Because the GFS mastodon was several tonnes larger than the common *Mammuthus americanus* approaching and even

exceeding body masses calculated for some species of *Mammuthus*, and it lived in a karstic, mountain terrain, such unique manual characteristics could have been adaptations to navigating steep terrain, while supporting an enormous body mass.

From surface scans of its elements, we constructed finite element models of its manus in Amira to test stresses and strains under loads from different gaits. Mass was estimated from allometric methods, and used to determine forces on the bones at various speeds. We applied distal forces, proximal constraints, and material properties for FEA in Strand7 and COMSOL Multiphysics. Maximum stresses of 8 Mpa at low speeds indicate that all elements had high safety factors, suggesting that the broad manus and divergent first digit enhanced potential capability to traverse high relief terrain. The unique manus features would have created a broader surface area, and the more mobile thumb might have had gripping or bracing capabilities, all of which would have made traversing the terrain easier.

### **Anatomical & Developmental Explorations of the Mammalian Skull**

#### **THE CARNIVORAN OSSICLES OF RANCHO LA BREA**

Hartstone-Rose, Adam, Elminowski, Erin E., Blume, Abby M., Dickinson, Edwin  
Biological Sciences, North Carolina State University,  
Raleigh, North Carolina, U.S.A.

The Rancho La Brea (RLB) fossil collection housed at the La Brea Tar Pits and Museum in Los Angeles, California contains the richest collection of carnivoran fossils in the world, representing nearly every bone in the skeleton, including the auditory ossicles. In this study, the ossicles of some of RLB's most iconic extinct carnivorans, *Canis dirus*, *Smilodon fatalis*, *Panthera atrox*, and *Arctodus simus* are compared in both size and overall morphology to those of extant analogs – ossicles of modern canids, felids, and ursids. Six measurements were taken on the malleus, five on the incus, and seven on the stapes. Principal Component Analyses (PCA) were used to explore morphological trends, and Geometric Mean (GM) was calculated to explore scaling differences. As expected, the majority of observed variation was driven by size. Although the most delicate ossicle, the stapes, was preserved in too few specimens for most statistical analyses, for the malleus and incus, ursids overlap in PCA morphospace with felids and not canids despite their closer phylogenetic relationship with the latter family. Also unexpectedly, the *S. fatalis* incus morphospace is more similar to that of canids than to other felid specimens. When examining principal component space within

individual families, *C. dirus* could not be distinguished from *C. lupus* in either the malleus or incus though *S. fatalis* occupied a separate morphospace from other felids. In terms of overall size, the *P. leo* malleus was surprisingly significantly larger in size than that of *P. tigris*, a finding that mirrors similarly surprising trends in the clavicles of these species. The ossicles of *P. atrox* are similar in shape to those of other congeners. While the ossicles of *A. simus* are absolutely large, like all other bears, they scale below the general carnivoran trend line suggesting, perhaps, less reliance on hearing in this lineage compared to felids and canids. In short, although there are phylogenetic and allometric trends in the anatomy of ossicles, there are also differences in shape that may relate instead to functional differences in these lineages and their extinct taxa.

**Funding Sources** North Carolina State University Office of Undergraduate Research.

## Cenozoic Herpetology

### OLDEST RECORD OF ALLIGATOR IN THE SOUTHEASTERN U.S.A. HAD SMALL BODY SIZE IN SUBTROPICAL ENVIRONMENT

Hastings, Alexander K.<sup>1</sup>, Schubert, Blaine<sup>2</sup>, Bourque, Jason<sup>3</sup>

<sup>1</sup>Paleontology, Science Museum of Minnesota, Minneapolis, Minnesota, U.S.A., <sup>2</sup>Department of Geosciences, East Tennessee State University, Johnson City, Tennessee, U.S.A., <sup>3</sup>Vertebrate Paleontology, Florida Museum of Natural History, Gainesville, Florida, U.S.A.

The earliest records of *Alligator* come from the latest Eocene of South Dakota and Nebraska. These belong to the most basal species for the genus, *A. prenasalis*, which can also be found in the earliest Oligocene strata from South Dakota. Fossil *Alligator* in Nebraska are not recovered again until the early Miocene, with *A. mcgrewi* in the Runningwater Formation. *Alligator mcgrewi* possesses more derived features than *A. prenasalis*, including a dorsally facing external naris, found in extant *Alligator*. Identifiable *Alligator* fossils from southeastern North America first appear in Florida from the early Miocene, belonging to the much larger species *A. olseni*, best known from the Thomas Farm locality (but with another report from the early Miocene of Texas). This has left a sizable gap of approximately 16 million years between early Oligocene and early Miocene *Alligator*.

Here we report *Alligator* fossils from the late Oligocene Brooksville fossil site in northern Florida. Brooksville has a diverse fauna, including the turtle *Xenochelys*, the lizard *Anolis*, the toad *Rhinophrynus*, the bat *Koopmanycteris*, and the early horse *Miohippus*. The most diagnostic of the *Alligator* fossils is a nearly complete small, right premaxilla, which bears the lateral notch that characterizes

the genus. The premaxilla also features a forward facing external naris, as in the ancestral *A. prenasalis*. Additional fossils include an articular, vertebrae, unguals, osteoderms, and isolated teeth. We further report additional material from two other Oligocene sites in Florida, the I-75 locality and the Live Oak locality, that also appear to come from a small species of *Alligator*.

The *Alligator* material presented here narrows the temporal gap significantly, now from the early to late Oligocene (about 8 million years). Interestingly, both the *Alligator* and *Xenochelys* from this site appear similar to late Eocene taxa from the north central U.S.A. Additionally, size and maturity indicators of the fossil material suggest at least the possibility that small body size was common in early *Alligator*, even as they shifted to the southeastern U.S.A. Alternatively, there may be fossil *Alligator* from before the late Oligocene, which have yet to be recovered.

## Education & Outreach

### INTERACTIVE DINOSAUR LESSONS FOR ALL AGES THAT EXPLAIN COMPLEX ANATOMY AND BODY SIZE TO HELP DISPEL COMMON MISCONCEPTIONS

Hastings, Alexander K.<sup>1</sup>, Ollanketo, Karla<sup>2</sup>, Glick, Sam<sup>2</sup>  
<sup>1</sup>Paleontology, Science Museum of Minnesota, Minneapolis, Minnesota, U.S.A., <sup>2</sup>Education, Science Museum of Minnesota, Saint Paul, Minnesota, U.S.A.

Although dinosaurs are a popular subject, posture and body size are often presented inaccurately in popular media, such as films and comic books. However, details of anatomy affecting posture as well as realistic body sizes are often difficult to convey through interactive lessons that make the information more memorable. We addressed three common misconceptions in a set of fun educational activities for all ages.

The first activity addresses the common depiction of sauropod dinosaurs with tails fully dragging, by using a simplified model of two sauropod caudal vertebrae. The vertebrae were cast from an original fossil, with a foam disc inserted between them to represent the intervertebral cartilaginous disc. An elastic band connects the neural arch of one vertebra to the next, simulating caudal ligaments that allow for lateral motion. Participants tested the model to see how the tail would move. Given that dorsoventral motion is tightly restricted, it reinforces that these dinosaur likely did not drag their tails.

The second is the most engaging, which addresses wrist pronation in theropod dinosaurs. Bipedal theropods were incapable of wrist pronation, such that their ‘palms’ would have been held toward the body, not rotated ‘palm’ down. This concept is reflected very well in prey capture. A set of knitted gloves was made with three fingers and a fabricated

dinosaur tail attached to a stiff board that can be held like a shield. One volunteer is the prey; the other is the predator. The predator needs to catch the prey using either palms down or palms in. Having palms in is a far simpler way to snatch the tail, illustrating not only the proper posture but also the anatomical benefit. A simple phrase to remember this has been remarkably effective: they were ‘clappers’ not ‘slappers.’

Last, we printed a banner with a life-size diagram of a *Tyrannosaurus rex* skull, specifically FMNH PR 2081, ‘Sue.’ Participants were invited to walk up to the banner and compare their own head to Sue’s. This helps show in very personal terms how large a *T. rex* actually is and also presents fun opportunities for photos.

We have found these simple lessons to be very effective and participants thus far have thoroughly enjoyed them. They have been used in outreach at the Science Museum of Minnesota, educator conferences and in traditional classroom settings. The lesson kit currently can be checked out from the museum’s Lending Library, so educators can teach these lessons in their classes.

#### **Late Cenozoic Mammalian Macroecology & Macroevolution**

##### **MIOCENE FOSSIL OR HOLOCENE ARTIFACT – *AGRIOTHERIUM SCHNEIDERI* MANDIBLE FROM SEDGWICK COUNTY, KANSAS**

Hawkins, Rebecca A.<sup>1</sup>, Everhart, Michael J.<sup>2</sup>

<sup>1</sup>Algonquin Consultants, Inc., Miami, Oklahoma, U.S.A.,

<sup>2</sup>Fort Hays State University, Sternberg Museum of Natural History, Hays, Kansas, U.S.A.

In March 2017, the partial right mandible (FHSM VP-19466) of the giant Miocene–Pliocene bear, *Agriotherium schneideri* (Ursidae, Agriotheriinae), was recovered from the sandy sediments of an exposed paleo stream channel in northern Sedgwick County, Kansas. Recent mechanical disturbance had created a ‘cutbank’ along the edge of a Holocene stream terrace, revealing older, underlying sediments and impacting an archaeological site (ca. 2000–3500 BP) on the terrace surface. Archaeologists working at the site, including the first author, found the mandible and immediately called the second author, a paleontologist. The overall size of the mandible, measurements of the teeth, presence of a ‘chin,’ and a large premasseteric fossa confirm the specimen to be *Agriotherium schneideri*. Collaborative research across the two disciplines raised the thorny question – made thornier by the eroded, mechanically disturbed context of the find locale – of the mandible’s origin. The closest Miocene/ Pliocene deposits, part of the Ogallala Formation, lie ca. 50 mi distant, and indeed, some Ogallala Formation orthoquartzites were used at the site to manufacture stone tools. Had the site’s

ancient occupants brought the mandible home along with some Ogallala toolstone? The use of fossils by pre-Western American Indian societies on the Plains is well documented, and for the hunter-gatherer occupants of the site, familiar with butchered animal bones, the mandible would have been easily recognizable as that of a giant carnivore worthy of showing to others. Examination of the sediments adhering to the mandible and its recovery location, carefully marked by archaeologists, along with further excavation of some fragments from the cutbank, suggest that the fossil had eroded from underlying terrace deposits, not the archaeological site on top. However, the terrace deposits are clearly Pleistocene in age, and the relatively complete and un-abraded condition of the mandible would preclude long distance stream transport. As well, although fragmentary remains attributable to *Agriotherium* have been previously identified in Kansas, all have been found only in Miocene/ Pliocene localities, and no other Miocene/ Pliocene fossils have been reported from Sedgwick County.

#### **Cenozoic Herpetology**

##### **NORTH BY NORTH-WET: A NEW ANILIID SNAKE TAXON FROM THE MIDDLE EOCENE OF WYOMING AND A REAPPRAISAL OF THE FOSSIL RECORD OF ‘ANILIID’ SNAKES**

Head, Jason

Zoology, University of Cambridge, Cambridge, U.K.

‘Anilioid’ pipe snakes are fossorial predators of elongate vertebrates and includes extant taxa from equatorial South America, South- and Southeast Asia, and a fossil record that consists primarily of isolated preloacal vertebrae from the Late Cretaceous through Cenozoic of the Americas, Europe, India, and Africa. Extant taxa are restricted to warm tropical gallery rainforests, and past extralimital distributions have been proposed to result from globally warm paleoenvironments. Molecular data strongly supports paraphyly of pipe snakes relative to other alethinophidians, which requires reappraisal of purported synapomorphies used to identify fossil taxa and resultant climatic and biogeographic histories.

On the basis of vertebral apomorphies optimized on molecular phylogenetic topologies, the vast majority of the reported ‘anilioid’ fossil record represents stem snakes and indeterminate macrostomatans erroneously assigned based on generalized features associated with fossoriality. Preloacal vertebrae from the middle Eocene Bridger Formation of Wyoming represent an unambiguous North American record of South American Aniliidae based on neural spine and prezygapophyseal apomorphies shared with extant *Anilius scytale* and, in combination with the revised fossil record, represents the only continental-scale

extralimital distributions of pipe snakes throughout their evolutionary history. Northern immigration of Central and South American squamates during earliest Eocene hyperthermals is well-documented; however, restriction of anillids to the more humid middle Eocene suggests that precipitation may be a stronger constraint on dispersal, as evidenced by high precipitation in the habitats of *Anilius*.

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## Dinosaur Systematics, Diversity & Ecology

### IMPLICATIONS OF THE DISTRIBUTION OF DISEASE AND INCIDENCE OF INJURIES IN NON-AVIAN MESOZOIC DINOSAURS

Heckert, Andrew B.<sup>1</sup>, Carrano, Matthew T.<sup>2</sup>, Ore, Zachary<sup>1</sup>, Howell, Logan S.<sup>1</sup>, Schneider, Katie<sup>1</sup>

<sup>1</sup>Geological & Environmental Sciences, Appalachian State University, Boone, North Carolina, U.S.A., <sup>2</sup>Paleobiology, National Museum of Natural History, Washington, District of Columbia, U.S.A.

As the fossil record of injuries and diseases, paleopathologies are one of the most direct insights to the paleobiology of extinct animals. Even with the vagaries of vertebrate taphonomy and the near-absolute requirement that they be expressed on hard parts, there are reports of more than 200 pathological dinosaur body fossil specimens in the peer-reviewed literature (many more are known from anecdotal evidence and various ‘gray literature’). Working from the null hypotheses that pathologies should be evenly distributed chronologically and taxonomically across Dinosauria, we have synthesized the existing peer-reviewed records (exclusive of eggs or trace fossils) to compile paleopathological occurrences by time, clade, body mass, and type (disease, injury, or both). We indexed pathologies across six epochs (Late Triassic, Early, Middle, and Late Jurassic; Early and Late Cretaceous), five major clades (Theropoda, Sauropodomorpha, Thyreophora, Marginocephalia, and Ornithopoda), and five orders of magnitude in body mass (from 1 kg to >10,000 kg).

The record is strongly biased geographically with ~70% of occurrences in North America and most others Eurasian; this likely reflects the predominance of North American dinosaur collections overall. Consequently, it mirrors the North American record of dinosaurs, with more than ~62% of the instances recorded in the Late Cretaceous and 18% more in the Late Jurassic. Normalizing these data to the fossil record is challenging but provides a further test of the null hypotheses. The paleopathological record broadly tracks the number of collections per epoch in the Paleobiology Database, with the exception being the Early

Cretaceous, where pathologies appear to be under-reported. The vast majority of pathologies (>80%) occur in specimens with an estimated mass >1000 kg; only theropods consistently have pathological occurrences at smaller body masses. This record also supports hypotheses regarding dinosaur behavior, namely that taxa that engaged in predatory or other antagonistic behaviors more often bear injuries (or a combination of injuries and diseases) than do other clades. Thus theropods and marginocephalians (principally ceratopsids) each represent >25% of paleopathologies and >33% of all injuries. By contrast, ornithopods, sauropods, and thyreophorans (stegosaurs and ankylosaurs) each account for <20% of pathological occurrences and experienced diseases at a higher rate than they did injuries.

## Holocene & Pleistocene Mammalian Macroecology & Faunal Studies

### THE LEGACY OF MEGAFUNAL EXTINCTION: A FINE-SCALE EXAMINATION OF FUNCTIONAL DIVERSITY OVER THE LATE QUATERNARY

Hedberg, Carson<sup>2</sup>, Smith, Felisa A.<sup>2</sup>, Lyons, S. K.<sup>1</sup>

<sup>1</sup>Biology, University of Nebraska, Lincoln, Nebraska, U.S.A., <sup>2</sup>Biology, University of New Mexico, Albuquerque, New Mexico, U.S.A.

Functional traits are one of the fundamental axes of biological diversity. They reflect the interactions among species and with their environment, providing a link between diversity and ecosystem function. Under periods of biodiversity decline, the magnitude of functional diversity loss often differs from that of species richness, providing insight into how ecosystems are affected during disassembly. The fossil record provides the unique opportunity to explore how extinction and turnover affect community structure and functional composition through time. Here, we quantify changes in functional diversity of a mammal community in central Texas from the late Pleistocene to the present. This interval encompasses the Terminal Pleistocene megafaunal extinction, climatic shifts during the Holocene, and escalating human influence through historical to modern times. We constructed multidimensional functional space from ecologically relevant traits (body mass, diet, arboreality, cursoriality, soil disturbance, activity period, social group size, and migration habit) for six distinct temporal communities represented at the site. We further analyzed the most recent temporal community with the addition of introduced and domestic species to investigate the extent to which these species replace ecological function lost in the megafaunal extinction and subsequent regional extirpations. Declines in functional diversity are greater than expected given the decrease in species richness following the Terminal Pleistocene extinction and historical extirpations, implying lost taxa contributed higher than average ecological

function. Functional distinctiveness of remaining species increases through time leading to less functional redundancy in the community. However, introduced taxa increase functional diversity to levels similar to the Holocene and partially restore lost functional space occupied by late Pleistocene fauna. This site-specific analysis demonstrates the loss of megafauna has left modern ecosystems functionally depauperate and less resilient to future biodiversity loss.

**Funding Sources** The National Science Foundation DEB Award # 1555525.

### Evolution & Biology of Non-Avian Theropods

#### NEW DATA ON THE OOASSEMBLAGE OF THE CENOMANIAN-AGE MUSSENTUCHIT MEMBER, CEDAR MOUNTAIN FORMATION, UTAH

Hedge, Joshua<sup>1</sup>, Makovicky, Peter J.<sup>3</sup>, Cifelli, Richard<sup>2</sup>, Zanno, Lindsay E.<sup>1</sup>

<sup>1</sup>Biological Sciences, NC State University, Raleigh, North Carolina, U.S.A., <sup>2</sup>Biology, University of Oklahoma, Norman, Oklahoma, U.S.A., <sup>3</sup>University of Minnesota, Minneapolis, Minnesota, U.S.A.

Dinosaur eggshell from the Cenomanian-age Mussentuchit Member of the Cedar Mountain Formation (MM) was first discovered half a century ago and has since been the subject of considerable research. Despite a high degree of morphological and microstructural variation documented in multiple publications, only a single oospecies, *Macroelongatoolithus carlylei*, is currently recognized. This is unexpected given the high abundance of eggshell preserved throughout the MM with thousands of fragments accessioned within multiple institutions, a diverse, burgeoning dinosaur species record, and the presence of highly diverse ooassemblages from younger Late Cretaceous sediments of the Western Interior Basin. To further explore oodiversity from the MM, we preliminarily analyzed a subsample (n = 24) of the best-preserved representations of external eggshell morphotypes collected from the MM over the past decade, and assessed diagnostic eggshell characteristics (layering, thickness, ornamentation, pore structure).

Unsurprisingly, our sample is dominated by specimens referable to *Macroelongatoolithus* (n = 22) based on the most recent rediagnosis of the genus. Contention remains over the synonymization of various *Macroelongatoolithus* oospecies from Cretaceous deposits in North America and Asia. Although a recent comprehensive study of relatively complete *Macroelongatoolithus* eggs from the Wayan Formation in Idaho supports synonymization of *M. carlylei* and *M. xixiaensis*, the type materials of *M. carlylei* are fragments that derive from the MM. Recently discovered partial clutches from the MM contain smaller eggs and will

no doubt shed additional light on the ootaxonomy of *Macroelongatoolithus*. We note that *Continuoolithus*, as currently defined, cannot be differentiated from many of our *M. carlylei* specimens, highlighting previously recognized issues with applying ootaxonomy from fragments alone. We tentatively refer a single specimen (NCSM 33729), collected from a diverse microvertebrate locality, to *Undulatoolithus* (Elongatoolithidae) on the basis of extremely prominent, undulating ornamentation with a ridge height of 0.6–0.84 mm that comprises half the eggshell thickness, a ML:CL ratio of 1.7–1.9, and a non-distinct ML:CL boundary. To date, *Undulatoolithus* has not been documented outside Upper Cretaceous deposits in China; making this, to our knowledge, a first record in North America.

**Funding Sources** National Science Foundation, Frontier Research in Earth Science award (#1925973).

### Fishes & Chondrichthyans: Evolution & Distribution

#### MORPHOLOGICAL DIVERSITY IN AN ACTINOPTERYGIAN FISH FOLLOWING THE END-DEVONIAN MASS EXTINCTION

Henderson, Struan, Giles, Sam

University of Birmingham, Birmingham, U.K.

In the aftermath of the end-Devonian mass extinction, aquatic faunas underwent significant restructuring, with actinopterygians and chondrichthyans replacing placoderms and piscine sarcopterygians. The Tournaisian (~359–347 Ma), immediately succeeding the end-Devonian, is therefore a key interval in the history of the Actinopterygii, a group that now dominates global aquatic ecosystems. Empty niches following mass extinctions potentially allow for high taxonomic diversity and morphological disparity in surviving lineages. Understanding of whether actinopterygians fulfilled this potential in the Tournaisian is curtailed by poor comprehension of the available taxa: of nearly 30 described species, only three have been included in phylogenetic analyses. The majority of taxa are known only from brief descriptions and idealised line drawings made in the 19<sup>th</sup> and early 20<sup>th</sup> centuries, with few being re-examined since the advent of CT scanning. *Carboveles ovensi* is a notable example: known from several fossils from the Tournaisian of Scotland, it was originally described nearly a century ago, and its taxonomic validity is uncertain. CT scanning reveals that the jaws and palate possess an extensive covering of enlarged conical teeth, as well as a melange of characters shared with both Devonian and Carboniferous taxa. Preliminary phylogenetic analyses resolve *Carboveles* in a polytomy with other Carboniferous taxa; an unsurprising result given the near-absence of contemporaneous taxa and detailed anatomical data. More importantly, our results suggest that actinopterygians diversified morphologically in the immediate aftermath of

the end-Devonian. *Carbovels* highlights that the fundamental descriptive and taxonomic aspects of paleontology are essential to understanding the actinopterygian rise to dominance.

**Funding Sources** The Royal Society – Dorothy Hodgkin Fellowship Enhancement Award.

## Bird Biology & Evolution

### A COLLECTION OF *METOOLITHUS NEBRASKENSIS* FRAGMENTS FROM THE CHADRON AND BRULE FORMATIONS OF NORTHWESTERN NEBRASKA

Hendrix, Amanda L.<sup>1</sup>, Zelenitsky, Darla K.<sup>1</sup>, Therrien, François<sup>2</sup>

<sup>1</sup>Department of Geosciences, University of Calgary, Calgary, Alberta, Canada, <sup>2</sup>Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada

Fossil bird egg remains are rare in Paleogene deposits of North America, with fewer than 15 documented occurrences. Here we describe bird eggshell fragments (n >600) from the Eocene Chadron Formation (Big Cottonwood Creek member) and overlying Oligocene Brule Formation (Orella member) of northwestern Nebraska. Eggshell fragments were recovered from 19 separate sites over a geographically restricted area (~2 km<sup>2</sup>) near Toadstool Geologic Park. The eggshell is relatively thick, ranging from 0.5–0.85 mm (mean = 0.63 mm), excluding the height of the outer surface ornamentation. The outer eggshell surface shows a range of textures, varying from smooth to undulating and nodose ornamentation. Microscopic analyses reveal the presence of three microstructural layers, namely the mammillary, prismatic, and external layers. The eggshell exhibits an abrupt boundary between the mammillary and prismatic layers, and flaring of the prisms in the upper portion of the prismatic layer that corresponds to the presence of nodose ornamentation. Pores are oval to crescent shaped and occur only in the fragments characterized by a smooth or undulating surface texture. Measurements of pore areas from several fragments yield a porosity value of 0.73, plotting within the range of extant open-nesting avian taxa. Comparison of the eggshell fragments to the holotype egg of the oospecies *Metoolithus nebraskensis* indicate they fall within the range of morphological variation present in this egg and are thus assignable to this ootaxon. The observed variability in eggshell thickness and ornamentation in *M. nebraskensis* suggests inclusion of *Metoolithus jacksonae* from the Brule Formation of North Dakota as a junior synonym of this ootaxon. Because eggs of extant birds rarely have ornamentation, assignment of *M. nebraskensis* to an extant avian family is challenging, although eggshell thickness, egg size/mass, and eggshell

porosity correlate strongly with certain types of galloanserans. Our results expand the geologic and geographic range of *Metoolithus nebraskensis* and improve our understanding of North American bird egg remains during the first half of the Cenozoic.

**Funding Sources** NSERC Discovery Grant to DKZ.

## Preparators

### RECENT EFFORTS TO DIGITIZE IMAGES IN THE SECTION OF VERTEBRATE PALEONTOLOGY CARNEGIE MUSEUM OF NATURAL HISTORY USING THE VAUGHN PROJECT AS AN EXAMPLE

Henrici, Amy C., Stokes, Jacob  
Vertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.

The Section of Vertebrate Paleontology at Carnegie Museum of Natural History (CM) has over 90,000 cataloged specimens and a wealth of associated data, including correspondence, field images, and field notes. A series of grants over the past 44 years has provided funding to improve fossil storage and climate in the collection rooms. Efforts to organize and preserve paper archives and images during this time were initiated by the former Collection Manager. She did so by organizing them, housing them in archival materials, cataloging a large portion of the image collection (some of which dates to 1898), and having copy negatives and prints made from glass plates. More recent efforts to preserve images and associated data include digitizing cataloged images, cataloging and digitizing images that were not previously cataloged, and storing the physical images, such as slides, negative film, and prints, in appropriate archival holders. With the recent migration of the Section's database to Axiell Emu, scanned images can now be linked to their respective image catalog record and, as appropriate, specimen or site records.

The Vaughn project involves the recent acquisition of field-books and 35 mm slides related to a collection of late Paleozoic vertebrate fossils donated to the Section in 1988 by the late Peter P. Vaughn, formerly a professor at the University of California Los Angeles. These images record fossil sites, field camps, and the American Southwest between 1960–1973, a time before or during incorporation of some of the sites into national parks, monuments, recreation areas, and state parks. The slides were cataloged, scanned, uploaded to the Emu database, and stored in archival sleeves. Information used to catalog the slides came from various sources. Some slides had locality information written on them, whereas others bore slide numbers to link them to descriptions in Vaughn's field-books, while still others lacked notation. This information was augmented by David S Berman (Curator Emeritus at

CM), a former Vaughn student who helped collect many of the fossils, and one of us (ACH), who has been to many of the fossil sites, as well as the use of Internet mapping tools. The digitization of this important archival collection will help to ensure that it remains available to researchers in perpetuity.

## Mesozoic Herpetology

### FOSSIL TURTLES FROM THE LATE CRETACEOUS (TURONIAN) OF KUJI, IWATE PREFECTURE, NORTHERN JAPAN

Hirayama, Ren

Waseda University, Shinjuku-ku, Tokyo, Japan

The bone bed of the Tamagawa Formation located in Kuji City, Iwate Prefecture, northern Japan, has produced more than 2000 terrestrial and marine vertebrate remains of the Upper Cretaceous, with at least 20 taxa, such as turtles, crocodylomorphs, dinosaurs, choristoderan, and chondrichthyans so far. The estimated age of  $90.51 \pm 0.54$  Ma (late Turonian), was obtained for the bone bed based on uranium-lead (U-Pb) dating of the volcanic ash layer overlying the bone bed. All terrestrial vertebrate fossils from the bone bed inter-bedded by marine sandstone layers are isolated and fragmentary except for two partially articulated turtle shells of the genus *Adocus*. These occurrences suggest they were transported by river stream near the mouth. Non-marine turtles (Order Testudines) are the most abundant vertebrates (788 specimens in total), identified as *Adocus* (Adocidae: 253 specimens), Trionychidae (79 specimens), Nanhsiungchelyidae (10 specimens), Carettochelyidae (six specimens), and Lindholmemydidae (11 specimens). Most turtle remains are isolated shell elements. *Adocus* from the Tamagawa Formation seems the most derived species of this genus in the possession of very wide marginal scales and the loss of cervical scale of carapace. The largest specimen of *Adocus* in this locality suggests an individual with at least a 60 cm long shell. Soft-shelled turtles (Trionychidae) are generally medium-sized with a carapace about 30 cm long. Fine sculpture on the plastron and reduced eighth costals suggest its affinity with the extant *Rafetus-Apalone* clade. Presence of such advanced taxa from the Turonian implies that this group (Trionychia) had an earlier diversification in Asia during the Cretaceous than previously assumed.

## Symposium: Dietary Reconstruction

### INSIGHT ON TROPHIC LEVEL ESTIMATION THROUGH AMINO ACID $\Delta^{15}\text{N}$ VALUES FROM MADAGASCAN MEGAFaUNA

Hixon, Sean W.<sup>1</sup>, Smith, Emma A.<sup>2</sup>, Crowley, Brooke<sup>3</sup>, Perry, George<sup>6</sup>, Rakotozafy, Lucien M.<sup>4</sup>, Randrianasy, Jeannot<sup>5</sup>, Ranaivoarisoa, Jean F.<sup>5</sup>, Douglass, Kristina G.<sup>6</sup>, Kennett, Douglas J.<sup>1</sup>, Newsome, Seth<sup>7</sup>

<sup>1</sup>University of California, Santa Barbara, Goleta, California, U.S.A., <sup>2</sup>Museum of Natural History, Smithsonian Institution, Washington, District of Columbia, U.S.A., <sup>3</sup>University of Cincinnati, Cincinnati, Ohio, U.S.A., <sup>4</sup>Institute of Civilizations, Museum of Art & Archaeology, University of Antananarivo, Antananarivo, Madagascar, <sup>5</sup>University of Antananarivo, Antananarivo, Madagascar, <sup>6</sup>Pennsylvania State University, State College, Pennsylvania, U.S.A., <sup>7</sup>University of New Mexico, Albuquerque, New Mexico, U.S.A.

Predation by introduced predators and competition with introduced livestock could have contributed to the extinction of Madagascar's megaherbivores. Ancient terrestrial food webs may be reconstructed based on amino acid (AA) specific nitrogen isotope ( $\delta^{15}\text{N}$ ) values, yet little work has validated this proxy. Existing data suggest that extinct giant tortoises (*Aldabrachelys* spp.) and extant lemurs (e.g., *Propithecus verreauxi*) exploited drier habitat than introduced bovids (cows and goats) in the past. Knowledge about past introduced predator diet is limited, and many influences of diet and physiology on AA  $\delta^{15}\text{N}$  values are uncertain. We test assumptions underlying AA  $\delta^{15}\text{N}$ -based trophic level estimates using AA  $\delta^{15}\text{N}$  values in ancient herbivore bone collagen ( $n = 57$ ) and modern plants ( $n = 10$ ) from southwestern Madagascar. Specifically, we use  $\delta^{15}\text{N}$  values of 'source' Aas (e.g., phenylalanine) as a proxy for habitat aridity and infer trophic levels based on offsets between the  $\delta^{15}\text{N}$  values of consumer 'source' and 'trophic' Aas (typically  $\Delta^{15}\text{N}_{\text{Glu-Phe}} = \delta^{15}\text{N}_{\text{glutamic acid}} - \delta^{15}\text{N}_{\text{phenylalanine}}$ ). Based on existing AA  $\delta^{15}\text{N}$  data from plants and cows, we expected differences in  $\Delta^{15}\text{N}_{\text{Glu-Phe}}$  among plant photosynthetic groups and between ruminant and non-ruminant herbivores. Though bovid collagen carbon isotope ( $\delta^{13}\text{C}$ ) data indicate that these animals consumed a wide range of  $\text{C}_3$  and  $\text{C}_4$  plant combinations, we found no dependence of  $\Delta^{15}\text{N}_{\text{Glu-Phe}}$  on  $\delta^{13}\text{C}$  values ( $n = 19$ ,  $r = 0.24$ ,  $p = 0.31$ ). We also found no significant differences in the  $\Delta^{15}\text{N}_{\text{Glu-Phe}}$  values between bovids ( $n = 19$ ) and endemic non-ruminant herbivores such as pygmy hippos and two lemur species ( $n = 28$ ,  $t(45) = -1.38$ ,  $p = 0.18$ ). Additionally, a sample of Malagasy  $\text{C}_3$ ,  $\text{C}_4$ , and CAM plants ( $n = 10$ ) so far shows no dependence of plant  $\Delta^{15}\text{N}_{\text{Glu-Phe}}$  values on a plant's photosynthetic pathway, which is inconsistent with limited existing data on these producer groups. These data suggest that AA-based trophic level estimates may be independent of both the photosynthetic pathway of dietary plants and an herbivore's reliance on rumen microbes. Patterns in AA  $\delta^{15}\text{N}$  values among Malagasy plants and herbivores have potential to provide information on ancient food web structure in this system, yet more work is required to

identify the past diets of introduced predators on Madagascar and to refine AA-based trophic level estimates for terrestrial animals in general.

**Funding Sources** National Science Foundation Grants GRFP #2015213455 and Archaeology DDRI #1838393.

## **Fishes & Chondrichthyan: Evolution & Distribution**

### **THE LATE MISSISSIPPIAN (VISEAN) CHONDRICHTHYAN ASSEMBLAGE FROM THE JOPPA MEMBER OF THE STE. GENEVIEVE FORMATION AT MAMMOTH CAVE NATIONAL PARK, KENTUCKY**

Hodnett, John-Paul M.<sup>1</sup>, Elliott, David K.<sup>2</sup>, Toomey, Rickard<sup>3</sup>, Olson, Rick<sup>3</sup>, Wood, Jack<sup>4</sup>, Santucci, Vincent<sup>5</sup>

<sup>1</sup>Archaeology, Maryland-National Capital Parks and Planning Commission, Upper Marlboro, Maryland, U.S.A., <sup>2</sup>Division of Geology, Northern Arizona University, Flagstaff, Arizona, U.S.A., <sup>3</sup>SR&M, Mammoth Cave National Park, Mammoth Cave, Kentucky, U.S.A., <sup>4</sup>Geologic Resource Division, National Park Service, Lakewood, Colorado, U.S.A., <sup>5</sup>Geologic Resource Division, National Park Service, Washington, District of Columbia, U.S.A.

The groundwater carving of the cave system at Mammoth Cave National Park (MACA) has produced one of the longest cave systems, over 400 miles in length, on the planet. These extensive underground passageways cut through Late Mississippian marine limestones that contain vertebrate remains, primarily those of cartilaginous fishes. Of interest here is the Visean age Joppa Member of the Ste. Genevieve Formation which, until now, had no published record of vertebrate fossils. Over 100 specimens of chondrichthyans were collected or documented in situ within the walls and ceiling of two passageways at MACA. At present 23 taxa, representing at least 11 orders of chondrichthyans have been identified from the Ste. Genevieve Formation at MACA. Symmoriform chondrichthyans are represented by *?Stethacanthus* sp. and *Denea* sp. Phoeodontiforms are represented by *Thrinacodus* cf. *T. incurvus* and an indeterminate form, and the xenacanthimorph *Bransonella* sp. Is present. Ctenacanthiform sharks are well represented by *Saivodus striatus*, which include the first endo-cranial cartilages preserved for this large ctenacanth taxon, *Cladodus* sp., *Glikmanius* sp., and a small indeterminate form. Euchondrocephalians are diverse with the enigmatic taxon *Chomatodus* sp. The most commonly encountered chondrichthyan at MACA, as well as *Venustodus* sp. At least two species of *Orodus*, and an indeterminate form. Petalodontiforms include *Janassa* sp., *Petalodus* sp., *?Tanodus* sp. And an indeterminate form. Holocephalans are diverse within the MACA St. Genevieve assemblage

and include *Helodus* sp., *Psephodus* sp., *Deltodus* sp., *Sandalodus* sp., *Psammodus* sp., and *Deltoptychius* sp.

The chondrichthyan assemblage from the St. Genevieve Formation at MACA adds important data to the Visean marine vertebrate record of North America. Other North American Visean shark records are known, however, very few of these faunas have been described well enough to allow comparison with each other and with more comprehensively studied assemblages in Europe, Asia, Africa, and Australia.

## **Fishes & Chondrichthyan: Evolution & Distribution**

### **SYSTEMATICS AND BIOGEOGRAPHY OF NEW FOSSIL WRASSES FROM THE LATE MIOCENE OF FLORIDA**

Hoeflich, Jennifer C.<sup>1</sup>, Bloch, Jonathan I.<sup>2</sup>

<sup>1</sup>Biology, University of Florida, Gainesville, Florida, U.S.A., <sup>2</sup>Florida Museum of Natural History, University of Florida, Gainesville, Florida, U.S.A.

The wrasse family Labridae consists of over 630 species classified in ~87 genera that are widespread in extant marine ecosystems spanning tropical, subtropical, and temperate waters of the Atlantic, Indian, and Pacific Oceans. While the fossil record of labrids spans the Eocene-Quaternary with variable representation across all continents, the only extant genera with fossil records are limited to the tribe *Scarini*. Recent work at the Montbrook locality, a late Miocene fossil site representing a near coastal river deposit in North Florida, has resulted in the discovery of several fossil wrasses: *Bodianus* sp. nov., which is represented by infrapharyngeal and dentary fossils; *Halichoeres* cf. *H. bivittatus*, which is represented by infrapharyngeal and premaxillary fossils, as well as other currently unidentified labrid fossils. These specimens are remarkable for their complete preservation, including associated dentitions. Based on vertebrate biochronology, the Montbrook fossil locality is late Hemphillian (ca. 5–5.5 my) in age and the labrid fossils represent some of the earliest records of their genera and respective subtribes found in North America and the earliest known from Florida. This labrid fauna is also notable in being close in time to the closure of the Central American Seaway. In particular, the fossil *Bodianus* sp. Nov. is found to be nested within species classified in the subgenus *Verreo*, a group of temperate Indo-Pacific wrasses, not with the Atlantic *Bodianus* species, thereby indicating that the Western Atlantic fauna and the Indo-Pacific fauna were experiencing interchange. Meanwhile, the *Halichoeres* represents an early member of the modern Eastern Atlantic *Halichoeres* group, which rapidly diversified following the closure of the Central American Seaway, including into

specialized niches such as juvenile cleaners. As such, these labrids belong to an intermediate Western Atlantic fauna.  
**Funding Sources** NSF (DBI-1756306) to JIB.

### Permo-Triassic Tetrapods

#### A DIVERSE EARLY TRIASSIC ARCHOSAUMORPH TOOTH ASSEMBLAGE FROM THE BURGERSDORP FORMATION OF SOUTH AFRICA

Hoffman, Devin K.<sup>1</sup>, Hancox, John<sup>2</sup>, Nesbitt, Sterling J.<sup>1</sup>  
<sup>1</sup>Department of Geosciences, Virginia Tech, Blacksburg, Virginia, U.S.A., <sup>2</sup>Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa

The end-Permian mass extinction destabilized global ecosystems, and these ecosystems and their taxonomic diversity did not recover until the Middle, or possibly Late, Triassic. One clade to radiate following the end-Permian mass extinction and achieved great taxonomic and ecological diversity was the Archosauromorpha. However, the paucity of Early Triassic assemblages limits reconstruction of the timing of ecological recovery, preventing determining if this delayed recovery is an accurate signal, or the result of preservation bias. The Driefontein locality from the Lower Triassic (*Cynognathus* Assemblage Zone, *Langbergia-Garjainia* Subzone) from the Beaufort Group, South Africa preserves a rich vertebrate assemblage in the classic Permo-Triassic transition with few gaps in the record. As articulated specimens are rare in the Driefontein assemblage, we used teeth, isolated and within jaws, to capture ecological disparity as a proxy for diet. All in situ teeth belong to the only confirmed archosauromorph reptile known from the Driefontein locality, the erythrosuchid, *Garjainia madiba*, but the abundant isolated material likely preserves more morphotypes. To quantify tooth morphology, we collected linear measurements from 170 isolated (of thousands) and in situ teeth. We used total crown heights and tooth base ratio (= base length/base width) to generate a morphospace for the tooth assemblage. One morphotype falls within *Garjainia* morphospace (possibly plesiomorphic for archosauromorphs), there are three clusters that fall completely outside this space. We also made qualitative scorings as a separate measure of tooth disparity in order to capture features not shown by overall shape, ordinated using non-metric multi-dimensional scaling. This analysis improves separation of tooth morphotypes in ordination and provides a comparison to description. We find the *Garjainia*-like morphotype retains the same features as in situ teeth despite being much smaller, possibly indicating little ontogenetic change in tooth morphology. Additionally, the isolated teeth reveal two new

carnivorous/insectivorous morphotypes and at least one morphotype correlated with herbivory. The presence of multiple tooth morphotypes, including probable herbivores, indicates that the Driefontein locality preserves a diverse ( $n > 5$ ) archosauromorph assemblage. This indicates ecosystems, at least by faunal dietary guilds, may have stabilized from the end-Permian mass extinction in the Early Triassic.

**Funding Sources** DKH was funded by NSF GRFP and a Geological Society of America Graduate Student Grant.

### Quantitative Methods

#### UTILITY OF MICROCT IN CEMENTUM-BASED AGE ESTIMATION OF PALEOGENE *CORYPHODON*

Hoffmann, Simone<sup>1</sup>, D'Emic, Michael<sup>2</sup>, Skonieczny, Kristen<sup>1</sup>, Mayback, Danika<sup>3</sup>  
<sup>1</sup>New York Institute of Technology, Old Westbury, New York, U.S.A., <sup>2</sup>Adelphi University, Garden City, New York, U.S.A., <sup>3</sup>Illinois State University, Normal, Illinois, U.S.A.

*Coryphodon* is one of the first placental mammals to evolve large body size after the K–Pg boundary and is hypothesized to have undergone dwarfing in the Eocene as a response to climatic changes. It is unknown whether *Coryphodon* achieved its large body size through extended or accelerated development and if the rapid temperature changes during and after the Paleocene–Eocene Thermal Maximum impacted longevity. Cementum chronology has emerged as a tool to estimate individual ages in fossil specimens. Cementum is a continuously growing dental tissue that anchors the periodontal ligament to the surface of the tooth root. It is deposited in annual bands and in contrast to bone is usually not subjected to resorption. As such, it has the potential to estimate individual age more precisely. Typically, cementum is visualized through destructive thin sectioning, although submicron synchrotron imaging has recently been shown to be effective in detecting cementum growth layers. Here we explore the utility of high resolution micro computed tomography (microCT) for imaging the fine incremental cementum layers in Eocene *Coryphodon*. We sampled nine teeth from several Clarkforkian and Wasatchian biozones of the Bighorn Basin of Wyoming. Standard petrographic techniques were used to create ground thin sections; the teeth were sampled around the apical third of the root. Specimens were microCT scanned either before or after thin sectioning on a Bruker SkyScan 1173 at 15–20  $\mu\text{m}$  voxel resolution. Our preliminary data suggest that microCT is capable of detecting cementum growth lines in *Coryphodon*; however, somewhat less reliably than in standard petrographic thin sections. Five of the samples

were either completely or partly diagenetically altered and could not be used for analyses. Four samples preserved a near complete record of cementum increments ranging between 6–30 annual growth layers in the petrographic sections. Although dark and light bands were visible in microCT images of several specimens, the number of lines were usually much lower than in the standard petrographic thin sections. Only one specimen preserved a similar count in the petrographic sections (six lines) and microCT images (five lines). Although it is promising that cementum growth layers can be detected in microCT images, higher resolution might be necessary to reliably infer individual specimen ages.

**Funding Sources** Funding for this study was provided by the Keck Geology Consortium and the National Science Foundation (NSF-REU1659322).

### Symposium: Paleoneurology

#### PHYLOGENETIC SCALING OF THE OLFACTORY APPARATUS IN CROWN AVES

Hogan, Aneila<sup>1</sup>, Amy Balanoff<sup>2</sup>, Gabriel Bever<sup>1</sup>

<sup>1</sup>Functional Anatomy and Evolution, Johns Hopkins School of Medicine, Baltimore, Maryland, U.S.A., <sup>2</sup> Psychological and Brain Sciences, Johns Hopkins School of Medicine, Baltimore, Maryland, U.S.A.

There is a long-held assumption that birds are lacking in olfactory ability, but data suggest avians exhibit a high degree of phylogenetic variation in this sense, with some taxa expressing odor sensitivity comparable to that of mammals. That olfaction became an increasingly important sensory modality in Pan-Aves is corroborated by fossil evidence showing progressive, crownward increases in relative olfactory bulb sizes across non-avian theropods. A variety of morphologies characterize the relevant brain regions and nasal cavity of crown birds, with striking differences in both olfactory bulb (OB) and turbinated (OT) form. The phylogenetic and mechanistic details of the evolutionary transformations responsible for this variation are, however, far from worked out. Developmental data in chickens reveal a coordinated growth in OBs and OTs through ontogeny, a result that is unexpected as the olfactory epithelium lines more of the nasal cavity than just the OT. If a similar developmental pattern holds true across the crown one should expect a conserved pattern of phylogenetic isometry, with OBs and OTs increasing or decreasing concomitantly across the tree. To test this hypothesis, we sampled across all major avian crown clades, utilizing diceCT scans to extract volumes and surface areas of brain and nasal anatomy. Results indicate OBs and OTs do not scale isometrically across the crown as a whole, although certain lineages (such as Passeriformes) return an isometric pattern whereas others exhibit different rates of allometry. The observed

transitions of relative OB size in published fossil data considered with our results suggest the avian olfactory apparatus has a complex evolutionary history that likely reflects differing levels of constraint, evolvability, and structural tradeoffs. With future work incorporating more developmental, physiological, and fossil data, these results will aid in enhancing our understanding of this integral sensory system and its larger role in avian and craniofacial evolution.

**Funding Sources** NSF DEB-1457181, NSF DEB-1406849.

### Holocene & Pleistocene Mammalian Macroecology & Faunal Studies

#### SHIFTING FAUNAS AND CHANGING CLIMATE: NEW REMAINS OF MIDDLE TO LATE PLEISTOCENE EQUUS FROM SOUTHWESTERN RIVERSIDE COUNTY, CALIFORNIA

Hohman, Charlotte J.<sup>1</sup>, Scott, Eric<sup>2</sup>, Dooley, Alton C.<sup>3</sup>

<sup>1</sup>Department of Earth Sciences, Montana State University, Temecula, California, U.S.A., <sup>2</sup>Paleontology, Cogstone Resource Management, Orange, California, U.S.A., <sup>3</sup>Western Science Center, Hemet, California, U.S.A.

Horses (genus *Equus*) are common denizens of Pleistocene large mammal faunas throughout North America. In inland southern California, horses are among the most common large mammals represented in the middle Pleistocene fossil record. By the end of the Pleistocene, however, horses are largely outnumbered by bison (*Bison*). The shift from a horse-dominated community to one dominated by bison is not well documented from the region.

During the 2003 construction of the Harveston housing subdivision in Temecula, Southwestern Riverside County, California, paleontological mitigation uncovered numerous vertebrate fossils. The recovered fossil material comes from two units: the middle Pleistocene Pauba Formation (Irvingtonian North American Land Mammal Age [NALMA]), which is unconformably situated above an unnamed sandstone and conglomerate unit (>765,000 years old), and from a second unnamed sandstone overlying the Pauba Formation. The latter sandstone unit contains fossils of *Bison antiquus*, and so dates to the Rancholabrean NALMA.

*Equus* is the most common large mammal genus present in the Harveston sample. A larger and smaller morphotype of horse is present, as demonstrated by size differences in weight-bearing elements and teeth. The larger morphotype of horse is more common in the Harveston sample; preliminary metric data indicate that these large horses plot

slightly below the size range of *Equus scotti* (previously reported from the Pauba Formation) and the late Pleistocene species *E. occidentalis*. The smaller horse morphotype compares favorably in size with small horse fossils from San Josecito Cave, Nuevo León, Mexico. Large mammals identified in association with horses from the Pauba Formation include *Paramylodon*, *Odocoileus*, and *Hemiauchenia*. Large mammals exclusive of horses in the younger Rancholabrean assemblage include *Bison*, *Mammuthus*, *Hemiauchenia*, *Odocoileus*, and cf. *Antilocapra*. The faunal assemblage in the younger unit suggests that the Temecula Valley may have shifted to a more open and drier habitat at the onset of the late Pleistocene with the appearance of *Bison*. A detailed quantitative study of specimens from multiple localities across the southwest U.S.A. and northern Mexico is underway to more fully explore changes in megafaunal biogeography through time in this region.

### Mesozoic Herpetology

#### AN ASSESSMENT OF CLIMATE AND ENVIRONMENTAL CHANGES OF THE HELL CREEK FORMATION USING THE BIOSTRATIGRAPHY OF SIX TURTLE TAXA

Holbach, Brady P.  
Biology, Carthage, Kenosha, Wisconsin, U.S.A.

The Hell Creek Formation (HCF) preserves an array of fossil fauna and flora, including *Tyrannosaurus*, *Triceratops*, *Edmontosaurus*, and a variety of turtles. The goal of this study was to determine whether changes in turtle biostratigraphy (i.e., relative placement of taxa in the strata) correlated with changes in plant biostratigraphy uncovered by previous studies. The biostratigraphy of turtles was also used to assess possible changes in the HCF environment over time. Turtles are sensitive to changes in temperature and require specific niches to survive. No previous study has compared the biostratigraphy of turtles from multiple localities of the HCF in an attempt to find changes in distribution or diversity.

This work included turtle specimens belonging to: Adocidae, Baenidae, Chelydroidae, Compsemydidae, Macrobaenidae, and Trionychidae; individual specimens were identified to the lowest taxonomic group. Presence-absence graphs were constructed or obtained from the literature and were used to assess changes in turtle diversity from individual HCF localities over time. These localities were then compared to each other for changes in presence or absence of taxa across the HCF in eastern Montana and western North and South Dakota. No significant difference was seen between the changes in diversity of plant taxa and turtle taxa.

The presence-absence graphs revealed that the presence and relative abundance of most turtle taxa studied remained stable both over time and across the different HCF localities. However, in southeastern Montana, the marine turtles, Macrobaenidae, were absent below 37 meters below the K/Pg boundary, while Basilmyes, a terrestrial turtle, was primarily found above this point, suggesting a transition from a coastal marine environment to forested environment at 37 meters below the K/Pg boundary in this region. A complete absence of turtle fossils was found between 55 and 50 meters below the K/Pg boundary in all localities suggesting a period of rapid sediment deposition.

### Mesozoic & Early Cenozoic Mammalian Evolution

#### PHYLOGENETIC POSITION OF *OLBITHERIUM* (MAMMALIA, PERISSODACTYLA) BASED ON NEW MATERIAL FROM THE EARLY EOCENE WUTU FORMATION

Holbrook, Luke T.<sup>1</sup>, Li, Cheng-Sen<sup>2</sup>, Yang, Jian<sup>2</sup>, Smith, Thierry<sup>3</sup>

<sup>1</sup>Biological Sciences, Rowan University, Glassboro, New Jersey, U.S.A., <sup>2</sup>Chinese Academy of Sciences, Beijing, China, <sup>3</sup>Royal Belgian Institute of Natural Sciences, Brussels, Belgium

The genus *Olbitherium* was originally described in 2004 from the early Eocene of the Wutu Formation in China as a 'perissodactyl-like' archaic ungulate. Described material of *Olbitherium* consists of partial dentaries with lower cheek teeth, isolated upper molars, and an isolated upper premolar. Subsequent collaborative fieldwork by Belgian and Chinese researchers discovered new material including a partial skull, the anterior portion of the dentary, and associated postcrania. In their general form, the skull and postcrania are similar to those of early perissodactyls. The new material provides a more complete picture of the upper dentition, and the anterior dentary demonstrates the presence of three lower incisors and a large canine, both ancestral features for perissodactyls. A phylogenetic analysis was conducted to test the affinities of *Olbitherium*, using a matrix of 321 characters and 72 taxa of placental mammals emphasizing perissodactyls and other ungulates. The results produced four shortest trees of 1981 steps. In all four trees, *Olbitherium* is the sister-taxon to all perissodactyls except *Ghazijhippus*. In contrast, when scoring was restricted to the originally described material, the results produced 16 shortest trees of 1970 steps, and *Olbitherium* nests well within Perissodactyla as sister-taxon to a clade including *Lambdaotherium* and the brontotheriids *Eotitanops* and *Palaeosyops*. The new material not only supports the identification of *Olbitherium* as a perissodactyl, but it also suggests that it is significant for understanding the ancestral perissodactyl morphotype.

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### **Dinosaur Systematics, Diversity & Ecology**

#### **A JUVENILE LAMBEOSAURINE BONEBED FROM THE WAPITI FORMATION OF NORTHWESTERN ALBERTA, CANADA**

Holland, Brayden<sup>1</sup>, Campione, Nicolás E.<sup>1</sup>, Bell, Phil<sup>1</sup>, Fanti, Federico<sup>2</sup>, Vavrek, Matthew J.<sup>3</sup>, Sissons, Robin<sup>4</sup>, Wang, Yan-Yin<sup>4</sup>, Hamilton, Samantha<sup>4</sup>, Sullivan, Corwin<sup>4</sup>  
<sup>1</sup>University of New England, Armidale, New South Wales, Australia, <sup>2</sup>Alma Mater Studiorum - Università di Bologna, Bologna, Italy, <sup>3</sup>Cutbank Paleontological Consulting, Grande Prairie, Alberta, Canada, <sup>4</sup>University of Alberta, Edmonton, Alberta, Canada

Hadrosaurid dinosaur bonebeds are prevalent in Upper Cretaceous strata from the midwest of North America (especially southern Alberta, Canada, and Montana, U.S.A.), but are less documented from more northerly regions. In 2018, the Boreal Alberta Dinosaur Project (BADP) rediscovered a juvenile hadrosaurid bonebed, the Spring Creek Bonebed (originally discovered in 1988) within Unit 3 outcrops of the Wapiti Formation (upper Campanian, ~75 Ma ago) near the town of Grande Prairie in northwestern Alberta. During the 2018 and 2019 field seasons, excavation of Spring Creek Bonebed yielded >250 specimens, including the first cranial material from the site (maxilla, premaxilla, postorbital, quadrate, prementary, dentary) which are consistent with a Lambeosaurinae designation. A minimum number of eight individuals have so far been identified from right humeri and, given the consistent size and histology of like elements, we assign all remains hadrosaurid to a single, similarly-aged, lambeosaurine species. Histological analyses of eight humeri indicate that the lambeosaurines were late juveniles, still undergoing sustained growth at their time of death. Uniform lack of weathering, lack of preferential alignment, and the monodominant composition of the bonebed, suggest that the bonebed originated from a mass mortality event. The exclusive preservation of a seemingly discrete age class within the Spring Creek Bonebed indicates that age segregation was a possible life history strategy used by these animals to mitigate the negative effects of juveniles on the fitness of the herd. Age segregation was previously hypothesized based on other hadrosaurid bonebeds, and in other dinosaurs, and may relate to: 1) seasonal breeding and extended parental care, in which non-breeding individuals are excluded from the main herd, and/or 2) the reduced physical capacity of younger individuals to ‘keep up’ with the main herd,

potentially requiring a different food source. Until now, our understanding of hadrosaurids from the Wapiti Formation was restricted to the hadrosaurine *Edmontosaurus regalis*, whilst bonebed research was limited to two *Pachyrhinosaurus* bonebeds. The description of the Spring Creek Bonebed marks the second unambiguous lambeosaurine occurrence in the Wapiti Formation, with the potential to provide a greater understanding of North American dinosaur diversity during the Late Cretaceous.  
**Funding Sources** Australian Government's Research Training Program scholarship; Dinosaur Research Institute's student grant.

### **Biomechanics & Functional Morphology**

#### **MYOLOGY OF THE REPTILIA: 3D MODELING OF JAW MUSCLES AND ITS UTILITY IN PALEOBIOLOGY**

Holliday, Casey, Wilken, Alec, Sullivan, Samuel, Verhulst, Conner, Sellers, Kaleb, Lessner, Emily, Fortner, John D., Middleton, Kevin  
University of Missouri, Columbia, Missouri, U.S.A.

Sauropsid vertebrates (lepidosaurs, turtles, crocodylians and birds) have evolved a diversity of head shapes and feeding behaviors during their history. A key to understanding this great radiation of reptiles is the physiology of the jaw musculature that powers the feeding apparatus. However, we still know little about jaw muscle mechanics within lineages of reptiles or how this complicated musculoskeletal system has evolved to employ a variety of behaviors. New imaging and computational methods are now enabling an extraordinary view into the 3D anatomy and biomechanics of reptiles and other vertebrates. Here we illustrate several approaches to analyzing jaw muscle morphology and architecture using contrast imaging, 3D fiber tracking, biomechanical analysis, and data visualization methods that offer enormous potential for exploring the anatomy, function and evolution of jaw muscles. We first illustrate basic workflow of 3D jaw muscle visualization, morphometrics, and interpretation using crocodylian jaw muscle anatomy. Second, we show how homologous jaw muscle bellies evolve among lineages of different reptiles and birds to elicit different functional demands. Third, we show how the 3D architecture of small, deep protractor muscles correlate with different types of cranial kinesis among a sample of lizards and birds. Many of these muscles leave traceable osteological correlates in the fossil record of reptiles and other vertebrates that can better guide inferences of muscle functional anatomy. These new imaging and analytical approaches offer incredible potential for the quantification of soft tissue morphology

and have remarkable applications to comparative biomechanics, ecomorphology, and paleobiology.

**Funding Sources** NSF IOS 1457319; NSF EAR 1631684.

## Education & Outreach

### PALEONTOLOGY ENGAGEMENT IN RURAL PUBLIC SCIENCE EXPOS

Holliday, Casey, Wilken, Alec, Sullivan, Samuel, Lessner, Emily, Sellers, Kaleb, Middleton, Kevin, Ward, Carol  
University of Missouri, Columbia, Missouri, U.S.A.

Most rural communities are not located near museums of natural history or other public paleontological exhibitions. This puts significant onus on local faculty versed in evolutionary biology and paleontology to develop events and activities that attract the interest of the public. This responsibility is heightened by the Broader Impacts initiatives of NSF, Next Generation Science Standards and ultimately the Engagement mission of Land Grant universities like the University Missouri. For the past ten years, faculty and students have been hosting a number of paleontological public outreach activities around Mizzou including science cafes, expos, and open houses to increase science exposure and literacy among the public of Central Missouri. Leveraged by our substantial imaging, 3D modeling and printing resources, and community partners, popular interactions have included tablecloth timelines, phylogenies with 3D printed homologous bones, Little Lascaux cave painting, 3D muscle fiber physiology exhibits, dissections, live raptors and of course Mesozoic fight club with inflatable outfits. Many of these exhibits are built to be easily transportable as part of our pop-up museum experience. These efforts have not only helped foster a pipeline of Central Missouri students into integrative anatomy and paleontology and forged lasting relationships with local families and community groups, but also have offered invaluable science communication training experiences for the next generation of young scientists who develop and execute many of these exhibits and events.

**Funding Sources** NSF IOS 1457319; NSF EAR 1631684.

## Mesozoic & Early Cenozoic Mammalian Evolution

### THE ANATOMICAL, LOCOMOTORY, AND SENSORY CHARACTERISTICS OF *TETRACLAENODON*, THE EARLIEST PHENACODONTID

Holpin, Sofia<sup>1</sup>, Shelley, Sarah L.<sup>2</sup>, Bertrand, Ornella C.<sup>1</sup>, Williamson, Thomas E.<sup>3</sup>, Brusatte, Stephen<sup>1</sup>

<sup>1</sup>School of Geosciences, University of Edinburgh, Edinburgh, U.K., <sup>2</sup>Mammals, Carnegie Museums,

Pittsburgh, Pennsylvania, U.S.A., <sup>3</sup>Paleontology, New Mexico Museum of Natural History, Albuquerque, New Mexico, U.S.A.

With the dawn of the Paleogene, the mammalian survivors of the Cretaceous–Paleogene mass extinction, 66 million years ago, found themselves in an emptied landscape. Within a million years of the bolide impact, placental mammals reached a diversity and abundance never seen during the Age of Dinosaurs. The North American ‘condylarths’ were amongst the first mammals to diversify during the early Paleogene and are often considered the ancestral ‘stock’ from which other euungulate groups evolved. Amongst these, Phenacodontidae are often regarded to lie at the base of the perissodactyl family tree, but their phylogenetic position, and that of other ‘condylarths’, remain contentious. *Tetraclaenodon*, a medium-sized herbivorous phenacodontid from the Torrejonian (~64 to ~62 Ma) of North America is generally recognized as the oldest member of Phenacodontidae, and thus is instrumental for untangling the evolutionary relationships of ‘condylarths’ and perissodactyls.

Here we present new information on *Tetraclaenodon* based on a description of new and previously known fossil material from the San Juan Basin of New Mexico, U.S.A., which we studied using high-resolution computed tomography (CT) scanning. From CT scans of the cranium, we segmented the brain endocast, which is relatively small and smooth (lissencephalic), similar to that of other Paleocene mammals. The petrosal lobules, which are involved in eye movement coordination, are small. The semi-circular canals associated with balance, provide an agility score of 3 indicating that *Tetraclaenodon* was probably moderately agile, similar to the extant raccoon dog or the aardwolf. A multivariate analysis of tarsal measurements for a sample of Paleocene and extant mammals, which informs locomotor style, indicates that *Tetraclaenodon* was most suited to terrestrial locomotion. This is in line with anatomical and myological features of the limbs of *Tetraclaenodon* and other phenacodontids, early perissodactyls and extant mammals. These findings contradict previous studies that designated *Tetraclaenodon* as a scansorial mammal, capable of habitually climbing trees. Our results shed light on the locomotory adaptations of *Tetraclaenodon* in comparison to more cursorial phenacodontids and perissodactyls, such as *Phenacodus* and *Hyrachus*. The earliest member of the perissodactyl stem lineage apparently lacked the more cursorial adaptations of their relatives in the late Paleocene and onwards.

**Funding Sources** European Research Council Starting Grant (ERC StG 2017, 756226, PalM), National Science Foundation (EAR- 1654952).

## Evolution & Biology of Non-Avian Theropods

## TAXONOMIC DIVERSITY, GUILD STRUCTURE, AND ONTOGENETIC NICHE SHIFTS IN THEROPOD CARNIVORE COMMUNITIES: IMPLICATIONS FOR PALEOECOLOGY AND LIFE HISTORY STRATEGIES IN TYRANT DINOSAURS

Holtz, Thomas R.  
Dept. of Geology, University of Maryland, College Park,  
Maryland, U.S.A.

Well-sampled dinosaur communities from the Jurassic through the early Late Cretaceous show greater taxonomic diversity and morphological disparity among larger (>50 kg) carnivorous theropod taxa than communities of the Campano-Maastrichtian, particularly to those of eastern/central Asia and Laramidia. This study tests the skewness of adult body size within cenograms of theropod guilds and confirms that the large carnivore sizes in Asiamerican assemblages are monopolized by tyrannosaurids, with adult medium-sized (50–500 kg) predators rare or absent compared to earlier communities. The distribution of carnivore sizes in various communities is compared to the species abundance of potential prey species recorded in these same faunas, to examine if the skewed distribution of Asiamerican populations reflects a decrease in herbivore taxon abundance. Recent high-quality biostratigraphic studies of several of dinosaur-bearing formations allows for a more precise use of ‘instantaneous’ biotic diversity that might be inflated by binning successive time intervals. When patterns of theropod diversity are compared to potential prey diversity in these communities, the distinctiveness of tyrannosaurid-dominated faunas is especially apparent.

The ‘missing middle-sized’ members of these guilds would be alleviated by subadults of tyrannosaurid species serving as the mid-sized predators. Hypothesized growth curves of tyrannosaurids are compared to those of likely prey species and to other large theropod dinosaurs, which suggest that the onset of the rapid growth phase in tyrant dinosaurs may be heterochronically delayed from the ancestral state.

### Symposium: Dietary Reconstruction

## MASHERS, GNASHERS, OR UNDERWATER SLASHERS? MOSASAUR MICROWEAR AND GEOCHEMISTRY EXPLORED AMONGST TWO DIFFERENT MOSASAUR COMMUNITIES IN THE LATE CRETACEOUS OF THE NETHERLANDS AND CANADA

Holwerda, Femke M.<sup>1</sup>, Bestwick, Jordan<sup>3</sup>, Purnell, Mark A.<sup>4</sup>, Schulp, Anne S.<sup>2</sup>

<sup>1</sup>Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada, <sup>2</sup>Faculty of Geosciences, Utrecht University, Utrecht, Netherlands, <sup>3</sup>School of Geography, Earth and Environmental Sciences, University of Birmingham, Birmingham, U.K., <sup>4</sup>School of Geography, Geology and the Environment, University of Leicester, Leicester, U.K.

Mosasaurus gained marine dominance as apex predators in the last 30 Ma of the Cretaceous. Though most genera are cosmopolitan, regional ecological structures with different taxonomic components existed. Coexistence of genera in a regional setting was likely facilitated by dietary niche differentiation, which was proven in an earlier study on two-dimensional and three-dimensional dental microwear texture analysis on type Maastrichtian mosasaurs from the Netherlands. Therein, large apex predators *Mosasaurus hoffmanni* and *Prognathodon saturator* displayed a mix of piscivorous, sarcophagous, and osteophagous signals in their dental microwear, whereas the smallest mosasaur, specialist *Carinodens belgicus*, showed a durophagous diet. The smaller mosasaur *Plioplatecarpus marshi* also displayed a tendency to durophagy, contrary to what its tooth morphology indicates.

A second group studied for community comparison is the mosasaurs from the Bearpaw Formation, Campanian of Alberta, Canada, on the northern border of the Western Interior Seaway. Here, *Mosasaurus missourensis* and *Prognathodon* sp. are identified as apex predators, showing a similar combination of ‘soft’ and ‘hard’ dietary habit traces in their 2D microwear as the type Maastrichtian mosasaurs. Interestingly, also here a plioplatecarpine, *Plioplatecarpus primaevus*, displays durophagous microwear signals, contrary to what its tooth morphology indicates. It is likely that these plioplatecarpines fed on ammonites and other soft invertebrates, besides softer prey (fish and squid), and were thus not solely piscivorous. Indeed, EDX analysis, measuring Sr and Ba elements, shows a distinct dietary niche for *Plioplatecarpus*, with low Ba content overlapping only with values of sharks, indicating near-shore foraging. Meanwhile, the apex predators overlap together with higher Ba rates, indicating more offshore feeding, and lower Sr levels than *Plioplatecarpus*, indicating higher trophic level.

The more common mosasaur at the Bearpaw Formation is *Mosasaurus missourensis*, which shows a difference in 2D microwear between its upper and lower jaws. The upper jaws show more scratches, thus more slashing movements, and lower jaws show more pits, thus more grinding of prey. Compared to *Prognathodon*, their skull kinetics show a higher intraspecific range, which may be why *Mosasaurus missourensis* was more successful in the region. Moreover, its EDX measurements show a higher range overall, indicating coverage of wider hunting grounds.

**Funding Sources** Femke Holwerda is Dr. Betsy Nicholls Post-Doctoral Fellow at the Royal Tyrrell Museum of

Palaeontology, which is funded by the Royal Tyrrell Museum Cooperating Society.

## Preparators

### CURATION OF THE MEHRTEN FORMATION

Hook, Juliet, McLeod, Samuel  
Vertebrate Paleontology, Natural History Museum of Los Angeles County, Altadena, California, U.S.A.

Collecting efforts throughout the past 50 years by Mr. Dennis Garber yielded a diverse Neogene vertebrate fossil assemblage from the Mehrten Formation in Stanislaus County, California, U.S.A. The collection consisting of well-preserved fish, birds, amphibians, reptiles, mammals, and plant material were donated to both the Natural History Museum of Los Angeles County and the University of California Museum of Paleontology. After limited publication on the material, resurgence in studies of the Hemphillian fossils reveal major insights into the paleoecology of the time. The collection holds the only known Californian occurrence of the *Hesperotestudo orthopygia* tortoise. This species presence supports previous paleobotanical evidence of a warmer Pliocene climate in the region compared to today. Most notably, the collection also includes the first and only fossilized coprolites from Borophagine canids exhibiting the bone-crushing behavior of the hypercarnivore's diet.

Supported by an anonymous donation, the Natural History Museum of Los Angeles County is facilitating future use and availability of this unique assemblage by completing the curation and digitization of newly acquired fossils discovered by Mr. Garber. Additional georeference data supplied by researchers at California State University Stanislaus provide missing contextual information of the Mehrten Formation localities. In order to process the collection, the following goals were established: inventory the material, sort and identify elements and taxonomic groups, catalog and archivally label elements, digitally photograph material, integrate the newly acquired fossils within the existing locality drawers, and supplement locality records.

The project resulted in the identification of over 400 elements from the 49 existing localities which were consequently labeled, stored in archival housing, cataloged, and photographed. Database locality records were updated to reflect accurate and extensive georeference data such as site photographs, GPS coordinates, lithologic descriptions, and collector interviews pertaining to the existing localities. Overall, the collection and its corresponding data are now housed and organized according to current best practices. The completion of the project provides for greater access to specimens and preservation of locality data from the Mehrten Formation so that a deeper understanding of the

paleoecology of Stanislaus County throughout the Neogene period can continue to develop.

**Funding Sources** The work was supported by an anonymous donation to the Vertebrate Paleontology Department at the Natural History Museum of Los Angeles County.

### Macroecology & Macroevolution

#### DEEP-TIME DEMOGRAPHIC INFERENCE SUGGESTS K-PG ECOLOGICAL RELEASE AS DRIVER OF NEOAVIAN ADAPTIVE RADIATION

Houde, Peter<sup>1</sup>, Braun, Edward L.<sup>2</sup>, Zhou, Lawrence<sup>1</sup>  
<sup>1</sup>Department of Biology, New Mexico State University, Las Cruces, New Mexico, U.S.A., <sup>2</sup>Department of Biology, University of Florida, Gainesville, Florida, U.S.A.

Assessing the applicability of theory to major adaptive radiations in deep time represents an extremely difficult problem in evolutionary biology. Neoaves (95% of living birds) is believed to have undergone a period of rapid diversification roughly coincident with and following the K-Pg boundary. We investigate whether basal neoavian lineages experienced ecological release in response to ecological opportunity, as evidenced by density compensation, a metric commonly employed in studies of more recent adaptive radiations. We estimated effective population size ( $N_e$ ) in basal lineages of birds using insertion/deletion mutations (indels) and gene trees generated from nucleotides, indels, or both in the context of well-understood relationships between gene tree dis/concordance (due to incomplete lineage sorting, 'ILS'), time, and demography couched in coalescent theory. We found that some lineages exhibited unexpectedly high gene tree discordance relative to the estimated number of generations between speciation events near the K-Pg boundary. The simplest explanation for this result is an increase in  $N_e$ , notwithstanding the potential effects of homoplasy, generation length, taxon and temporal sampling, tree topology, divergence time estimates, and metapopulation structure on  $N_e$  inference. Simply stated, we observed a spike in estimated  $N_e$  among some of the basal-most lineages of Neoaves beginning with the K-Pg boundary. This is consistent with density compensation in response to ecological opportunity. It suggests that the K-Pg mass extinction of heterospecific antagonists (e.g., Enantiornithes) spurred an explosive radiation of neoavian birds, whether or not it was adaptive. To the best of our knowledge, such demographic data have never previously been available for the ancestral lineages of major clades because it generally requires population sampling. The relevance of our results to the 'Ecological Theory of Adaptive Radiation' will ultimately hinge on complementary studies of rates of speciation and of

ecological specialization. Nevertheless, our result is yet another piece in an ever-accumulating collection of data that are consistent with and therefore afford confidence to the hypothesis that Neaves underwent an adaptive radiation in response to ecological release following the K-Pg mass extinction. Perhaps more importantly, we believe that our study represents proof-in-principle for a novel approach for estimating population demography in deep time.

## Taphonomy & Stratigraphy

### **DIMETRODONS DISASSEMBLING PREY: MULTIPLE TAPHONOMIC SIGNATURES AT CRADDOCK BONE BED, SEYMOUR, TX,**

Houpt, Tracy J.<sup>1</sup>, Flis, Chris J.<sup>1</sup>, Bakker, Robert T.<sup>2</sup>, Temple, David T.<sup>2</sup>

<sup>1</sup>Whiteside Museum of Natural History, Seymour, Texas, U.S.A., <sup>2</sup>Houston Museum of Natural Science, Houston, Texas, U.S.A.

Classic theory says that *Dimetrodon* and other sphenacodontids, although retaining many primitive features, are close to the ancestry of more advanced 'mammal-like reptiles' and true Mammalia. We have dissected the richest dimetrodont site, the Craddock Bone Bed, near Seymour, TX. A 2008–2013 test excavation of an area 33x40 m showed abundant bite marks and shed dimetrodont teeth; over the last seven years, we expanded the sampling across the entire bonebed outcrop, 240 m N to S, 34 m E to W, maximum depth 3.2 m. 99% of bones lie horizontally in successive thin silty mudstone units, 3–12 cm thick. Ninety-seven percent of shed teeth are dimetrodont. Body size correlate with taphonomic mode. The heaviest species, *Diadectes* sp., adult live weight estimated at 450 kg, occurs as isolated scattered vertebrae, with neural spine apices bitten off. The commonest small amniote, *Varanosaurus*, (FL 100 mm maximum), shows 'owl pellet' mode, i.e. little articulation and bones with very few bite marks and no calcareous rind, suggesting that body parts were swallowed whole and regurgitated or defecated cleanly. Small juvenile dimetrodons (FL 135 mm and less) show similar conditions. The commonest benthic non amniote, *Diplocaulus*, occurs as articulated skeletons with bite marks in the snout, suggesting that dimetrodons had attempted to remove the animal from its burrow.

Adult dimetrodons and subadult diadectids show severe damage. We mapped the percent of bone area damaged by bite marks. Heaviest damage occurs to thin, wide areas where thick muscles attached. Up to 60% of bone area was removed in scapulae and axis neural spines. Muscle attachments in distal humeri-- epicondyles and supinator crests - were removed, up to 25% of total humerus area. Entire proximal ends were removed in humeri and femora,

5–15% of total bone area. Edges of coracoids were bitten away, up to 10% of bone area, mean area removed in all bitten bones is 15%. In experiments, feeding by extant crocodiles and Komodo Dragons remove far less bone. Dinosaur feeding sites too show lower bone removal. Craddock Bone Bed bites seem precise: none occur on central shafts of femora or humeri; damage was concentrated on muscle sites at ends. The bone bed data agrees with that from White River mammals. We suspect that dimetrodont feeding behavior had evolved to higher precision than that of extant reptiles.

## Mammalian Skeletal Morphology

### **THE ECOLOGY OF FOSSIL HIPPOPOTAMIDS (MAMMALIA, CETARTIODACTYLA) EXAMINED IN THE LIGHT OF THE MICROANATOMY OF THEIR LONG BONES**

Houssaye, Alexandra<sup>1</sup>, Martin, Florian<sup>2</sup>, Etienne, Cyril<sup>1</sup>, Boisserie, Jean-Renaud<sup>2</sup>, Lihoreau, Fabrice<sup>3</sup>

<sup>1</sup>CNRS/MNHN, Paris, France, <sup>2</sup>Université de Poitiers, Poitiers, France, <sup>3</sup>Université de Montpellier, Montpellier, France

Hippopotamids are herbivorous mammals whose origin dates back to the late middle Eocene. This taxon includes animals of a wide variety of sizes and body proportions, ranging from small and gracile forms with slender limbs to massive and heavy forms. Many anthracotheres were previously considered to be semi-aquatic, but recent studies have revealed a diversity of ecologies. This study focuses on bone microanatomy, one of several indicators for inferring the ecology of extinct taxa. This microanatomical study of the stylopod bones of various hippopotamids and comparisons with diverse terrestrial and semi-aquatic quadruped mammals highlight converging specializations for a semi-aquatic lifestyle and load bearing. This consists of an increase in bone compactness by filling the medullary area with spongy bone and a thickening of the cortex. However, despite this convergence, comparisons between animals of similar weight suggest that excessive compactness is indicative of a semi-aquatic lifestyle. In this context, the microstructure of *Choeropsis liberiensis* seems to correspond to an animal that feeds mainly in forests but frequently invades water, whereas the microstructure of *Hippopotamus amphibius* has a stronger compactness corresponding to an animal that spends a large part of its time standing in the water or walking/swimming on the bottom. Consequently, this study suggests an essentially terrestrial lifestyle for various anthracotheres and some fossil hippopotamids, a slight degree of water dependence in the anthracothere *Brachyodus onoideus*, and a stronger degree in the anthracothere *Libycosaurus bahri* and the fossil

hippopotamid *Hexaprotodon garyam*, although less intense than in *Hippopotamus amphibius*. This demonstrates the importance of integrating bone microanatomy in future studies of hippopotamoid ecology. **Funding Sources** ANR-15-CE32-0010, ERC-2016-STG-715300.

## Mesozoic & Early Cenozoic Mammalian Evolution

### TESTING FOR A LATITUDINAL GRADIENT OF MORPHOLOGICAL DIVERSITY IN EARLY PALEOCENE EUTHERIAN MAMMALS FROM NORTH AMERICA

Hovatter, Brody, Grossnickle, David, Wilson, Gregory P. University of Washington, Seattle, Washington, U.S.A.

The latitudinal diversity gradient is well documented in extant vertebrate communities and has been observed in various intervals of the Phanerozoic. Most of the research on this pattern in mammals has focused on taxonomic richness, whereas morphological diversity has received less attention, particularly in the fossil record. Here, we investigate the latitudinal diversity gradient in mammals via dietary diversity and morphological disparity of early Paleocene eutherian mammals from the Western Interior of North America. We applied landmark-based 2D geometric morphometrics to penultimate upper molars of mammals from the Puercan and Torrejonian NALMAs across a north–south transect from western Canada to New Mexico. We compiled a specimen dataset from museum collections and the published literature, and subdivided it into three geographic bins (northern, central, southern) of approximately equal latitudinal extent.

Our results show that dental-shape disparity of Puercan eutherian mammals did not significantly differ across latitudinal bins. This is consistent with previous reports of a flat latitudinal gradient of taxonomic richness for this interval, but surprising given the differences in the taxonomic composition across this transect. In the Torrejonian, disparity decreased with latitude: the ‘southern’ fauna had substantially greater disparity than the ‘central’ and ‘northern’ faunas, suggesting the establishment of a latitudinal gradient in ecomorphological diversity in the wake of the end-Cretaceous mass extinction event. There are also distinctive patterns of morphospace occupation across latitudes within taxonomic groups (plesiadapiforms) and between closely related taxonomic groups (i.e., arctocyonid vs. peripitychid ‘archaic ungulates,’ and cimolestid vs. leptictid ‘insectivorans’). The morphospace patterns imply a greater reliance on plant-based diets in southern regions (e.g., peripitychids) and a higher prevalence of omnivory and carnivory in more northerly regions (e.g., plesiadapiforms and arctocyonids, respectively). More broadly, our findings point to early

Paleocene dietary divergence within clades (and grades) of eutherian mammals across latitudes that might have been driven by latitudinal differences in climate and vegetation. These results corroborate previously observed biogeographic differences in early Paleocene mammalian faunas and underscore the importance of evaluating morphological diversity in tandem with taxonomic diversity.

## Mammalian Skeletal Morphology

### HOW DID MASTODONS GROW? ONTOGENETIC LONG BONE GROWTH IN THE AMERICAN MASTODONS

Htun, Thein<sup>1</sup>, Prothero, Donald R.<sup>2</sup>, Hoffman, Jonathon<sup>3</sup>, Lukowski, Stephanie<sup>4</sup>

<sup>1</sup>Geological Sciences, California Polytechnic University, Pomona, Hollister, California, U.S.A., <sup>2</sup>Natural History Museum of L.A. County, Los Angeles, California, U.S.A., <sup>3</sup>Santa Barbara Museum of Natural History, Santa Barbara, California, U.S.A., <sup>4</sup>Snowmass Ice Age Discovery Center, Snowmass Village, Colorado, U.S.A.

Proboscideans, much like other terrestrial megafauna, are supported by thick robust limbs, which are necessary to accommodate their larger body mass. How do these limbs grow between different species? Having already looked at the pattern in elephants and mammoths, we investigated the growth curves of two different species of proboscideans (the newly named Western mastodon, *Mammot pacificum*, and the American mastodon, *Mammot americanum*) to determine their ontogenetic patterns, and compared their growth to data from extant African elephants. Contrary to expectations of increasing robustness, analysis of these measurements suggests that most elephant and mammoth limbs grew isometrically, with slopes not significantly different from 1.0. Only the ulna in some species shows slightly more robust growth, possibly because the huge head of elephantoids might require more robust support in the lower front limbs. In the case of the American mastodon, the slopes of front limbs (humerus, ulna) are all isometric (except for the ulna of *M. americanum*), while the slopes of the femora are significantly more gracile than expected. The slopes of the tibiae were mixed, with the genus *Mammot* showing negative allometry, while *M. pacificum* was more gracile and *M. americanum* was isometric. Most of these slopes are tightly constrained, since there is the full range of sizes, from huge adults to baby mastodons in the data set (over 24 specimens of each limb were measured), and the correlation coefficients are excellent ( $r$ -squared = 0.85 or higher for nearly every sample). This pattern contrasts strongly with that seen in other proboscideans, but the presence of some of the negative growth slopes may be due to the absence of

neonate specimens in our data set. In studies of living elephants, when neonates are included, the trend in the hindlimbs shifted from negatively allometric to isometric.

**Funding Sources** Cal Poly Pomona Geological Sciences Department, Cal Poly Pomona OUR student travel fund.

### Mesozoic & Early Cenozoic Mammalian Evolution

#### NEW TRICONODONTID (PAN-THERIA, MAMMALIA) FROM THE JURASSIC OF NORTH AMERICA AND CRANIAL-POSTCRANIAL DISPARITY IN THE BODY MASS ESTIMATIONS OF SMALL-BODIED MAMMALS

Huang, E. J., Bever, Gabriel S.

Johns Hopkins University, Baltimore, Maryland, U.S.A.

We report a new triconodontid mammal from the Upper Jurassic Morrison Formation, Fruita Paleontological Area, western Colorado. The taxon is based on a single associated, and partially articulated, skeleton that includes a left lower jaw with molars in situ, but also a wide array of postcranial elements. This may be the first occasion in a triconodontid where non-fragmentary, three-dimensional limb elements, in particular a nearly complete femur, are preserved in direct association with more taxonomically useful dental material. Phylogenetic analyses consistently recover the specimen within the stem therian radiation Triconodontidae, as sister to *Priacodon*. Diagnostic characters among triconodontids include a shallow jaw depth relative to molar size and a coronoid process positioned lateral to the last lower molar. The proximal end of the femur resembles that of *Morganucodon* and other stem therians, whereas the distal end may well be unique among Mesozoic mammals in the poor development of its intercondylar fossa.

The preservational details of the new specimen make it a useful subject for contrasting body mass estimations based on cranial versus postcranial measurements. Body mass is a critical quantity of all organisms that correlates with many other predictive biological characters, including metabolic rate, lifespan, and fecundity. There has been a heavy reliance on craniodental metrics for assessing body mass in Mesozoic mammals, which may or may not have important implications for assessing these important and relatively small-bodied lineages. We tested this hypothesis with a robust dataset of cranial and postcranial measurements from small-bodied mammals sampled across the mammalian crown clade. Linear regressions on recorded body mass indicate a universal correlation between the measurements and body mass and a clear difference in the precision of the estimators. Postcranial measurements generally outperform jaw and especially dental metrics in predicting body mass, with the superior-inferior breadth of the femoral head and the bicondylar

breadth of the femur providing the most precise estimations. Based on the derived postcranial estimators, the Fruita specimen weighed 20–35 grams, one-third of its estimated mass based on craniodental estimators. This supports the conclusion that previous mass estimates for the group are likely exaggerated, and may be promoting imprecise interpretations of Late Jurassic paleobiology.

### Dinosaur Systematics, Diversity & Ecology

#### NEW THESCELOSAURID (DINOSAURIA: ORNITHISCHIA) MATERIAL FROM THE WAPITI FORMATION (CAMPANIAN) OF NORTHERN ALBERTA, CANADA

Hudgins, Michael N.<sup>1</sup>, Bell, Phil<sup>2</sup>, Campione, Nicolás E.<sup>2</sup>, Fanti, Federico<sup>3</sup>, Sissons, Robin<sup>1</sup>, Vavrek, Matthew J.<sup>4</sup>, Larson, Derek W.<sup>5</sup>, Sullivan, Corwin<sup>1</sup>

<sup>1</sup>Biological Sciences, University of Alberta, Edmonton, Alberta, Canada, <sup>2</sup>School of Environmental and Rural Science, University of New England, Armidale, New South Wales, Australia, <sup>3</sup>Dipartimento di Scienze della Terra e Geologico-Ambientali, Università di Bologna, Bologna, Italy, <sup>4</sup>Grande Prairie, Grande Prairie, Alberta, Canada, <sup>5</sup>Philip J. Currie Dinosaur Museum, Wembley, Alberta, Canada

The neornithischian dinosaur clade Thescelosauridae flourished from the Aptian to the Maastrichtian. This diverse, but in some respects poorly studied, group of small-bodied herbivores existed in both North America and Asia and is divided taxonomically into Orodrominae and Thescelosaurinae. In the Campanian and Maastrichtian of southern Alberta, orodromines typically occur in the Belly River Group and thescelosaurines in the younger Edmonton Group. The shale deposits of the Bearpaw Formation laid down during a major Campanian transgression of the Western Interior Seaway separate the two stratigraphic groups and obscure thescelosaurid evolution during this interval. However, the Wapiti Formation, a non-marine fluvial deposit exposed in northern Alberta, includes strata that correlate with the transgressive Bearpaw Formation. Recent fieldwork in the Grande Prairie area has yielded new thescelosaurid material from the DC (Dinosaur-Chelonian) Bonebed, which lies within Unit 3 of the Wapiti Formation and roughly corresponds in age to the transition between the Bearpaw Formation and the overlying Edmonton Group in southern Alberta. The thescelosaurid material from the DC Bonebed comprises several disarticulated postcranial and cranial elements, including a femur, two fibulae, and a quadrate. The femur exhibits typical features of Thescelosauridae: a pendant fourth trochanter, a posteriorly directed femoral shaft, and an intertrochanteric notch, although it is more robust than those of known

thescelosaurines and orodromines. The fibulae are similar in morphology and size to North American thescelosaurines, but are larger than those of Asian thescelosaurines. The quadrate is morphologically similar to its thescelosaurine counterparts in both North America and Asia and is smaller than typical thescelosaurine quadrates but larger than orodromines. Preliminary phylogenetic analysis of the DC specimens, using a previously published character matrix and assuming that they all belonged to a single species, tentatively places the DC thescelosaurid in a polytomy with Orodrominae and Thescelosaurinae. The DC thescelosaurid specimens represent the first unambiguous osteological record of a thescelosaurid in the Wapiti Formation and of the thescelosaurid fauna that existed during, or perhaps just after, the deposition of the Bearpaw Formation.

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### Mesozoic & Early Cenozoic Mammalian Evolution

#### EVOLUTION OF MAMMALIAN ARBOREALITY AND THE K-PG MASS EXTINCTION

Hughes, Jonathan J.<sup>1</sup>, Berv, Jacob S.<sup>2</sup>, Chester, Stephen G.<sup>3</sup>, Sargis, Eric J.<sup>4</sup>, Field, Daniel J.<sup>5</sup>

<sup>1</sup>Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York, U.S.A.,

<sup>2</sup>Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan, U.S.A.,

<sup>3</sup>Brooklyn College, City University of New York, Brooklyn, New York, U.S.A., <sup>4</sup>Yale Peabody Museum, New Haven, Connecticut, U.S.A., <sup>5</sup>Department of Earth Sciences, University of Cambridge, Cambridge, U.K.

The Cretaceous–Paleogene (K–Pg) mass extinction 66.02 million years ago was characterized by a worldwide ecological catastrophe and rapid species turnover. Large-scale deforestation resulting from the Chicxulub asteroid impact influenced the evolutionary trajectories of multiple clades in terrestrial environments, such as biased survivorship favoring non-arboreal bird lineages. Here, we evaluate patterns of substrate preferences across the K–Pg boundary in mammals, a group that, like birds, underwent rapid diversification following the mass extinction event. Using Bayesian, likelihood, and parsimony ancestral state reconstructions, as well as using alternative phylogenetic topologies and contextualizing with available fossil evidence, we found that patterns of mammalian ecological selectivity were not as stark as those hypothesized for birds. We suggest that most, but not all, pre-K–Pg arboreal mammalian lineages did not survive the mass extinction event and infer post-extinction transitions to arboreality in

numerous independent mammalian lineages in the early Cenozoic. However, members of total-clade Primatomorpha (Primates + Dermoptera) and a major clade of marsupials (Petauroidea + Didelphimorphia) appear to have maintained arboreal habits across the K–Pg boundary, possibly indicating ecological flexibility during an interval of global forest instability.

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### Symposium: Dietary Reconstruction

#### A MULTI-PROXY APPROACH TO RECONSTRUCT THE PALEOECOLOGY OF THE RHINOCEROTIDAE (MAMMALIA, PERISSODACTYLA) FROM THE EARLY MIOCENE BÉON 1 LOCALITY, MONTRÉAL-DU-GERS, SW FRANCE

Hullot, Manon I.

Institut des Sciences de l'Evolution de Montpellier, Montpellier, France

With around 90 species, the mid-Orleanian Béon 1 locality (Occitanie, SW France) yielded one of the richest Miocene vertebrate assemblages in Europe. Rhinocerotidae are exceedingly dominant over other faunal components, with dental remains documenting four species: the teleoceratines *Brachypotherium brachypus* (minimum number of individuals [MNI]  $\approx$  5) and *Prosantorhinus douvillei* (MNI  $\approx$  40), the hornless rhinocerotine *Plesiaceratherium mirallesi* (MNI  $\approx$  38), and the early elasmotheriine *Hispanotherium beonense* (MNI  $\approx$  7). This abundance within ca. 500 m<sup>2</sup> raises questions about habitat capacity and niche partitioning as all species were strictly coeval. The four rhinoceroses are thought to inhabit different ecotopes, except for both teleoceratines, considered swamp dwellers. However, available  $\delta^{18}\text{O}$  data suggest discrepancies between *B. brachypus* and *P. douvillei*, either related to distinct evapotranspiration rates (*B. brachypus* being more hippo-like) or isotopic content of preferred food. Here, we propose a multi-proxy approach to better understand the ecology of these four rhinoceroses. We used dental microwear texture analysis to provide dietary preferences, enamel hypoplasia to assess environmental stresses, and mortality curves to give insights on populational structure. Dental microwear reveals significant differences between species and facets (MANOVA, p-values <0.05). All fossil specimens exhibit microwear patterns distinct from those of all extant species, yet suggesting soft browsing or mix-feeding. Only the shearing facet's signal of *P. mirallesi* falls within the range of grazing species. The microwear signals of *B. brachypus*

and *P. douvillei* point to distinct feeding preferences. The prevalence of enamel hypoplasia is very high at Béon 1 with about 23% of all teeth being affected. Proportions vary between species – 10.5% in *H. beonense* teeth vs. 25.4% in *P. mirallesi* ones – and dental loci, but P4 and molars are more impacted by hypoplasia, suggesting both weaning-related (P4) and environmental stresses (e.g., seasonality; M2–M3). The mortality curves of all species are relatively similar (Khi2, p-value >0.1), with three modes: around weaning, around sexual maturity, and late in life. This suggests similar socialities. Furthermore, *Prosantorhinus douvillei* and *H. beonense* show a population structure similar to that of the extant *Rhinoceros unicornis* in Chitwan National Park (India) with about 20% of juveniles, 20% of subadults, and 40% of adults.

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## Late Cenozoic Mammalian Macroecology & Macroevolution

### CONTRASTING THE BODY MASS EVOLUTION OF ENTOPYCHINE AND GEOMYINE GOPHERS

Hunt, Molly E.<sup>1</sup>, Calede, Jonathan<sup>2</sup>, Jiménez-Hidalgo, Eduardo<sup>3</sup>, Claxton, Alexander<sup>4</sup>

<sup>1</sup>School of Earth Sciences, The Ohio State University, Columbus, Ohio, U.S.A., <sup>2</sup>Department of Evolution, Ecology, and Organismal Biology and School of Earth Sciences, The Ohio State University, Columbus, Ohio, U.S.A., <sup>3</sup>Laboratorio de Paleobiología, Universidad del Mar, Oaxaca, Mexico, <sup>4</sup>Department of Evolution, Ecology, and Organismal Biology, The Ohio State University, Columbus, Ohio, U.S.A.

Pocket gophers (family Geomyidae) are the dominant burrowing rodents in North America today. They also were the dominant taxa in that role during much of the Oligocene. The extant subfamily of gophers, the Geomyinae, has been hypothesized to diversify with climatic and environmental changes during the Blancan whereas the extinct subfamily Entoptychinae diversified during the Arikareean, possibly as a response to the opening of the environment.

In this study, we explore the pattern of body size evolution within these two clades as a tool to constrain the processes at play in the radiation of burrowing rodents. Body mass is a critical property of animals that is linked to many ecological characteristics, locomotion, and habitat. Body mass can also easily be estimated both in modern taxa and in the fossil record. In this study, we use upper and lower tooththrow lengths from 266 fossil specimens and body mass data from museum collections and the literature for extant

specimens. We also used the well-resolved published phylogenetic framework of geomyines and an unpublished phylogenetic tree of entoptychines currently in development.

The results of our analysis show that the evolution of body size in Entoptychinae follows an Ornstein-Uhlenbeck model whereas the body size evolution within Geomyinae follows a directional model. The ancestral entoptychine was a mid-sized rodent (for the clade). Small body size evolved at least three times across three different genera; so did large body size. Within Geomyinae, the genus *Thomomys* remained constrained to small body sizes whereas several genera (e.g., *Heterogeomys*, *Zygogeomys*) evolved to only include large species.

Within Entoptychinae, there is no significant difference in body size among the genera *Entoptychus*, *Gregorymys*, and *Pleurolicus*; the rare genus *Ziamys* is significantly smaller. However, species from the western U.S.A. and Mexico are larger than those found in the Great Plains. There also appears to be a consistent pattern of association between a large and a small species living contemporaneously within a given region.

Ongoing analyses will help refine the timing of the evolution of body size in Geomyidae and help shed light on its possible association with locomotion and heterochronous environmental changes across North America.

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## Permo-Triassic Tetrapods

### A BASAL NONMAMMALIAFORM CYNODONT FROM THE LATE PERMIAN OF ZAMBIA: NEW EVIDENCE FOR THE ORIGIN OF MAMMAL-LIKE CRANIAL-POSTCRANIAL NEUROMECHANICAL COORDINATION

Huttenlocker, Adam<sup>1</sup>, Sidor, Christian A.<sup>2</sup>

<sup>1</sup>Department of Integrative Anatomical Sciences, University of Southern California, Los Angeles, California, U.S.A., <sup>2</sup>Department of Biology and Burke Museum, University of Washington, Seattle, Washington, U.S.A.

Nonmammaliaform cynodonts were a diverse group of Permo-Triassic synapsids whose morphological evolution documented the beginning of many classic mammalian traits. Here, we report a new cynodont from the upper Permian Madumabisa Mudstone Formation of Zambia's Luangwa Basin. The specimen, a relatively complete and undistorted cranium and articulated mandible with associated postcranial elements, is interpreted as the most

complete and well-preserved example of a charassognathid cynodont. High-resolution micro-computed tomography further reveals hitherto unknown details of charassognathid endocranial and postcranial anatomy, including inset postcanine tooth rows, a well-differentiated masseteric fossa, an epipterygoid processus ascendens unjoined to the frontal, incipiently biconcave exoccipital condyles, and an acromion process and triceps tubercle on the scapula. A phylogenetic analysis of 110 morphological characters from 25 therapsid taxa, including 15 Permo-Triassic cynodonts, supports a sister-taxon relationship between the new taxon and *Abdalodon* within a monophyletic Charassognathidae (which also includes *Charassognathus*) and places the family near the base of Cynodontia. Though incomplete, the specimen includes associated and partially articulated anterior postcranial elements, permitting inferences of cranial-postcranial function during the earliest stages of cynodont evolution. This includes evidence of correlated transformations in the feeding system, neck and shoulder, that are consistent with novel mammal-like locomotor and feeding behaviors in the earliest cynodonts. Lastly, given prior reports of charassognathids in the Karoo Basin of South Africa, the new record suggests that charassognathid cynodonts, like procynosuchids, were geographically widespread by Lopingian times. Continued collecting in the Madumabisa Mudstone Formation will lead to a better understanding of Permian cynodont diversity and biostratigraphy, as well as the biogeographic structure of southern Pangean vertebrate assemblages prior to the Permo-Triassic mass extinction.

### Paleozoic Tetrapods & Lissamphibians

#### ON THE TAXONOMIC STATUS OF FRAGMENTARY FOSSIL ANURANS FOUND FROM THE LOWER CRETACEOUS OHYAMASHIMO FORMATION OF THE SASAYAMA GROUP, HYOGO, JAPAN

Ikeda, Tadahiro, Ota, Hidetoshi  
Institute of Natural and Environmental Sciences,  
University of Hyogo, Sanda, Hyogo, Japan

Abundant anuran fossils including a few articulated skeletons and numerous fragmentary skeletal elements, such as tibiofibulae, femora, humeri, and ilia, have been recovered from the Lower Cretaceous Ohyamashimo Formation of the Sasayama Group at Kamitaki, Tamba City, Hyogo Prefecture, Japan. Of these, two relatively well-preserved articulated specimens were previously described as distinct taxa, *Hyogobatrachus wadai* and *Tambabatrachus kawazu*, on the basis of detailed comparisons with each other, as well as with other Mesozoic and primitive extant anurans. On the other hand, taxonomic identities of fragmentary materials remain to be

determined, partly due to the lack of reliable information regarding detailed characteristics in individual elements for those described taxa.

Recently, we obtained high resolution CT images for the unique types of *H. wadai* and *T. kawazu* using a Nikon-XTH225. Reconstructed 3D models of their skeletal elements from the CT data clarified detailed characteristics in individual elements of the specimens, such as shapes of proximal and distal ends of the tibiofibula and femur, proximal end of the humerus, and of the ilial shaft. The results revealed visible differences between those types that are unlikely attributable to individual or sexual variation, but supposedly reflect between-species differences. Then, we preliminarily investigated corresponding character states in more than ninety isolated skeletal elements (femurs, tibiofibulae, humeruses, radioulnas, ilia, and urostyles). As a result, approximately 50% and 40% of these materials were assigned to *H. wadai* and *T. kawazu*, respectively, whereas the other 10% remained unidentified. Although most of the unidentified materials showed poor preservation state that prevented their accurate taxonomic identification, some ilia therein included features apparently different from those of both types, such as relatively curved shafts. We thus suspect that the late Early Cretaceous anuran fauna in the current Kamitaki region was dominated by *H. wadai* and *T. kawazu*, but with at least one additional, less frequent, and presumably undescribed taxon. For a convincing conclusion on this issue, further efforts are desired to recover articulated skeletal specimens of anurans that are comparable to the types of *H. wadai* and *T. kawazu*, but with curved ilium shafts.

**Funding Sources** JSPS KAKENHI Grant Number JP17K18442.

### Evolution & Biology of Non-Avian Theropods

#### PALEOBIODIVERSITY OF THEROPOD DINOSAURS FROM THE UPPER CRETACEOUS LAÑO SITE, NORTHERN IBERIAN PENINSULA

Isasmendi, Erik<sup>3</sup>, Torices, Angelica<sup>2</sup>, Canudo, José Ignacio<sup>1</sup>, Pereda-Suberbiola, Xabier<sup>3</sup>

<sup>1</sup>Universidad de Zaragoza, Zaragoza, Spain, <sup>2</sup>Universidad de La Rioja, Logroño, Spain, <sup>3</sup>Universidad del País Vasco/Euskal Herriko Unibertsitatea, Leioa, Spain

Laño is one of the most important and best studied Upper Cretaceous vertebrate sites of Europe, and it is considered a reference to understand the paleobiodiversity and evolution of European latest Cretaceous faunas.

Located in the northern part of the Iberian Peninsula, near the city of Vitoria-Gasteiz, the site is situated at the Sub-Cantabrian Synclinorium of the Basque-Cantabrian Basin, where during the upper Campanian an intertropical braided river system was developed. The vertebrate fossils come from two sandy and silty fossiliferous beds. The small

vertebrate sample was recovered from screenwashing, whereas the large vertebrate sample was found via surface prospecting and excavation. The vertebrate association of Laño consist of nearly 40 species of continental vertebrates, including actinopterygians, lissamphibians, chelonians, squamates, crocodylomorphs, dinosaurs, pterosaurs, and mammals. Dinosaurs include theropods, titanosaurian sauropods, ankylosaurs, and ornithopods.

In this work, 227 theropod teeth have been studied, where 107 were previously unpublished. From the Laño theropod teeth sample, eight morphotypes and six taxa have been identified: cf. *Arcovenator*, cf. *Paronychodon*, cf. *Richardoestesia*, Paraves indet., cf. Dromaeosauridae indet., and cf. *Pyroraptor*. Therefore, this study corroborates the presence of cf. *Richardoestesia*, cf. Dromaeosauridae indet., and cf. *Pyroraptor*, and recognizes the presence of cf. *Arcovenator*, cf. *Paronychodon*, and Paraves indet. The Laño theropods are represented by one medium- to large-sized theropod and five small-bodied theropods. In addition to the teeth, postcranial remains found in Laño suggest the presence of a (still undescribed) ornithomimosaur and the large ground bird *Gargantuavis*.

The European Upper Cretaceous vertebrate sites are mainly situated in the Ibero-Armorican Domain and Central Europe. The theropod assemblage of these areas during the latest Cretaceous consists of a mixture of Gondwanan and Laurasian faunas with mainly abelisauroids, dromaeosaurids, birds, cf. *Richardoestesia*, and cf. *Paronychodon*.

In conclusion, the Laño site shows unusual paleobiodiversity for a single site. Possibly it is the richest and most diverse European uppermost Cretaceous site for theropod dinosaurs. The theropod association has similarities with other Campanian–Maastrichtian sites of the Ibero-Armorican Domain.

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## Fishes & Chondrichthyans: Evolution & Distribution

### THE HOLOTYPE OF THE PALEOZOIC CHONDRICHTHYAN *PSEPHODUS MINUTUS* IS A GASTROPOD STEINKERN

Itano, Wayne

Museum of Natural History, University of Colorado, Boulder, Colorado, U.S.A.

In the original 1901 description, the holotype of *Psephodus minutus* was interpreted as a set of three articulated tooth plates of a chondrichthyan fish. The specimen, NHMUK PV P52479, now in the collections of the NHMUK (Natural History Museum, London), was examined by the author in December, 2019. The type locality is in the hamlet of Summit, in the metropolitan county of Greater Manchester, England. The bedrock in the vicinity of Summit lies within the Marsden Formation (Marsdenian, Lower Pennsylvanian). NHMUK PV P52479 bears a superficial resemblance to a set of three articulated tooth plates of *Psephodus magnus*, NHMUK PV P2397, which were figured in an 1883 publication and would likely have been known to the author that described *P. minutus*. Aside from the difference in scale, being much smaller, NHMUK PV P52479 differs from NHMUK PV P2397 in lacking tubular dentine and lacking crenulations along the edges of the 'tooth plates.' The inclinations of the margins between the three 'plates', relative to the longitudinal axis of the set of 'plates,' are consistent with the outline of three whorls of a dextrally (normally) coiled gastropod shell. In all probability, NHMUK PV P52479 is a steinkern (internal mold) of an indeterminate high-spired gastropod. *Psephodus minutus* is thus rendered as a nomen nudum. The affinities of the holotype of *P. minutus* seem to have escaped scrutiny until now because (1) the original description did not include a figure and (2) access to the specimen was difficult for an extended period. In the original description, the holotype was stated to be in the personal collection of the author. About 30 years after the description, the specimen was transferred to the Leeds City Museum, where it was examined by another author who published a crude line drawing in 1933. The specimen was transferred from the Leeds City Museum to the NHMUK in October 1959. *Psephodus* is something of a 'wastebasket' taxon, many Paleozoic chondrichthyan tooth plates having been referred to it that are not clearly close to the type species, *P. magnus*. For example, tooth plates of some nominal species do not have crenulated edges. Although the range of nominal occurrences of *Psephodus* is from the Devonian to the Permian, well-documented occurrences may be restricted to the Carboniferous. Removal of *P. minutus* may further restrict the range to the Mississippian.

## Quantitative Methods

### THE CAPACITY OF QUANTITATIVE SHAPE ANALYSIS WITH GEOMETRIC MORPHOMETRIC METHODS FOR TAXONOMIC DELIMITATION USING MID-TRUNK SNAKE VERTEBRAE.

Jacisin, John J., Lawing, Anna M.

Ecology & Conservation Biology, Texas A&M University, College Station, Texas, U.S.A.

Snake vertebrae are usually identified via qualitative descriptions of morphological traits, and less commonly with quantified linear measurements and ratios. The dearth of spectacular specimens and the difficulty of identifying and describing snake elements in a scientifically replicable way has long hindered progress in fossil snake research. Attempts to identify between (e.g., *Coluber* and *Masticophis*) or within (e.g., natricines) some snake groups are often onerous. Geometric morphometrics (GMM) is a method to quantify shapes in an objective way. Given the difficulties associated with identifying closely related snake taxa, GMM may be a potentially powerful method to assist the identification process.

We used GMM to explore the viability of quantitative shape analysis as a delimitation and identification tool for snake trunk vertebrae. We photographed 505 trunk vertebrae in anterior view for landmarking, spanning 10 families, 16 subfamilies, 90 genera, and 188 extant species, mostly from North America. We Procrustes superimposed landmarks to translate, rotate, and scale landmark schemes associated with each specimen. We ordinated the superimposed landmarks with a Principal Component Analysis and used Linear Discriminant Functions to test the reliability of taxonomic assignments based on the shape captured by our landmark scheme. Principal components 1-5 capture ~80% of total shape variance and suggest that neural spine height (PC1; 39.5%), prezygapophyseal orientation (PC2; 19.9%), outer vs. inner articulation width (PC3; 11.6%), cotylar shape and orientation of rib articulations (PC4; 5.4%), and prezygapophyseal articular facet relative size and orientation (PC5; 3.9%) are the greatest foci of shape variation. Results based on anterior vertebral shape classified vertebrae with 94.0% (family), 85.0% (subfamily), 67.2% (genus), and 56.8% (species) accuracy. We found that taxonomic groups with small sample sizes and closely related groups are more difficult to delimit in shape space. Our shape space provides a new framework that can be referenced to assist in assigning snake trunk vertebrae to a taxonomic affiliation. Although GMM is a powerful tool with the capacity to assist in the delimitation of snake vertebrae, it is not precise enough alone to provide high confidence in delimitation for some groups. Thus, qualitative descriptions and traditional morphometrics should continue to be used alongside qualitative shape analysis to identify snake vertebrae.

## Mesozoic Herpetology

### AN EXCEPTIONALLY WELL PRESERVED PTEROSAUR FROM THE MIDDLE JURASSIC OF SCOTLAND

Jagielska, Natalia<sup>1</sup>, Brusatte, Stephen<sup>1</sup>, O'Sullivan, Michael<sup>3</sup>, Butler, Ian<sup>1</sup>, Challands, Tom<sup>1</sup>, Clark, Neil<sup>4</sup>,

Fraser, Nicholas<sup>2</sup>, Penny, Amelia<sup>1</sup>, Ross, Dugald<sup>5</sup>, Wilkinson, Mark<sup>1</sup>

<sup>1</sup>School of Geosciences, University of Edinburgh, Edinburgh, U.K., <sup>2</sup>Department of Natural Sciences, National Museums Scotland, Edinburgh, U.K., <sup>3</sup>University of Portsmouth, Portsmouth, U.K., <sup>4</sup>The Hunterian, University of Glasgow, Glasgow, U.K., <sup>5</sup>Staffin Museum, Staffin, U.K.

An incomplete fossil record limits understanding of pterosaurian macroevolution during the Middle Jurassic, a period associated with diversification of many major pterosaur clades. The European Middle Jurassic pterosaurian record, until now, has consisted of numerous non-taxon specific specimens and included a single named genus, based on a partially preserved dentary. Here we describe a new three-dimensionally preserved partial skeleton from the Bathonian Lealt Shale Formation of Skye, Scotland, that helps fill the Middle Jurassic pterosaur gap. It is the most complete fossil from the Jurassic sequence of the Scottish Hebrides, which commonly yields ichnofossils but only fragmentary archosaur remains, and the first nearly complete Middle Jurassic pterosaur from outside of China. The new pterosaur is mostly articulated and includes the skull (which retains delicate palatal, hyoid, and neurocranial elements), complete cervical and caudal vertebral series, fully preserved paired forelimbs with partially preserved wing phalanges, a disarticulated dorsal vertebral series and ribcage, and a poorly preserved sacral, pelvis and hindlimb region. It is the largest non-pterodactyloid on record, with an estimated 2 m wide wingspan. The specimen represents a new genus and species diagnosed by several autapomorphies, including slender, curved humeral shaft; large teardrop-shaped lower temporal fenestra; a novel 'jugo-lacrima' fossa, and unique palatal arrangement with trident-shaped anterior vomer. We conducted a phylogenetic analysis by combining several published datasets, which placed the new Scottish pterosaur within the paraphyletic array of non-monofenestratans commonly called the Rhamphorhynchinae, where it shares cranial similarities to the similarly-aged Chinese *Angustinaripterus longicephalus*. We imaged the skull using microCT, which reveals a brain endocast with a large cerebellum and floccular region wrapped by thin, curved semi-circular canals of the inner ear, similar to closely related *Rhamphorhynchus muensteri*. Along with the highly diverse but fragmentary Taynton Limestone Formation assemblage of England, the new specimen challenges the long-considered notion that the European Middle Jurassic was a time of low pterosaur diversity and anatomical disparity.

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## Anatomical & Developmental Explorations of the Mammalian Skull

### AN EYE FOR A TOOTH: WAS *THYLACOSMILUS* REALLY A 'MARSUPIAL SABERTOOTH' PREDATOR?

Janis, Christine<sup>1</sup>, Figueirido, Borja<sup>2</sup>, DeSantis, Larisa<sup>3</sup>, Lautenschlager, Stephan<sup>4</sup>

<sup>1</sup>University of Bristol, Bristol, U.K., <sup>2</sup>University of Malaga, Malaga, Spain, <sup>3</sup>Vanderbilt University, Nashville, Tennessee, U.S.A., <sup>4</sup>University of Birmingham, Birmingham, U.K.

*Thylacosmilus atrox* (Metatheria: Sparassodonta: Borhyaenoidea: Thylacosmilidae), from the Pliocene of Argentina, is popularly known as the 'marsupial sabertooth,' and is frequently used as an example of convergence between marsupials and placentals. However, apart from its impressive upper canines (which, unlike those of placental sabertooths are triangular rather than blade-shaped) it has many anomalous craniodental features (of which, only the ever-growing canines can be attributed to it being a metatherian). Most notably, it lacks an incisor battery: placental sabertooths have stout, projecting incisors, probably necessary for getting meat off the bone. In addition, the jaw symphyses are unfused, the postcanine teeth are small and have blunted wear, the palate is somewhat domed, and the jaw adductor attachment areas are small. Additionally, while there is evidence of strong muscles to resist torsion of the head on the neck there is little for muscles to exert a powerful head strike, which is how sabertooths are presumed to have killed their prey. *Thylacosmilus* was less cursorial than any sabertooth, and lacked retractile claws.

Our quantitative studies confirm distinct differences between *Thylacosmilus* and placental sabertooths. Correspondence analysis of discrete craniodental characters distinguishes sabertooths from conical-toothed (regular) cats, but shows *Thylacosmilus* to be distinctly different from all of these. Finite element analysis shows the skull of *Thylacosmilus* to be less stress-resistant to stabbing than that of the sabertooth cat *Smilodon fatalis*, but more resistant to a pulling-back motion with the canines (both the triangular canines and the postorbital bar aid this action). Dental microwear texture analysis shows that *Thylacosmilus* ate soft food, either fresh flesh or internal organs, but note that the blunt gross dental wear is unlike the shearing wear of meat-eaters.

We conclude that *Thylacosmilus* was morphologically ill-equipped for sabertooth predatory behavior, and should not be held as an example of convergence on this ecomorph. What its mode of life actually was is more difficult to determine, although it appears to have been unlike any

known mammal, extant or extinct. We note that the virtual lack of incisors, together with a domed palate, are suggestive of a large tongue, and propose that *Thylacosmilus* was a specialized scavenger, using its canines to open carcasses, and its tongue to aid in extracting the internal organs.

### Symposium: Dietary Reconstruction

#### STRONTIUM CONTENT AND ISOTOPES REVEAL ECOLOGICAL NICHE COMPLEXITY IN NORTH AFRICAN CRETACEOUS DINOSAURS

Jarochovska, Emilia<sup>2</sup>, Shirley, Bryan O.<sup>2</sup>, Grohgan, Madleen<sup>2</sup>, Leonhard, Isabella<sup>2</sup>, Holwerda, Femke M.<sup>1</sup>

<sup>1</sup>Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada, <sup>2</sup>Geozentrum Nordbayern, Friedrich-Alexander University Erlangen-Nuernberg, Erlangen, Germany

The Cretaceous Kem Kem beds, Morocco, are well-known for their theropod taxa (*Spinosaurus*, *Carcharodontosaurus*), but herbivores are rare, with a paucity in body fossils. Their teeth are more abundant, though not as numerous as for theropods. These teeth are used as paleoenvironmental proxies. Because dental enamel incorporates trace elements via water and food uptake, the elemental composition may reflect trophic level, ecological niche, or paleoenvironment. In particular, the Sr/Ca vs Ba/Ca ratio works as a proxy for trophic level, because calcium is preferentially incorporated over strontium, so strontium levels are lower in carnivores than herbivores. Moreover, strontium isotope ratios (<sup>87</sup>Sr/<sup>86</sup>Sr) may reflect migratory behavior, because Sr levels reflect different habitat substrate conditions.

Sr/Ca vs Ba/Ca content was measured from both sauropod and theropod teeth. Interestingly, only the semi-aquatic *Spinosaurus* showed distinct Sr/Ca levels, whereas *Carcharodontosaurus* shows an overlap with the sauropods. Titanosauriform sauropods show the highest Ba/Ca range with a relatively narrow Sr/Ca range, whereas rebbachisaurid sauropods show the reverse, possibly reflecting a differentiation in foraging behavior, and possibly indicating grazing and browsing, respectively. Moreover, possible titanosaurs show no overlap in ratio with either titanosauriform or rebbachisaurid sauropods, tentatively indicating three different herbivorous foraging strategies, which is supported by two-dimensional dental microwear analysis. Although it is unclear why theropods and sauropods should overlap in values, a likely explanation is the probable use of rare common water sources in arid regions. *Spinosaurus* and *Carcharodontosaurus* clearly separate in Sr/Ca values, reflecting different hunting grounds: riverine and terrestrial, respectively. The <sup>87</sup>Sr/<sup>86</sup>Sr isotope signal shows

the widest range for *Carcharodontosaurus*, followed by the sauropods, indicating these terrestrial carnivores roamed over a large hunting ground. Sauropods might have been seasonal migrants, which explains the lack of sauropod body fossils in the region.

**Funding Sources** Funded by a scholarship supporting faculty-specific gender equality targets at the Friedrich-Alexander University Erlangen-Nürnberg (FAU).

## Mesozoic Herpetology

### A RARE PLASTOMENID TURTLE (TESTUDINES: PLASTOMENIDAE) FROM THE END OF THE CRETACEOUS IN NORTH DAKOTA AND SURVIVORSHIP OF PLASTOMENIDS ACROSS THE CRETACEOUS-PALEOGENE BOUNDARY

Jasinski, Steven E.<sup>1</sup>, Heckert, Andrew B.<sup>2</sup>, Lichtig, Asher J.<sup>3</sup>, Sailer, Ciara<sup>2</sup>, Dodson, Peter<sup>4</sup>

<sup>1</sup>Department of Paleontology and Geology, State Museum of Pennsylvania, Harrisburg, Pennsylvania, U.S.A.,

<sup>2</sup>Department of Geological and Environmental Sciences, Appalachian State University, Boone, North Carolina, U.S.A.,

<sup>3</sup>Department of Paleontology, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, U.S.A.,

<sup>4</sup>Department of Biomedical Sciences, University of Pennsylvania, Philadelphia, Pennsylvania, U.S.A.

Plastomenidae is a clade of fossil turtles that has recently undergone significant revision. North American plastomenids are currently known from the Late Cretaceous (Maastrichtian) to the Eocene, and some genera are known to survive the end-Cretaceous extinction (e.g., *Hutchemys*) while others go extinct at the end of the Cretaceous (e.g., *Gilmoremys*). Only one taxon is known to survive past the Paleocene into the Eocene (*Plastomenus thomasi*). *Hutchemys* is represented by several species, although the majority are known from the Paleocene, with only a single species present in the Cretaceous.

A specimen from the latest Cretaceous Hell Creek Formation of southwestern North Dakota provides important new information for the genus while also representing the eastern-most Cretaceous record of the genus. Represented by an incomplete carapace, it is identified as a plastomenid by a nuchal that is at least four times wider than long and the presence of a preneural. It is assigned to *Hutchemys* by the presence of surface sculpturing that fades towards the center of the carapace and distally split costals. The specimen is distinct from other known *Hutchemys* species by several features, including aspects of the nuchal, costals, and placement of a carapacial constriction. It is thus the second species of *Hutchemys* known from the Cretaceous, and with its most closely related species *H. tetanetron*, may potentially

provide a direct evolutionary anagenetic lineage from this Cretaceous species to *H. tetanetron*. It also represents a third plastomenid evolutionary lineage present in the Hell Creek assemblage of North Dakota, together with *Gilmoremys lancensis* and *Helopanoplia distincta*, while also representing the most derived of these plastomenids. Additionally, a phylogenetic analysis recovers a basal clade comprised of the Asian genera *Perochelys*, *Petrochelys*, *Kuhnemys*, and *Gobiapalone* within Plastomenidae that persisted from the Aptian to the Santonian. A derived clade of North American plastomenids is comprised of *Aspideretoides*, *Atoposemys*, *Gilmoremys*, *Helopanoplia*, and *Hutchemys*. The analysis suggests that this group of turtles originated in Asia during the middle-late Early Cretaceous and subsequently went extinct in Asia by the end of the Santonian, with members of the clade migrating to North America before the Campanian and complete extinction of Plastomenidae by the Lutetian.

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## Permo-Triassic Tetrapods

### THE PHYLOGENETIC PLACEMENT OF AN ENIGMATIC REPTILE FROM THE EARLY TRIASSIC TRANSANTARCTIC MOUNTAINS

Jenkins, Kelsey M.<sup>1</sup>, Lewis, Patrick J.<sup>2</sup>, Choiniere, Jonah N.<sup>3</sup>, Bhullar, Bhart-Anjan S.<sup>1</sup>

<sup>1</sup>Earth and Planetary Sciences, Yale University, New Haven, Connecticut, U.S.A.,

<sup>2</sup>Biological Sciences, Sam Houston State University, Huntsville, Texas, U.S.A.,

<sup>3</sup>Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa

The phylogenetic placement of *Palacrodon* has been contentious since its initial description, with workers naming it as either a rhynchocephalian, lizard, procolophonid, eosuchian, or archosauromorph. The uncertainty surrounding the phylogenetic affinity of *Palacrodon* in large part stems from the fact that nearly all the specimens found are teeth and fragmentary portions of tooth-bearing bone. *Palacrodon* bears characteristic labiolingually elongate, molariform, cuspidate teeth reminiscent of herbivorous reptiles like extinct trilophosaurs and polyglyphanodonts and modern shell-crushing lizards. Because previous workers lacked any other skeletal material, *Palacrodon* has never been placed within a phylogeny. Though its phylogenetic affinity is uncertain, *Palacrodon* is a cosmopolitan genus spanning most of the Triassic, with specimens found in the Early Triassic of Antarctica, Early-Middle Triassic of South Africa, and the Late Triassic of Arizona. The only

specimen of *Palacrodon* possessing more than dentition is from the Early Triassic lower Fremouw Formation of Antarctica (specimen number BP/1/5296). That formation is the sedimentary sequence immediately preceding the Permian-Triassic mass extinction boundary in the Transantarctic Mountains and represents the only known Early Triassic paleopolar deposit with abundant tetrapod material. The Antarctic specimen of *Palacrodon* was described from the impression of a latex peel as a partial small skull belonging to an unknown diapsid reptile initially named *Fremouwsaurus geludens*, which was later synonymized with *Palacrodon*. We CT scanned the Antarctic specimen and found that previously undescribed skeletal elements are preserved in BP/1/5296. These include limb bones, ribs, phalanges, caudal vertebrae, ankle bones, and an ilium. Of the cranial elements, portions of the right maxilla, lacrimal, prefrontal, jugal, postorbital, ectopterygoid, and dentary are preserved. Both parsimony and Bayesian analyses found *Palacrodon* to be a stem saurian with close affinities to drepanosauromorphs. This finding suggests that *Palacrodon* is the earliest known drepanosaur, extending the temporal range of the clade by nearly 20 million years. *Palacrodon* is also the only known drepanosauromorph from the southern hemisphere. Further analysis of these new skeletal elements will now allow a more thorough understanding of the behavior and niche of *Palacrodon* and primitive drepanosaurs generally.

## Evolution & Biology of Non-Avian Theropods

### DECOUPLED RATES OF BODY SIZE EVOLUTION AND DENTAL MORPHOLOGY IN THEROPOD DINOSAURS

Jevnikar, Evan M., Zanno, Lindsay E., Gates, Terry A. Vertebrate Paleontology, NC State University, Raleigh, North Carolina, U.S.A.

Theropod dinosaurs are hypothesized to have filled a wide variety of ecological niches during their >230 million-year evolutionary history, prompting the speculation that ecological innovations drove diversification trends. This idea is supported by studies attempting to identify broad evolutionary patterns in theropod evolution using body size, locomotor mode, or compilations of phylogenetically informative traits, as eco-evolutionary data. Results of these studies suggest that in contrast to the general pattern among dinosaurs, at least some non-avian theropods (maniraptorans) experienced persistently high evolutionary rates, making them an exception to a general trend of niche saturation in post-Triassic dinosaurs. Here we use tooth shape data as a proxy for dietary ecology, to explore whether observed high rates of evolution in the clade can be explained by continued bursts of innovation in dietary ecology specifically.

We coupled tooth measurements and body mass data from 58 non-avian theropods with a variety of phylogenetic comparative methods over 100 time-scaled trees. Evolutionary rates and phenotypic trends were calculated using the R package RRPhylo. To explore sampling bias, we conducted sensitivity studies by subsampling 75% of the species from each time scaled tree. Our analyses uniformly recover five peaks in evolutionary rates during the Mesozoic, which likely correspond to heterogeneous sampling. However, the magnitude of these peaks varies between body-size evolution and tooth morphology. We recover a low rate of tooth evolution prior to the mid-Cretaceous, at which point rates become markedly higher through the Campanian. Conversely, the rate of body mass evolution increases from the Triassic through Early Cretaceous and thereafter declines, trending toward zero up to the K-Pg boundary.

Our results complement previous research on the importance of ecological innovation in theropod evolution and add a new perspective: decoupling of body size evolution from dental innovation. Rate discrepancies between the evolution of body size and tooth shape in Cretaceous theropods may reflect nuanced trends between maniraptorans (small-bodied theropods hypothesized to have had distinctly diverse feeding ecologies) and other Cretaceous theropod clades, that merit parsing out in future studies.

## Paleozoic Tetrapods & Lissamphibians

### PATTERNS OF CAUDOSACRAL VERTEBRAE WITH REFERENCE TO THE EVOLUTION OF FERTILIZATION MODES IN SALAMANDERS (AMPHIBIA: CAUDATA)

Jia, Jia<sup>1</sup>, Gardner, James<sup>2</sup>, Anderson, Jason<sup>3</sup>, Jiang, Jian-Ping<sup>4</sup>, Gao, Ke-Qin<sup>1</sup>

<sup>1</sup>School of Earth and Space Sciences, Peking University, Beijing, China, <sup>2</sup>Royal Tyrrell Museum, Drumheller, Alberta, Canada, <sup>3</sup>Department of Comparative Biology and Experimental Medicine, University of Calgary, Calgary, Alberta, Canada, <sup>4</sup>Chengdu Institute of Biology, Chengdu, Sichuan, China

Salamanders have two modes of fertilization: Cryptobranchoidea are external fertilizers, typically with females depositing eggs on substrate, which are fertilized by sperm released from males; Salamandroidea are internal fertilizers, with the male depositing spermatophores (sperm packet) that are inserted into, or picked up by, the cloaca of the female and stored for later internal fertilization. Internal fertilization is widely thought to have originated only once, because it is part of a suite of related features (e.g., complex tail display and differentiation of cloacal glands) unique to salamandroids. In living

salamanders, the cloaca opens directly below the last caudosacral, which ventrally bears the first complete haemal arch in the tail. Thus, cloacal position in fossil salamanders can be determined relative to the last caudosacral. Little attention has been paid to caudosacrals in the two major salamander clades. By direct examination under microscope and micro-CT scanning of 221 specimens representing 46 extant and extinct species in Cryptobranchoidea and Salamandroidea, we found that caudosacral counts vary from two to seven in extinct and one to four in extant cryptobranchoids, and three to four in extinct and two to three in living salamandroids. These data show caudosacral counts (1) are more variable in Cryptobranchoidea than in Salamandroidea; and (2) become less variable through time in both clades. Thus, regardless of geological age, the position of the cloaca is more stable in internal vs. in external fertilizers. However, caudosacral patterns alone cannot be used to differentiate external from internal fertilizers. Previous investigations, supplemented by our diceCT data on some hynobiid taxa (e.g., *Batrachuperus*), confirm that the haemal arch on the last caudosacral or the first few caudals is the origin for a set of muscles (e.g., *M. ischio-caudalis*, *M. caudocruralis*, *M. caudofemoralis*) that flex the base of the tail and/or compress the cloaca. We hypothesize that stabilization of the cloacal position in internal fertilizers was driven by the demands for complex tail movement during courtship and fertilization. In contrast, the more variable cloacal position in external fertilizers may be linked to a looser constraint on muscle flexibility because tail displays are less common in cryptobranchoids than in salamandroids.

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## Mesozoic Herpetology

### THE OLDEST OCCURRENCE OF A YAGUARASURINE MOSASAUROID FROM THE LATE CENOMANIAN–EARLY TURONIAN OF COAHUILA, NORTHERN MEXICO

Jiménez-Huidobro, Paulina<sup>1</sup>, López-Conde, Oliver A.<sup>2</sup>, Chavarría-Arellano, María L.<sup>2</sup>, Porras-Múzquiz, Héctor<sup>3</sup>

<sup>1</sup>Geosciences, Universität Bonn, Bonn, Germany, <sup>2</sup>Universidad Nacional Autónoma de México, Ciudad de México, Mexico, <sup>3</sup>Museo Paleontológico de Múzquiz, Santa Rosa de Múzquiz, Mexico

Mosasauroidea is a clade that includes obligatorily and potentially aquatic forms. The group is divided in two families: the facultatively aquatic Aigialosauridae and the diverse family Mosasauridae. The latter family is divided in two facultatively aquatic subfamilies, Tethysaurinae and Yaguarasaurinae, and four obligatorily aquatic

subfamilies, Halisaurinae, Plioplatecarpinae, Tylosaurinae, and Mosasaurinae, with the exception of the semi-aquatic mosasaurine *Dallasaurus turneri*. The older records correspond to aigialosaur mosasauroids from the Cenomanian of the Mediterranean Tethys, while most of the occurrences of Mosasauridae appear from the Turonian to the Maastrichtian. Here we present the oldest record of the subfamily Yaguarasaurinae from the late Cenomanian–early Turonian beds of Coahuila, Northern Mexico. The specimen corresponds to a complete right surangular in lateral view that presents the following characters: (1), ‘V’-shaped suture line between surangular and articular; (2), dorsal margin of the surangular slightly concave; (3), small or absent contribution of the surangular to the glenoid. These three characters support the assignation of the specimen to the subfamily Yaguarasaurinae. However, the specimen does not present characters enough for assignation beyond subfamily level, making impossible to differentiate it into a genus and species. Records of Cenomanian mosasauroid faunas are scarce globally, except by the aigialosaurs from the Mediterranean Tethys. The yaguarasaurine specimen reported here extends the temporal range of the subfamily Yaguarasaurinae back to the late Cenomanian and early Turonian, while it was previously known from the mid Turonian. Moreover, the specimen represents the oldest mosasauroid from North America. These early records of mosasauroids are crucial to understand the transition from plesio pelvic–plesio pedal to hydropelvic–hydropedal derived mosasaurs, since the group represents one of the more dramatic cases of radiation to aquatic environments within Squamata during the Late Cretaceous.

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## Fishes & Chondrichthyans: Evolution & Distribution

### A LARGE MIDDLE DEVONIAN EUBRACHYTHORACID ‘PLACODERM’ (ARTHRODIRA) FROM NORTHERN GONDWANA

Jobbins, Melina E.<sup>1</sup>, Rücklin, Martin<sup>2</sup>, Argyriou, Thodoris<sup>3</sup>, Klug, Christian<sup>1</sup>

<sup>1</sup>University of Zurich, Zurich, Switzerland, <sup>2</sup>Naturalis Biodiversity Center, Leiden, Netherlands, <sup>3</sup>CR2P, MNHN-CNRS-Sorbonne Université, Paris, France

The evolutionary history of jawed vertebrates and especially the origin of jaws and teeth are debated. The fossil record is crucial in understanding the early evolutionary steps in these innovations. Especially different evolutionary stages in ‘placoderms’ are informative as they are probably representing a grade on the stem towards extant gnathostomes. Arthrodirans, derived ‘placoderms’, play a crucial role with teeth being

described in *Compagopiscis* from the Late Devonian of Australia. The Devonian of Morocco has become famous for its rich occurrences of ‘placoderms’, particularly arthrodires. While Late Devonian strata can be rich in ‘placoderms’, the Middle Devonian yields fewer placoderm remains. Here, we describe a large jaw element of an eubrachythoracid arthrodire from the Middle Devonian of Morocco with teeth. This gnathal element was found isolated, which suggests that it was loosely attached to the skull and postmortem transported. This posterior superognathal displays various morphological adaptations including a strong dentition. This new specimen is among the very limited record of brachythoracid gnathal elements from the Middle Devonian worldwide. The jawbone displays features considered apomorphies known from Late Devonian eubrachythoracid arthrodires. It has one posterior and one lateral row of conical teeth oriented postero-lingually, with a gentle dorsal curvature. CT-images revealed the preservation of internal structures in these teeth, including a pulp cavity and dentinous tissue. This marks the first record of confirmed teeth in arthrodires in the Middle Devonian. The teeth’s posterior orientation and the traces of a putative occlusal contact on the lingual side of the bone implies that these teeth were hardly functional. A possible scenario, similar to *Compagopiscis* and *Plourdosteus*, would be that functional teeth were present during an earlier developmental stage of the animal and have been worn entirely. Unlike most other known eubrachythoracid posterior superognathals, this specimen does not present a mesial tooth. Additionally, its ventral margin is smooth and teeth deprived. Its morphological features suggest a close relationship with plourdosteids, in particular *Plourdosteus*. The size of this arthrodire implies that the animal was rather large. The abundance of phacopid trilobites like *Drotops* in the same layer makes these arthropods likely candidates as a food source for this big fish.

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## Marine Reptile Diversity & Biology

### THE ECOLOGICAL DIVERSIFICATION AND EVOLUTION OF TELEOSAUROIDEA (CROCODYLOMORPHA, THALATTOSUCHIA), WITH INSIGHTS INTO THEIR MANDIBULAR BIOMECHANICS

Johnson, Michela M.<sup>1</sup>, Foffa, Davide<sup>2</sup>, Young, Mark T.<sup>1</sup>, Brusatte, Stephen<sup>1</sup>

<sup>1</sup>School of Geosciences, University of Edinburgh, Edinburgh, U.K, Canada, <sup>2</sup>National Museum of Scotland, Edinburgh, U.K.

Throughout the Jurassic, a wealth of marine reptiles dominated ocean waters, including plesiosaurs, ichthyosaurs and thalattosuchian crocodylomorphs. Jurassic ecosystems were characterized by high niche partitioning and spatial variation in dietary ecology. However, while the ecological diversity of many marine reptile lineages is well known, the overall ecological diversification of Teleosauroidea (one of the two major groups within thalattosuchians) has never been explored. Teleosauroids were previously considered to have a morphologically conservative body plan; however, they were in fact morphofunctionally diverse and evolved a bizarre body-plan (e.g., proportionally large heads). Here we investigate the ecology and feeding specializations of teleosauroids, using morphological and functional cranio-dental characteristics. We assembled the most comprehensive dataset of multiple teleosauroid taxa (twenty species) and ran a principal component analysis (PCA) and canonical variate analysis (CVA) to categorize them into various feeding guilds based on seventeen dental characteristics (41 specimens), as well as sixteen functionally significant mandibular characters (nineteen specimens). The results were examined in conjunction with our comprehensive thalattosuchian phylogeny (153 taxa and 502 characters) to evaluate macroevolutionary patterns and significant ecological shifts. Multiple taxa fall into the pierce and crushing guilds (as well as intermediate forms), and there is increased bite efficiency shifting from longirostry to brevirostry in the subclade Machimosaurini. Teleosauroid taxa with slender teeth and an elongate mandible have a lower mechanical advantage than taxa with robust teeth and/or a shortened mandible. One teleosauroid subgroup displays the following ecological shift: from 1) slender, pointed tooth apices and an elongate gracile mandible; to 2) more robust, pointed teeth with a slightly deeper mandible; and finally, 3) rounded teeth and a deep-set, shortened mandible with enlarged musculature. A second teleosauroid subgroup is more phenotypically plastic. As a clade, non-machimosaurin teleosauroids display a slight array of overlap, particularly in the dental analyses; this suggests that multiple taxa may have exploited relatively similar food sources and may have lived in similar habitats. However, this contradicts the cranial anatomy, which shows an extraordinary number of diverse characteristics within teleosauroid species.

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## Colbert Poster Prize/Evolution & Biology of Non-Avian Theropods

### SIZE-EQUALIZED FINITE ELEMENT MODELS OF ADULT *TYRANNOSAURUS REX* CRANIA SUGGEST LOWER STRAIN LEVELS THAN

## JUVENILES IN ASSOCIATION WITH THE ONTOGENETIC SHIFT TO EXTREME OSTEOPHAGY

Johnson-Ransom, Evan D.<sup>1</sup>, Gignac, Paul<sup>1</sup>, Erickson, Gregory M.<sup>2</sup>, Snively, Eric<sup>1</sup>

<sup>1</sup>Center for Health Sciences, Oklahoma State University, Tulsa, Oklahoma, U.S.A., <sup>2</sup>Department of Biological Science and Mechanical and Physical Properties Laboratory, National High Magnetic Field Laboratory, Florida State University, Tallahassee, Florida, U.S.A.

Considerable focus has been directed at understanding the feeding anatomy of adult *Tyrannosaurus rex*, but rarely have the biomechanics of juveniles been appraised. For example, rapid growth in *T. rex* is thought to enable ontogenetic dietary transitions in which small gracile-snouted juveniles with narrow teeth developed into large adults with deep snouts and reinforced dentitions that facilitated extreme osteophagy (= bone pulverization). Morphology-driven exclusion and opportunity, as is observed in modern crocodylians, supports the stratification of juvenile and adult *T. rex* niches through the partitioning of prey resources based on differences in feeding capacities. How the demands of prey acquisition and processing are reflected in the skull morphology and jaw mechanics of juvenile *T. rex* relative to their adult counterparts is not quantitatively understood. Gaining this insight would help address the functional morphology contributing to developmental niche partitioning in this apex predator. Here we use 3D finite element analysis to quantify how the crania of a juvenile *T. rex* (BMRP 2002.4) responded to estimated bite forces, in comparison to a large adult individual (MOR 555). Analogous to the American alligator (*Alligator mississippiensis*), modeling results indicate that *T. rex* underwent substantial transformations in morphology manifesting in substantial differences in cranial stresses and strains. Specifically, the juvenile specimen showed high strain during biting because of its relatively gracile cranium in contrast to the adult, which was capable of handling disproportionately high forces for its size. Although our results indicate that juvenile *T. rex* showed capacities to bite into bone, only adults were able to deeply puncture, catastrophically fracture, and wedge apart bone, requisite capacities for extreme osteophagy. These results are concordant with trace evidence from tyrannosaur-inflicted bite marks. Thus, our findings support theories that at least one substantial dietary shift(s) occurred during *T. rex* ontogeny (i.e., from a bone slicer to one that could comminute bone).

### Biomechanics & Functional Morphology

## EVOLVING ON THEIR OWN LANDSCAPE: UNRAVELLING FUNCTIONAL TRADE-OFFS IN SYNAPSID AXIAL EVOLUTION

Jones, Katrina E.<sup>1</sup>, Dickson, Blake V.<sup>1</sup>, Angielczyk, Ken<sup>2</sup>, Pierce, Stephanie E.<sup>1</sup>

<sup>1</sup>Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts, U.S.A., <sup>2</sup>Field Museum of Natural History, Chicago, Illinois, U.S.A.

The origin of mammals from their forerunners, the non-mammalian synapsids (NMS), is an iconic locomotor transition in vertebrate evolution. Extant reptiles share superficial morphological and functional similarities to NMS in their limb skeleton, and have therefore been used as a model for the ancestral synapsid locomotor condition. Based on this similarity, and data from trackways, it is presumed that NMS vertebral function likely also resembled that of reptiles. Specifically, that early synapsids used exaggerated lateral trunk bending to increase stride length during locomotion instead of the sagittal bending that characterizes fast mammalian gaits. However, synapsid vertebral evolution is much less well understood than limb evolution, so this hypothesis remains untested.

Here, we quantified morphology and function in synapsid trunk vertebrae to test the hypothesis that extinct NMS resembled reptiles in their axial locomotor mode. We used three dimensional geometric morphometric data on the shapes of five dorsal vertebrae in a broad array of extant tetrapods (n = 73) and NMS (n = 13) to construct functionally-informed adaptive landscapes. Based on form-function relationships from inter-vertebral joint experiments on extant amniotes (cat, n = 10; and tegu lizard, n = 8), we derived functional traits for simulated vertebrae in a grid spanning the morphospace. From this functional variation, we generated four performance surfaces - stiffness, torsion, anterior mobility, and posterior mobility, which we then combined into adaptive landscapes that optimized functional traits for 'reptile', 'mammal, and 'NMS' groups.

We recovered unique adaptive landscapes for reptiles, mammals, and NMS, indicating that each group is characterized by a different combination of functional trade-offs, and refuting the hypothesis of functional similarity between extant reptiles and early synapsids. Instead, reptiles are highly optimized for lateral bending in the posterior trunk, whereas NMS exhibit intermediate levels of lateral bending and strong optimization for stiffness. By contrast, all four traits contributed to the mammal adaptive landscape, reflecting the remarkable functional diversity and regionalization of their axial skeleton. Our work highlights the challenges of applying extant models to the fossil record, and suggests that divergent selection pressures were important in synapsid and sauropsid vertebral evolution.

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### **Colbert Poster Prize/Mesozoic & Early Cenozoic Mammalian Evolution**

#### **A LARGE, PREDATORY BAT (CHIROPTERA, PHILISIDAE) FROM THE MIDDLE EOCENE OF LIBYA**

Jones, Matthew F.<sup>1</sup>, Beard, K. Christopher<sup>1</sup>, Salem, Mustafa<sup>2</sup>, Jaeger, Jean-Jacques<sup>3</sup>

<sup>1</sup>Biodiversity Institute & Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, Kansas, U.S.A., <sup>2</sup>Geology Department, Tripoli University, Tripoli, Libya, <sup>3</sup>Laboratoire Paléontologie, Evolution, Paléoécosystèmes, Paléoprimatologie, UMR 7262 CNRS, Université de Poitiers, Poitiers, France

At least four genera of unusually large Eocene bats are currently known from Europe and North Africa. Large bats belonging to the extinct family Philisidae are known from the middle Eocene of Algeria, Egypt, and Tunisia. We report an upper first molar belonging to a new species of the philisid *Witwatia* from the middle Eocene Dur At-Talah escarpment of central Libya. This new species differs from other *Witwatia* species in lacking a postprotocrista and possessing a larger talon expansion. Dur At-Talah is estimated to be approximately 38–39 million years old based on biostratigraphy and magnetostratigraphy, making the Libyan species of *Witwatia* slightly older than *W. eremicus* and *W. schlosseri* from Egypt and younger than *W. sigei* from Algeria and Tunisia. Using the matrix published by Ravel and colleagues in 2014, we performed a phylogenetic analysis of the Libyan *Witwatia* and other members of Philisidae. Our analysis recovered the Libyan taxon as the most basal species within *Witwatia*, with the other three species forming a polytomy in the strict consensus tree. As in the previous analysis, we recover *Witwatia* to be nested within a paraphyletic *Philisis*. The Libyan *Witwatia* is among the largest known Eocene bats and provides further evidence that bats evolved to exploit large animalivorous niches relatively early in the Paleogene.

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### **Bird Biology & Evolution**

**FROM BONES TO FEATHERS:  
RECONSTRUCTING THE EXTINCT  
PLEISTOCENE COUCAL ‘CENTROPUS  
MAXIMUS’**

Jordan, Lucy, Drabsch, Bernadette, Howells, Andrew  
School of Creative Industries, University of Newcastle,  
Newcastle, New South Wales, Australia

*Centropus maximus* is a large extinct coucal from early–mid Pleistocene Australia. It is known from two partial post-cranial skeletons recovered from the *Thylacoleo* cave system in the Nullarbor Plain and formally described in 2016. Three extinct coucal species are known in Australia, but only one of these, *Centropus colossus*, has ever been illustrated. This is typical for Cenozoic Era birds, a consequence of few novel characteristics, a lack of interest in this period, and a scientific focus on description alone. This study reconstructs *C. maximus* from the individual skeletal elements up to a full colour representation. This follows the standard methodology for paleoart, where the external appearance of reptilian and mammalian subject matter often reflects the underlying anatomy. Evaluating the merits of this approach for avian subjects, where the anatomy is hidden under a feathered exterior, is a key objective of this project.

The second objective investigated coloration and markings, based on the two most likely factors of influence: phylogenetic relationships and habitat requirements. The visual appearance of 30 extant species of *Centropus* were compared along these two axes to establish patterns and possible order of primacy. The final color scheme for *C. maximus* ultimately drew more on the three-tone plumage of the African coucals that live in a similar habitat over the only extant Australian species, *C. phasianinus*. This is an introductory study with further research aiming to establish a framework for illustrating individual Cenozoic birds, differentiating similar species and applicable across different orders.

### **Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

#### **PALEOCLIMATIC RECONSTRUCTION OF THE LATE PLEISTOCENE FROM SERBIA BASED ON RODENT ASSEMBLAGES**

Jovanovic, Mihailo P.<sup>1</sup>, Bogičević, Katarina<sup>2</sup>, Agusti, Jordi<sup>1</sup>, Blain, Hugues-Alexandre<sup>1</sup>

<sup>1</sup>Universitat Rovira i Virgili, Tarragona, Spain, Tarragona, Spain, <sup>2</sup>Paleontology, University of Belgrade, Faculty of Mining and Geology, Belgrade, Serbia

Investigation of small mammal fossils, especially rodents, is very useful for Pleistocene terrestrial environment reconstructions. Serbia, within the Balkan Peninsula, is an interesting place to study the transition between the late Pleistocene and Holocene because it contributes to knowledge about the formation of the current biodiversity

in the central Balkan. Furthermore, research is increasingly focusing on the possible climatic and environmental causes that led to Neanderthal extinction and the transition between the last Neanderthals and Early Anatomically Modern Humans (i.e., *Homo sapiens*); Serbia is an ideal place to investigate this transition.

The bioclimatic model poses the hypothesis that a significant correlation between climate and mammal communities exists, and that by using the series of mathematical functions that have been previously established, we are able to calculate climatic factors such as temperature values (average, maximal, and minimal), average annual precipitation, duration of cold months, and number of dry months.

In accordance with this research, it was necessary to establish a simplified chronology of deposits in Baranica, Hadzi Prodanova and Pešturina caves, for the last 60,000 years (Mousterian–Aurignacian–Gravettian succession). The analysis showed that there were no dramatic climatic oscillations during MIS 2 and MIS 3. Results suggest that the Balkans had a milder and more humid climate during MIS 2 compared to Central Europe, with average temperature ranging from 2.2 to 4.5 degrees Celsius lower than present. This suggests that climate change was not a crucial factor in extinction of the Neanderthals, instead the Balkans possibly acted as a refugium for the last Neanderthals, similar to the Iberian and Apennine Peninsulas.

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#### **Late Cenozoic Mammalian Macroecology & Macroevolution**

#### **THE FIRST SPECIMEN OF *DEINOTHERIUM INDICUM* (MAMMALIA, PROBOSCIDEA, DEINOTHERIIDAE) FROM THE LATE MIOCENE OF KUTCH, INDIA**

Jukar, Advait M.<sup>1</sup>, Singh, Ningthoujam P.<sup>2</sup>, Patnaik, Rajeev<sup>2</sup>, Sharma, K M.<sup>3</sup>, Singh, Nongmaithem A.<sup>3</sup>, Singh, Yumlembam P.<sup>3</sup>

<sup>1</sup>Paleobiology, Smithsonian Institution, Washington, District of Columbia, U.S.A., <sup>2</sup>Department of Geology, Panjab University, Chandigarh, India, <sup>3</sup>Department of Geology, Central University of Punjab, City Campus, Bathinda, Punjab, India

In the Indian Subcontinent, deinotheres are largely known from dental remains found in Miocene deposits. Both large and small species have been described from here. Hitherto this study, only small deinotheres species had been identified from Kutch in western India. In the fossiliferous Tapar beds in Kutch, dental remains were referred to the

small species *Deinotherium sindiense*, but the specimens are too fragmentary to be systematically diagnostic. We describe a large p4 of a deinotheres from Tapar and show that it is morphologically most similar to *Deinotherium indicum*, a large species of deinotheres, thus confirming the identity of deinotheres at Tapar. *Deinotherium indicum* from Tapar is the first occurrence of the species in the region, and is larger than other deinotheres specimens identified from Kutch. This new specimen constrains the age of the Tapar beds to the Tortonian and increases the biogeographic range of this species, formerly only known from two localities on the subcontinent. This specimen also highlights the morphological diversity of South Asian deinotheres p4s and allowing us to reassess dental apomorphies used to delimit Indian deinotheres species. This specimen also points at the ecological replacement of small deinotheres species by *D. indicum* in the late Neogene.

#### **Permo-Triassic Tetrapods**

#### **NEW LATE PERMIAN DICYNODONTOIDS (SYNAPSIDA: ANOMODONTIA) FROM THE UPPER MADUMABISA MUDSTONE FORMATION (LUANGWA BASIN, ZAMBIA)**

Kammerer, Christian F.<sup>1</sup>, Angielczyk, Ken<sup>2</sup>, Peacock, Brandon R.<sup>3</sup>, Sidor, Christian A.<sup>4</sup>, Smith, Roger M.<sup>5</sup>, Tolan, Stephen<sup>6</sup>, Viglietti, Pia A.<sup>2</sup>

<sup>1</sup>North Carolina Museum of Natural Sciences, Raleigh, North Carolina, U.S.A., <sup>2</sup>Field Museum of Natural History, Chicago, Illinois, U.S.A., <sup>3</sup>Idaho State University, Pocatello, Idaho, U.S.A., <sup>4</sup>Burke Museum, University of Washington, Seattle, Washington, U.S.A., <sup>5</sup>Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, Gauteng, South Africa, <sup>6</sup>Chipembele Wildlife Education Centre, Mfuwe, Zambia

Fieldwork in the Zambian Madumabisa Mudstone Formation (MMF) has revealed a rich upper Permian tetrapod fauna, including an extensive record of dicynodont therapsids. A single dicynodontoid species (*Dicynodon huenei*) was previously recognized in this assemblage, but new discoveries of numerous, well-preserved skulls indicate the presence of multiple morphotypes (Morphotypes A–E). To determine the relationships of these morphotypes, we included them in an expanded phylogenetic analysis of Dicynodontia.

Morphotypes A–C are basal (i.e., non-lystrosaurid, non-kannemeyeriiform) dicynodontoids. Morphotype A shares many features with South African *Daptocephalus leoniceps* and Tanzanian *D. huenei* (e.g., sharply sloping snout, broad interorbital region), and is recovered as a member of *Daptocephalus*. It differs from other species of *Daptocephalus* in its short temporal fenestra. Morphotype B is distinguished by a low, flat snout and thickened

zygoma, similar to the Tanzanian *Dicynodon angielczyki*. Morphotype C may also represent *Dicynodon*, but differs from known specimens in having a premaxilla-frontal contact. Morphotypes D and E are recovered as lystrosaurids: both show the clade's characteristic deflected snout and septomaxilla-lacrimal contact. Morphotype D shares a 'U'-shaped naso-frontal ridge and expanded prefrontal bosses with *Euptychognathus bathyrhynchus*, a basal lystrosaurid known from Tanzania and South Africa. It differs in its extremely broad skull; we consider it a new species of *Euptychognathus*. Morphotype E represents a new taxon characterized by autapomorphic fossae on the opisthotics, and is more closely related to *Lystrosaurus* than *Euptychognathus*.

The Zambian dicynodontoids support several patterns in the geographic and temporal distribution of African dicynodonts. Basal dicynodontoid genera are cosmopolitan (e.g., *Dicynodon*, *Daptocephalus* in all major African basins), but with locally endemic species. Lystrosaurids are more prevalent in Zambia than in South Africa or Tanzania, indicating the strong influence of local conditions on interbasinal abundance. Zambian dicynodontoids are restricted to the uppermost portions of the MMF, replacing cryptodont dicynodonts (e.g., *Aulacephalodon*) as the dominant herbivores. Dicynodontoids and cryptodonts were previously thought to broadly co-occur in the Karoo Basin, but stratigraphic refinements indicate clade-level turnover there as well, suggesting regional change in large herbivores in the latest Permian.

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#### **Quantitative Methods**

### **IDENTIFYING JURASSIC THEROPOD GENERA USING GIS MAPS OF TOOTH SERRATIONS**

Kane, Miriam

physical and environmental sciences, colorado mesa university, Grand Junction, Colorado, U.S.A.

Theropods are carnivorous dinosaurs that have serrations on their teeth; a serration is a row of sharp tooth-like projections found on the edges of theropod dinosaur teeth. There are two main theories surrounding the origin and purpose of serrations on theropod teeth. In the first theory, serrations are thought to help maintain the strength and integrity of the tooth along the curve of the tooth. The second, and more widely accepted theory, is that serrations evolved to aid in the killing of prey, which helped theropods become the apex predators of their time. Many attempts have been made to morphometrically analyze theropod teeth as an aid in their identification, including measurements of serration density and the microanatomy of the denticles. However, none of these techniques have

been able to successfully identify theropod genera from isolated teeth and teeth fragments. The purpose of this study was to use GIS mapping of tooth serrations of previously identified theropod teeth acquired from museum collections, to establish criteria for identifying theropod genera based on tooth serration geometries.

This study used photographs of 92 theropod teeth and ARCMAP GIS software to characterize the geometry of serrations on *Ceratosaurus*, *Marshosaurus*, and *Allosaurus* teeth. By using the software to digitize the serration outline on each tooth, this study was able to identify patterns among each individual genus using qualitative observations. *Ceratosaurus* denticles typically have mushroom- and tapered-shaped denticles with relatively little space between individual denticles and a deep interdenticular dentition. *Allosaurus* serrations display a blocky shape, and there is a relatively large space in between individual denticles and a relatively shallow interdenticular dentition. *Marshosaurus* serrations show jagged puzzle-like shaped denticles with a moderate amount of space between individual denticles and a deep interdenticular dentition. Using these specific denticle patterns, unidentified theropod teeth were successfully classified as either allosaur or ceratosaur genera using qualitative observations that led to defining characteristics of the serrations of each genus. This study shows justification for future efforts to identify theropod genera from a detailed study of individual tooth fragments.

### **Evolution & Biology of Non-Avian Theropods**

#### **THEROPOD AND BIRD TRACKS IN THE NUBIA SANDSTONE, EASTERN DESERT, EGYPT**

Kassab, Walid<sup>1</sup>, Abdel Gawad, Mohamed<sup>1</sup>, Abu El-Kheir, Gebely<sup>2</sup>

<sup>1</sup>Geology, Cairo University, Giza, Egypt, <sup>2</sup>Geology, New Valley University, Kharga, Egypt

Vertebrate-media contacts are treasured for interpreting ancient environmental, ecological, and climatic settings within the geological record. Sixteen tetrapod footprints were found in the Upper Cretaceous strata, the 'Nubian Sandstone', in the South Eastern Desert of Egypt. The Nubian sandstone is subdivided into three informal members. The lower member attaining 60 m in thickness. It is marked by reddish brown, trough cross bedding ranging from coarse to medium grained sandstone interbedded by thin beds of varicolored mudstone which reflect a deposition in braided fluvial channels and a flood plain system. The middle member reaches 40 m in thickness. It is characterized by reddish white- to yellow planar cross bedding containing medium-grained sandstone with ferruginous siltstone intercalations

interpreted as a meandering fluvial channel and flood plain deposits. The upper member attains 100 m in thickness. Displays an upward coarsening repeated cycles of rippled siltstone to fine sandstone and a tabular cross bedded, yellowish white, fine to medium grained sandstone which contains those vertebrate footprints, invertebrate trace fossils and frequent plant leaves and roots which reflect deposition in coastal to deltaic regime. The preservation of these footprints is poor. Sixteen tetrapod tracks are recorded at the base of the upper member of the Nubia sandstone, on an inclined surface of fine-grained rippled sandstone. Twelve of them are interlocked with each other as they are a trackway of more than three tetrapods of different groups, the other four are found distributed on the same surface far from each other. All the twelve interlocked tracks are from numerous theropod dinosaurs, while three of the separate tracks might be for huge birds. Twelve tracks are defined as monodactyl, one track is didactyl and three tracks are tridactyl. The tracks are described between semiplantigrade and digitigrade. This discovery marks the second record of tetrapod footprints in Egypt and the first record of tetrapod footprints in the Eastern Desert, Egypt.

#### **Dinosaur Systematics, Diversity & Ecology**

#### **REEVALUATING THE AFFINITIES OF A HATCHLING-SIZE HUMERUS ORIGINALLY ASSIGNED TO THE RARE LAMBEOSAURINE *PARASAUROLOPHUS TUBICEN* (DINOSAURIA: HADROSAURIDAE)**

Kastroll, Lindsay M.<sup>1</sup>, Jasinski, Steven<sup>2</sup>

<sup>1</sup>California University of Pennsylvania, California, Pennsylvania, U.S.A., <sup>2</sup>The State Museum of Pennsylvania, Harrisburg, Pennsylvania, U.S.A.

The specimen SMP VP-2202 (State Museum of Pennsylvania) from the Upper Cretaceous Kirtland Formation of New Mexico was initially described as the left humerus of a hatchling cf. *Parasaurolophus tubicen* in 2011. However, the 41 mm long humerus has a shorter and more robust shaft compared to known, ontogenetically older lambeosaurine humeral elements. This calls into question the validity of the original diagnosis for this specimen and prompts a review of the affinities for the specimen.

A morphometric analysis was performed using seven dimensions of significant features of the humerus, with emphasis on the deltopectoral crest. Measurements from SMP VP-2202 were compared to those collected from a sample of hadrosaurids (saurolophines and lambeosaurines), ceratopsians, and ankylosaurians of different ontogenetic stages in order to determine which group the specimen most closely aligned with. Specimens

housed at the State Museum of Pennsylvania were directly measured in millimeters using digital calipers. Other specimens were measured from images in published material using ImageJ: only images that clearly showed the entire humerus and included a scale bar were used. This allowed specimens with confident referrals to be included in the sample. Dimensions, such as total humeral length compared to width of the deltopectoral crest, were computed and compared for each family and subfamily. Resulting values were plotted and corresponding trendlines were also compared between different subsets of the sample.

The results of this study agree with the original findings that SMP VP-2202 is a hadrosaurid with an oddly robust shaft and distal end. Among hadrosaurids, while both saurolophines and lambeosaurines have comparable dimensions that cause their humeral morphology to be similar, there are some features that potentially separate out members of the subfamilies, including more distinct deltopectoral crests in the latter. However, the apparently abnormal proportions in the specimen may be due to distortion during fossilization or ontogenetic change, making any attempts to identify the specimen beyond the family level uncertain. Regardless, these findings suggest that this method can be used to differentiate fossil material of these groups and can be used to aid in taxonomic decisions of hard-to-determine fossils. Additionally, they may have implications for ontogenetic changes in hadrosaurids, including potential ontogenetic change in locomotion style.

#### **Symposium: Paleoneurology**

#### **EFFECTS OF STRUCTURAL CONSTRAINTS OF SKULL ON BRAIN MORPHOLOGY IN BIRDS: A CASE STUDY WITH THE TEMPORAL FOSSA**

Kawabe, Soichiro

Fukui Prefectural University, Eiheijicho, Fukui, Japan

The relationship between morphology and ecology is critical when analyzing the brain of birds. However, multiple studies have demonstrated that ecological differences do not necessarily reflect the variations in brain morphology in birds. This may be because birds are highly specialized to flight, an adaptation which could physically constrain skull morphology. Yet, how skull structural constraints affect brain morphology in birds is poorly understood quantitatively. The present study investigates the temporal fossa, which is the most conspicuous part of the avian neural cranium and varies greatly in development among species. Through analyzing the relationship between temporal fossa surface area and brain morphology using geometric morphometric methods, I found that the size of temporal fossa explains approximately 6% of the variation in brain morphology in birds. On the other hand, about 8% of the variation in brain morphology in birds is

apparently explained by the allometry effect. Therefore, the developmental change of the temporal fossa is unignorable in constraining the brain morphology in birds. Because the surface area of the temporal fossa may correlate with the size of the jaw adductor muscles, the development of these muscles may indirectly affect their brain morphology. As demonstrated, structural constraints of the skull in birds must be clarified to elucidate the relationship between their brain morphology and ecology.

## Marine Mammals

### RECOGNITION OF THE DEEP-DIVING CETACEAN FAUNA FROM THE MIDDLE MIOCENE OF THE WESTERN NORTH PACIFIC

Kawatani, Ayako<sup>1</sup>, Kohno, Naoki<sup>2</sup>

<sup>1</sup>University of Tsukuba, Tsukuba, Japan, <sup>2</sup>National Museum of Nature and Science, Tsukuba, Japan

The toothed whales of the family Ziphiidae and the Physeteridae are the most mysterious groups in the Cetacea, despite having a cosmopolitan distribution, because of their deep-diving behavior. Among them, the ziphiids are thought to have originated and diversified in the Southern Ocean, and the ancestors of these deep-diving whales would have lived initially in epipelagic and/or neritic oceans. But, the processes involved in their adaptation and diversification to deep-sea environments are still uncertain. The late middle Miocene Tsurushi Formation (ca. 12 Ma), distributed on the Sado Island in the Sea of Japan along the western margin of the North Pacific, has produced a lot of well-preserved fossil ziphiids, including at least six crania with ear bones and many rostra: at this time, the Sea of Japan was a deep sea over 1000 meters in depth.

Interestingly, these fossil ziphiids from the Tsurushi Formation are more similar to those of extant species in the genera *Berardius*, *Ziphius*, and *Mesoplodon*, respectively, than other species in the genera of fossil ziphiids in overall morphology. This suggests that these are the first reliable middle Miocene records of taxa that belong to these genera. Among these taxa, the oldest known record is for *Berardius*, which goes back geochronologically only as far as the Pleistocene. So, these new fossils from the Tsurushi Formation fill the gap of evolutionary history for at least the genus *Berardius*. More interestingly, the new fossils have distinct characters that indicate adaptation to deep-diving behavior. Another aspect of the toothed whales from the Tsurushi Formation is the existence of the *Physeter*-like sperm whale skull with the tympanoperiotic that looks like a morphologically miniature replica of the extant sperm whale. Thus, the western North Pacific, including the Sea of Japan, may have been one of the areas for the evolution and radiation of deep-diving whales, including ziphiids and physeterids, that led to the extant taxa. Since the

*Berardius*-like ziphiid and *Physeter*-like sperm whale had lived in the western North Pacific, including the Sea of Japan, by 12 Ma, these discoveries may become the key to elucidating the timing of the expansion of the ziphiids from the southern oceans to the northern oceans, including the North Pacific, and also the processes involved in the development of the deep-diving adaptations of the ziphiids and a physeterid during the middle Miocene in the North Pacific.

## Permo-Triassic Tetrapods

### INSIGHT INTO THE OSTEOLOGY OF AN EARLY AETOSAURIAN ARCHOSAUR FROM MICRO-CT SCANNING

Keeble, Emily<sup>1</sup>, Parker, William<sup>2</sup>, Nesbitt, Sterling J.<sup>3</sup>, Stocker, Michelle R.<sup>3</sup>, Hutchinson, John R.<sup>1</sup>

<sup>1</sup>Structure and Motion Laboratory, Royal Veterinary College, Fleet, U.K., <sup>2</sup>Division of Science and Resource Management, Petrified Forest National Park, Petrified Forest, Arizona, U.S.A., <sup>3</sup>Virginia Tech, Blacksburg, Virginia, U.S.A.

Studying the anatomy of aetosaurs (Triassic armored pseudosuchian archosaurs) can present difficult problems. Despite the existence of many articulated specimens, their distinctive carapace often obscures internal anatomy, and the physical removal of this structure can put fossils at risk of damage. CT scanning provides a non-destructive way of studying these animals, and its usefulness in paleontology has been repeatedly demonstrated in recent years. Indeed, CT scanning has already been used to uncover new anatomical details of *Coahomasuchus* hidden within an articulated specimen, to study the neuroanatomy of *Neoaetosauroides*, and to visualize the 3D shape of the caudal anatomy of *Stagonolepis*. However, articulated specimens can be difficult to successfully scan due to the volume of matrix around the carapace that may need to be penetrated and the size of many of the specimens. This can lead to poor quality scans that are little use in comparing the finer points of anatomy. Here we present new 3D image data of material from a partly-disarticulated specimen of cf. *Coahomasuchus kahleorum* (TMM 31100-437) that is ideal for micro-CT scanning, allowing for high resolution scans and 3D modelling of joint articulations. The specimen is in many regions disarticulated and less crushed than the holotype, so the 3D shapes of elements are clearer. In particular, new features of the femur and neural arch anatomy can be seen for the first time unobscured, as well as improved detail of the scapulocoracoid, ulna, fibula, astragalus, calcaneum, and cervical and trunk vertebrae; and excellent preservation of the skull. Sections of thoracic osteoderms with articulated ribs provide more information about the likely in vivo arrangement of these structures allowing a more accurate reconstruction of the combined

skeleton and carapace in relation to each other. Overall we have obtained an improved understanding of the skeletal morphology of this pivotal early actosaur and present the first 3D (partial) skeletal reconstruction as a step toward analyses of its locomotor biomechanics.

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### **Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

#### **GRASSHOPPER MICE OF UNUSUAL SIZE: CLIMATE- AND EXTINCTION-DRIVEN ECOLOGICAL SHIFTS IN *ONYCHOMYS* OVER 22,000 YEARS AT HALL'S CAVE**

Keller, Jonathan S.<sup>1</sup>, Lyons, S. K.<sup>2</sup>, Newsome, Seth<sup>1</sup>, Smith, Felisa A.<sup>1</sup>

<sup>1</sup>Biology, University of New Mexico, Albuquerque, New Mexico, U.S.A., <sup>2</sup>Biology, University of Nebraska, Lincoln, NE, Nebraska, U.S.A.

Despite considerable climate change and the anthropogenic extinction of megafauna restructuring ecosystems, many North American micromammals persisted in situ from the late Pleistocene to the present. To understand their long-term ecological responses to climate change and biodiversity loss at the terminal Pleistocene, we studied the 0–22 ka fossil record of the grasshopper mouse *Onychomys* at Hall's Cave in Texas. We examined its ecology by estimating body size from tooth row length and using carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotope analyses to trace dietary niche through this turbulent time. While past work characterized slight small herbivore ecological responses, we report strong, climate- and extinction-driven body size and isotopic niche shifts in invertivorous *Onychomys* mice. Consistent with Bergmann's rule, *Onychomys* body size generally responded inversely to temperature. Immediately post-extinction, however, *Onychomys* body size nearly doubled despite warming temperatures, suggesting megafaunal extinction effects outweighed *Onychomys*' typical climate response. Isotopic data demonstrate fossil *Onychomys* exclusively occupied the secondary consumer/predator niche in contrast to more omnivorous moderns. Post-extinction *Onychomys* shifted toward C4-isospace, suggesting they and their prey consumed more resources released by the megafaunal grazers' extinction. *Onychomys* body size and  $\delta^{15}\text{N}$  (trophic level) also correlated, with the largest individuals being the most carnivorous. Post-extinction, hypercarnivorous Hall's Cave *Onychomys* represent the largest modern or fossil specimens recorded. These results emphasize megafaunal extinction's ecologically transformative effects in the light of modern anthropogenic extinctions.

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### **Mesozoic Herpetology**

#### **A PROBABLE *TORETOCNEMUS* (REPTILIA: ICHTHYOSAURIA) PARTIAL SKULL FROM THE LATE TRIASSIC ANTIMONIO FORMATION OF SONORA, MEXICO**

Kelley, Neil P.<sup>1</sup>, Johnson, Lila<sup>2</sup>, Gibson, Brandt<sup>1</sup>

<sup>1</sup>Earth & Environmental Sciences, Vanderbilt University, Nashville, Tennessee, U.S.A., <sup>2</sup>Biological Sciences, Vanderbilt University, Nashville, Tennessee, U.S.A.

The Triassic ichthyosaur genus *Toretocnemus* is a relatively poorly known taxon occupying an important place in ichthyosaur evolutionary history. Although limited material make its precise placement uncertain, in many phylogenetic analyses *Toretocnemus* occupies a position close the emergence of the 'advanced ichthyosaur' clade Euichthyosauria, which includes all Jurassic and later ichthyosaurs. This clade is characterized by modifications in the skull and dentition as well as limbs and tail that reflect changes in feeding ecology and swimming efficiency, which may have facilitated the persistence of this clade across the Triassic–Jurassic boundary. First described over a century ago, *Toretocnemus* is known primarily from fragmentary specimens from multiple western North American localities spanning Alaska to Mexico. Each of these occurrences derive from accreted terranes that were situated off the continental margin along eastern Panthalassa during the Triassic. While investigating shastasaurid remains from the Carnian-aged Antimonio Formation of Sonora, Mexico, we identified a partial rostrum that does not resemble the morphology of the other specimens with which it is catalogued. Micro-CT scanning of this specimen confirmed the distinctive morphology that sets it apart from the other remains. The upper jaw exhibits well-preserved premaxillae, maxillae, and vomers, as well as taphonomically displaced nasals. The lower jaw exhibits well-preserved surangulars and relatively well-preserved dentaries, as well as highly splintered splenials. Forty-eight closely packed isodont conical teeth are present in the specimen, including 13 replacement teeth. A lack of distinct alveoli or visible connection to the jawbones and tight tooth packing within a dental groove suggests aulacodont tooth implantation. Additional small conical to columnar structures within the dentigerous margin are difficult to identify, but may represent remnants of periodontal ligaments or malformed nonfunctional teeth. Although incomplete, the specimen resembles the holotype skull of *Toretocnemus californicus* from equivalent aged rocks in northern California. This specimen supports previous reports of isolated vertebrae from the Antimonio Formation referred to *Toretocnemus*.

This additional record underscores the broad regional distribution of small to medium-sized euichthyosaurus, living alongside larger bodied shastasaurid ichthyosaurs during a transitional period of ichthyosaur evolution.

## Mesozoic Herpetology

### NEW INFORMATION ON *KERESDRAKON VILSONI* (PTEROSAURIA, AZHDARCHOIDEA, TAPEJAROMORPHA) FROM A CRETACEOUS BONEBED IN BRAZIL

Kellner, Alexander W.<sup>3</sup>, Weinschütz, Luiz C.<sup>1</sup>, Sayão, Juliana<sup>4</sup>, Bantim, Renan A.<sup>2</sup>, Holgado, Borja<sup>3</sup>

<sup>1</sup>CENPALEO – Centro Paleontológico da Universidade do Contestado, Universidade do Contestado, Mafra, Santa Catarina, Brazil, <sup>2</sup>Laboratório de Paleontologia, Universidade regional do Cariri (URCA), Crato, Ceará, Brazil, <sup>3</sup>Laboratory of Systematics and taphonomy of Fossil Vertebrates, Departamento de Geologia e Paleontologia, Museu Nacional, Rio de Janeiro, Rio de Janeiro, Brazil, <sup>4</sup>Laboratório de Paleobiologia e Microestruturas, Centro Acadêmico de Vitória, Universidade Federal de Pernambuco, Vitória de Santo Antão, Pernambuco, Brazil

The sole pterosaur bonebed from Brazil, designated cemitério dos pterossauros (pterosaur graveyard), is located in the southern part of Brazil, more specifically at the region of Cruzeiro do Oeste (Paraná State). The site recently yielded the basal tapejaromorph *Keresdrakon vilsoni*. The deposit is formed by sandstones of the Goio-Erê Formation (Turonian–Campanian) of the Bauru Group, and the site represents an oasis in a Cretaceous desert region. *Keresdrakon* shows a low skull with an elongated, toothless, and pointed rostrum, that is longer than in tapejarids and chaoyangopterids but shorter than in the azhdarchid *Quetzalcoatlus*. No premaxillary sagittal crest is present. The lower jaw bears a comparatively thick ventral dentary crest and further shows a blunt longitudinal ridge on the dorsal surface of the posterior half of the dentary. The appendicular skeleton is highly pneumatized: the humerus has a pneumatic foramen on the ventral surface, at the base of the deltopectoral crest; ulna, radius, carpus, and distal syncarpal are also pierced with pneumatic foramina; and the first wing phalanx shows two pneumatic foramina on the ventral surface close to the proximal articulation, a feature not previously reported in any other pterosaur. Cervical vertebrae are comparatively short, differing from the elongated condition of azhdarchids, bearing a tall and blade-like neural spine. They are lightly built, with the anterior and posterior articular surfaces showing three developed pneumatic foramina above and lateral to the neural canal. The lateral surface of the centrum is pierced by a large depression that ends in a pneumatic foramen that is smaller in tapejarids

and absent in azhdarchids and chaoyangopterids. Some cervical vertebrae show additional foramina on the ventral surface bordering the hypapophysis, rarely reported in flying reptiles. The sternal articulation of the coracoid is dorsoventrally flattened and very asymmetrical, with a much longer posterior component. It lacks a deep sternal flange, which is present in azhdarchids, but shows a well-developed tubercle on the ventroposterior margin that has been reported in tapejarids. The sternum is quadrangular, with a shallow and elongated cristospine. On the dorsal surface, close to the origin of the cristospine, the sternum is pierced by a large foramen that appears to be pneumatic. The discovery of *Keresdrakon* expands the occurrence of non-tapejarid azhdarchoid pterosaurs in South America.

**Funding Sources** FAPERJ (#E-26/202.893/2015), CNPQ (#420687/2016-5, #313461/2018-0, #140789/2016-2, #311715/2017-6) and FUNCAP (#BMD-0124-00302.01.01/19).

## Holocene & Pleistocene Mammalian Macroecology & Faunal Studies

### WHEN GRAZERS DIDN'T JUST EAT GRASS: DIETARY PREFERENCES OF BISON AND HORSE IN NORTHERN ALASKA

Kelly, Abigail A.<sup>1</sup>, Miller, Joshua H.<sup>1</sup>, DeSantis, Larisa<sup>2</sup>, Wooller, Matthew J.<sup>3</sup>, Seaton, C. Tom<sup>4</sup>, Druckenmiller, Patrick S.<sup>5</sup>

<sup>1</sup>University of Cincinnati, Cincinnati, Ohio, U.S.A., <sup>2</sup>Vanderbilt University, Nashville, Tennessee, U.S.A., <sup>3</sup>University of Alaska, Fairbanks, Alaska, U.S.A., <sup>4</sup>Alaska Department of Fish and Game, Fairbanks, Alaska, U.S.A., <sup>5</sup>University of Alaska Museum, Fairbanks, Alaska, U.S.A.

In the late Pleistocene, the North Slope of Alaska hosted a diverse and abundant assemblage of large herbivores, including steppe bison, horse, woolly mammoth, musk oxen, caribou, and saiga antelope. Following the end-Pleistocene megafaunal extinctions, Holocene diversity was reduced to caribou, musk oxen, and moose. Diverse large mammal communities of the late Pleistocene may have been supported by more nutritious forage and/or dietary niche partitioning. Within this context, herbivores in the far north provide an important case study. While bison, horses, and mammoths were once common in the far north, Holocene arctic grazers are rare or entirely missing. To evaluate competing mechanistic hypotheses for supporting high Pleistocene herbivore biomass, we characterized the diets of the two most common late Pleistocene herbivores on the North Slope of Alaska: bison and horse (*Bison priscus*; n = 20; *Equus* sp.; n = 36, both housed in the University of Alaska Museum of the North) via dental mesowear analysis and dental microwear texture analysis (DMTA). Because grass-based diets are uniquely

abrasive, grazers typically have blunter mesowear profiles and more highly scratched enamel microwear surfaces. To interpret Pleistocene diets from DMTA data, we use a multivariate Discriminant Function model trained on published DMTA data for 23 ungulate species with known diets, as well as two extant bison populations in Alaska. Living bison include an introduced plains bison herd (*B. b. bison*) located near Delta Junction (n = 8), and a reintroduced population of Wood Bison (*B. b. athabascae*; n = 15). We find that late Pleistocene bison and horses have DMTA signatures more similar to modern 'intermediate' mixed feeders, rather than grazers. Both extant Alaska bison populations showed DMTA signatures more similar to grazers. Pleistocene bison mesowear profiles also had marginally, though not significantly, higher relief than extant bison ( $p = 0.19$ ), consistent with less grass-dominated diets in the late Pleistocene. Finally, there were no differences in DMTA values between late Pleistocene bison and horses, suggesting that the two most common large herbivores of northern Alaska were eating foods with similar textural properties, suggesting limited niche partitioning. Our results indicate that abundant and diverse Pleistocene mammal communities of northern Alaska were more likely maintained by higher quality forage availability as opposed to dietary niche partitioning.

**Funding Sources** Funding for this project was provided by student grants from the University of Cincinnati Sigma Xi, Geological Society of America, and American Society of Mammalogists.

## Education & Outreach

### AUGMENTING THE REALITY OF WYOMING'S RICH FOSSIL RESOURCES: DOES AUGMENTED REALITY ENHANCE MUSEUM VISITOR EXPERIENCE AND OUTREACH?

Kerr, Tyler<sup>2</sup>, Vietti, Laura A.<sup>1</sup>

<sup>1</sup>Geological Museum, University of Wyoming, Laramie, Wyoming, U.S.A., <sup>2</sup>Engineering Education and Research Building Student Innovation Center, University of Wyoming, Laramie, Wyoming, U.S.A.

The use of augmented reality (AR), technology that superimposes computer-generated images or models on a user's real-world view, as an educational tool is an increasingly growing field of interest. In an effort to make the University of Wyoming (UW) Geological Museum's fossil collections more accessible and to provide a new and engaging learning tool about Wyoming's fossil record, we developed a free downloadable AR app called *WyoFossil* that superimposes 3D models of our fossil specimens on cards. As the user changes either the orientation of the camera or the card, they see 360-degree views of a selected 3D model. We designed and printed five educational AR

cards and made them available to museum visitors to take home, and also made them globally accessible for download on the museum website. Users were asked to take a quick survey to better understand how they envision using the cards in the future, what they liked, and if it enhanced their visit or inspired a visit to the UW Geological Museum. Here, we present the general design of our AR cards, results from the initial user survey distributed with the cards, and results from a survey sent out one year later.

Of the 300+ initial survey responses, we found that overall the responses were very favorable towards the *WyoFossil* app and cards. Over 90% of the responses indicated that the AR cards enhanced their museum visit, and 60% indicated the app/cards inspired them to visit the museum. We are pleased to report that 70% of the users felt more connected with Wyoming paleontology, that 75% users felt the AR cards were like taking a fossil home with them. Users indicated they will primarily use the cards as mementos and show-and-tell, but many indicated they intended to use them for school, research, and art.

From the 54 responses submitted one year later, 62% of users still had the AR cards and 72% have interacted with the cards since initially collecting them. Users indicated that these cards were still be used for show and tell, art or mementos, as well as school and research related projects. One year later, 91% of users stated that the AR cards enhanced their museum visit and 74% indicated that the cards inspired them to visit the museum. 94% of responses agreed that the AR cards made them feel more connected to Wyoming paleontology. Based on both survey results, we believe the app did in fact improve visitor experience and strengthened the scholarship and outreach use of our displays and collections.

**Funding Sources** Paleontological Society Outreach and Education Grant.

## Late Cenozoic Mammalian Macroecology & Macroevolution

### PROBOSCIDEANS (MAMMALIA) FROM THE MIO-PLIOCENE OF NORTHERN PAKISTAN

Khan, Muhammad A., Abbas, Sayyed G.  
Zoology, University of the Punjab, Lahore, Punjab, Pakistan

This research work provides a comprehensive new collection of the Siwalik Mio-Pliocene proboscideans from Northern Pakistan. The collected specimens are more than 60 in number and include tusks, deciduous and permanent premolars, and molars. Some of the specimens are reported for the first time from the Siwaliks and are new to the Siwalik paleontology of the subcontinent. The complete hemimandibles of *Deinotherium pentapotamiae*,

the lower tusk of *Protanancus chinjiensis*, the juvenile and adult lower tusks of *Konobelodon* sp., and the deciduous premolars of *Gomphotherium browni* have been reported for the first time from the Siwalik Group. The specimens belong to ten species, eight genera, and five families viz Deinotheriidae, Amebelodontidae, Gomphotheriidae, and Stegodontiidae. The stratigraphic range of *Protanancuschinjiensis* has been extended from the Chinji Formation to the Dhok Pathan Formation of the Siwalik Group. *Konobelodon* sp. has been reported for the first time from the Chinji Formation of the Lower Siwalik Subgroup. The status of *Stegolophodon latidens* has been validated. The new proboscidean material comes from the Siwalik localities, namely Chabbar Syedan, Padhri, Hasnot, and Dhok Gojriand Lehri of district Jhelum; Chinji, Lawa, Bhilomar, Kundal Nala northern, Sethi-Nagri, Dhok Pathan, and Naraghi of district Chakwal; Dhok Mila of district Attock and Kanhatti of district Khushab, northern Pakistan. The localities date from 18–3.5 Ma. The Siwalik Mio–Pliocene proboscideans exhibit diversity in their habitats, ranging from damp and swampy places to open grasslands, and have mixed diets, ranging from grazers to browsers or even diggers.

**Funding Sources** University of the Punjab, Lahore, Pakistan.

### Mammalian Skeletal Morphology

#### FUNCTIONAL ANATOMY OF THE MUSTELID HINDLIMB SKELETON AND THE POTENTIAL INFLUENCE OF CLIMBING AND SWIMMING LOCOMOTOR HABITS ON MORPHOLOGICAL DIVERSIFICATION

Kilbourne, Brandon  
Evolutionary Morphology, Museum für Naturkunde Berlin, Berlin, Berlin, Germany

Though form-function relationships of the mammalian locomotor system have been investigated for over a century, relatively recent models of trait evolution provide a means to rigorously test whether biomechanical demands actually govern the diversification of limb morphology. Using mustelid mammals, an ecologically diverse carnivoran lineage that includes specialists for climbing (e.g., martens), digging (e.g., badgers), and swimming (e.g., otters), I investigated whether hindlimb skeletal morphology functionally distinguishes these distinct locomotor habits among mustelids in addition to more generalist species (e.g., weasels). Sampled skeletal traits included 13 linear femoral, tibial, fibular, and calcaneal traits consisting of lengths, diameters, and muscle in-lever lengths. These traits were used in a principal components analysis, so as to visualize the distribution of mustelid locomotor habits in phenotypic space. After this initial

analysis, individual linear traits were fitted with competing models of trait diversification, including models in which traits diversify under a primary influence of locomotor habit. Mustelids specialized for climbing occupy a region of phenotypic space characterized by a gracile limb skeleton, whereas those specialized for digging and swimming occupy regions characterized by a more robust limb skeleton, though swimming and digging specialists have hindlimbs of differing proportions. A model of adaptive diversification according to locomotor habit was the best fitting model for the majority of the individual traits. More specifically, selective regimes for climbing and swimming were the best fitting model for several sampled traits. These results are contrary to the findings of previous studies on limb bone cross-sectional areas, which were found to most likely diversify according to Brownian motion. These results suggest that the origin of climbing and swimming locomotor habits were major, if not adaptive, events during limb evolution in mustelids, if not mammals more broadly. Additionally, traits with differing biomechanical roles should be analyzed for a complete picture of locomotor system evolution.

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### Taphonomy & Stratigraphy

#### STRATIGRAPHIC DISTRIBUTION OF VERTEBRATES FROM THE LATE CRETACEOUS WESTERN INTERIOR SEAWAY IN MANITOBA, CANADA

Kilmury, Aaron A., Brink, Kirstin  
Geological Sciences, University of Manitoba, Winnipeg, Manitoba, Canada

New stratigraphic information on Cretaceous deposits of the Western Interior Seaway in Manitoba, Canada, including an updated lithostratigraphic framework, radiometric ages, and foraminiferal zones made available over the last decade have improved historically challenging regional correlations with coeval deposits. However, data is currently lacking in terms of vertebrate biostratigraphy. An understanding of the distribution of vertebrates in Manitoba is essential in order to test hypotheses of faunal provinciality, habitat preferences, and temporal and spatial changes in faunal assemblages.

In order to examine faunal occurrences, a dataset was compiled of specimens previously collected from Manitoba that are housed in museums across Canada and reported in the literature. Specimens were grouped by genus and arranged by lithostratigraphic member. Those with taxonomic uncertainty were identified to the highest possible level and those with stratigraphic uncertainty

appointed to a probable member based on preservation and rock matrix properties.

Results show that the Cenomanian faunas represented in the Belle Fourche Member of the Ashville Formation and the Keld member of the Favel Formation indicate a relatively high diversity chondrichthyan and osteichthyan assemblage and low diversity avian and reptilian assemblage, whereas the early Campanian fauna represented in the Pierre Shale Formation indicates a relatively high diversity osteichthyan and reptilian assemblage and low diversity avian and chondrichthyan assemblage. In terms of stratigraphic distribution, the chondrichthyans *Squalicorax* and *Cretalamna* and osteichthyans *Enchodus* and *Protosphyraena* have the longest taxonomic durations, ranging from the Cenomanian to Campanian. Reptilian and avian taxa have much shorter durations, being mostly limited to the Campanian with the exception of polycotyloid plesiosaurs, which range from the Cenomanian to Campanian.

This study has revealed members other than the Pembina and Belle Fourche are underrepresented by museum fossil collections. Future work will include collecting new specimens to offset historical collection biases, biostratigraphic correlations between the Cretaceous marine units of the Canadian prairie provinces and territories and U.S.A., as well as paleoecological analyses and quantifying temporal faunal changes in order to address questions concerning evolutionary patterns, ecosystem function, and extirpation events within the Western Interior Seaway.

## **Taphonomy & Stratigraphy**

### **A TAPHONOMIC STUDY OF THE COLONIAL DINOSAUR NESTING GROUND FOUND IN THE UPPER CRETACEOUS NATURAL LEVEE DEPOSITS (WIDO VOLCANICS), WI ISLAND, SOUTH KOREA**

Kim, Seongyeong<sup>1</sup>, Lee, Yuong-Nam<sup>1</sup>, Hwang, In Gul<sup>3</sup>, Gihm, Yong Sik<sup>2</sup>, Kim, Noe-Heon<sup>1</sup>, Choi, Seung<sup>1</sup>

<sup>1</sup>Seoul National University, Seoul, Korea (the Republic of), <sup>2</sup>Kyungpook National University, Daegu, Korea (the Republic of), <sup>3</sup>Korea Institute of Geoscience and Mineral Resources, Daejeon, Korea (the Republic of)

Floodplain mudstones are the most common lithology of dinosaur egg deposits. Despite this dominance, the paleoenvironment of the mudstones is poorly known due to their homogeneous features. Here we describe the dinosaur egg-bearing deposits in the lower Daeri Andesite of the Wido Volcanics (Coniacian–Santonian), Wi Island, South Korea, from paleontological and taphonomical points of view. The egg site produced three different ootaxa. Two are dinosaur eggs, which include new faveoololithid eggs (*Propagoolithus widoensis*) and possible new

dromaeosaurid eggs (*Reticuloolithus acicularis*). The third type (*Aenigmaoolithus vesicularis*) is neither a dinosaur nor a bird egg. *Propagoolithus widoensis* is mainly preserved as in situ clutches associated with isolated eggs and eggshell fragments. The strata containing most of the clutches consist of compound paleosols formed in a natural levee environment, based on sandstones with an erosive bottom that exhibit a gradual upward increase in the degree of paleosol development. The sedimentological and pedological analyses at this site indicate that the nesting ground was extended along a certain area within the natural levee. The elevated position may have an advantage for the dinosaurs to watch over predators during the incubation period. With this setting, the nesters could also avoid being flooded and/or wet substrate tightly bound by plant roots in low land. *Propagoolithus widoensis* differs from the other ootaxa in its numerous closely-spaced pore canals, reflecting that the eggs had been covered with sediments after oviposition, which significantly increased preservation potential. Those clutches occur in nine different stratigraphic horizons with close spacing (<1 m) in the lateral direction, suggesting paleontological site fidelity on the study area and gregarious nesting behavior of these nesters. The absence of body fossils of hatchlings or embryos from many hatched clutches may suggest that they left the colony immediately after hatching. This study suggests that massive terrestrial mudstones should be carefully observed based on sedimentological and pedological analyses for fruitful interpretation of the paleo-nesting environment.

**Funding Sources** National Research Foundation of Korea (grant number 2019R1A2B5B02070240) to Yuong-Nam Lee.

## **Symposium: Dietary Reconstruction**

### **BREATH AND TOOTH ENAMEL OF SMALL MAMMALS FROM FEEDING-CONTROLLED EXPERIMENTS FOR STABLE CARBON ISOTOPES**

Kimura, Yuri<sup>1</sup>, Yamada, Keita<sup>2</sup>, Casanovas-Vilar, Isaac<sup>6</sup>, Cerling, Thure E.<sup>3</sup>, Seki, Azumi<sup>4</sup>, Suzuki, Nozomi<sup>5</sup>

<sup>1</sup>National Museum of Nature and Science, Tsukuba, Japan, <sup>2</sup>Tokyo Institute of Technology, Yokohama, Japan, <sup>3</sup>University of Utah, Salt Lake City, Utah, U.S.A., <sup>4</sup>Hamri Co. LTD., Ibaraki, Japan, <sup>5</sup>Daito Cacao Co. LTD, Tokyo, Japan, <sup>6</sup>Institut Català de Paleontologia Miquel Crusafont, Cerdanyola del Valès, Spain

Stable isotopes have been used as powerful tracers to infer food sources, predator-prey interactions, dietary niche, and seasonal migrations for mammals in modern and paleocommunities. Independent of morphology and community analyses, isotopic inferences add intricate

paleoecological information even when fossil assemblages are hindered by taphonomic biases. Original isotopic signals of digested products and fluid intake are assimilated in various tissues of animals through biological processes, which results in isotopic enrichment. Thus, comprehensive understanding of isotope-based ecological inferences requires empirical values or priori estimates of the isotopic enrichment/fractionation factors. For large herbivorous mammals, an empirically measured average of -14 per mil has been used as the isotopic enrichment factor between diet and tooth enamel. Nevertheless, for small mammals, such empirical measures are limited and result in great uncertainty in recently proposed regression lines between body mass and controlled diet.

We herein report feeding-controlled experiments on three species of rodents: *Rattus rattus* (rats), *Mesocricetus auratus* (golden hamster), and *Meriones unguiculatus* (Mongolian gerbil) for isotopic enrichment factors between consumed products and enamel of each tooth position in small mammals and explore interspecific variation and intra-dentition variations in the species. The rodents were raised with commercial rat chow and water of known isotope values. The mothers and their offspring were examined for breath and tooth enamel samples. The cubs were separated from their mother at Day 20 and fed with the same rat chow after Day 20 (= weaning). The whole experiments were properly conducted and approved in accordance with the Guidelines for the Care and Use of Laboratory Animals (AAALAC International). During lactation, cubs show more negative  $\delta C$  values than mothers by a few per mil due to the milk effect. The effect is greater in gerbils than in rats and hamsters, suggesting that gerbil milk is more lipid-rich than others. In tooth enamel, carbon isotope values highly correlate with the timing of tooth eruption. The data also suggest that breast-feeding mothers and weaned cubs digest more protein selectively from the bulk diet, which leads to positive isotopic shift toward cancelling out the milk effect. These effects must be considered when rodent molars are to be used for isotopic paleoecology.

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### **Dinosaur Systematics, Diversity & Ecology**

#### **AVIAN-LIKE ENDOCRANIAL TRAITS OF A JUVENILE *PSITTACOSAURUS LUJIATUNENSIS* AND THE PEDOMORPHIC NATURE OF THE BIRD BRAIN**

King, Logan<sup>1</sup>, Zhao, Qi<sup>2</sup>, Rayfield, Emily<sup>1</sup>, Benton, Michael J.<sup>1</sup>

<sup>1</sup>School of Earth Sciences, University of Bristol, Bristol, U.K., <sup>2</sup>Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China

Bird and derived maniraptoran brains are frequently described as having an ‘S’-shaped form, reduced olfactory lobes on a short olfactory tract, expanded cerebral hemispheres, and laterally oriented optic lobes. This brain shape deviates from basal archosaur brains, which are less expansive dorsally and are oriented all along the same plane. The general bird brain layout has been preserved on endocasts dating back to the Eocene in avialans and as far back as the Cretaceous in maniraptorans. These characters of the bird brain are derived and are thought to pertain to a wider clade, possibly Paraves, Maniraptora, Theropods, or even Dinosauria. Through study of CT scans, we find these same characters, with the exception of the reduced olfactory bulbs, are present on the endocast of IVPP V15451, a sub-yearling *Psittacosaurus lujiatunensis*, a basal ceratopsian dinosaur. IVPP V15451 has flexure angles that are less than 90°, olfactory bulbs that are 23.3% of the width of its cerebrum, a cerebrum with a width that is 70% of the total endocranial length, and optic lobes that are laterally situated (but not anterolaterally). When compared to endocasts of *Struthio camelus* and other extinct and extant birds, IVPP V15451 has an S-shaped brain with expanded cerebrum. This is not, however, the case in older *Psittacosaurus* where the brain first elongates, somewhat as in an alligator, and then shortens again to a partially bird-like structure. This suggests that the brains of crown Aves are in fact a mosaic of pedomorphic non-avian dinosaur and adult Aves features. Cerebral expansion (as evidenced in *Psittacosaurus* and *Dysalotosaurus*) occurs in juvenile non-dinosaurs and potentially shifts the optic lobes from a dorsal position to a lateral orientation early in ontogeny. Retention of a drastically expanded cerebrum in adults supports the recent suggestion that bird skulls and brains are pedomorphic modifications from crocodiles. Throughout Avialae and Aves the cerebrum continuously expands to the point that the cerebral width is up to 92–95% of the total endocranial length. This in turn forces the optic lobes further anterolaterally, thus making the exaggerated cerebrum and anteriorly facing, elongated optic lobes true markers of ‘bird-like’ endocranial anatomy.

### **Fishes & Chondrichthyans: Evolution & Distribution**

#### **PRELIMINARY ANALYSIS OF THREE LATE CRETACEOUS MARINE VERTEBRATE ASSEMBLAGES FROM THE PEEDEE FORMATION AT ALLISONS FERRY, CAINS LANDING, AND BURCHES FERRY, FLORENCE COUNTY, SOUTH CAROLINA**

Kirkpatrick, Donald R.<sup>1</sup>, Cicimurri, David J.<sup>2</sup>

<sup>1</sup>Horry County Museum, Conway, South Carolina, U.S.A.,

<sup>2</sup>Natural History, South Carolina State Museum, Columbia, South Carolina, U.S.A.

Late Cretaceous (Maastrichtian) marine vertebrate faunas were recovered from Peedee Formation strata exposed along the west bank of the Great Pee Dee River at Burches Ferry, Cains Landing, and Allison's Ferry, Florence County, South Carolina. Peedee Formation strata are oldest at Burches Ferry and youngest at Allison's Ferry, with Cains Landing stratigraphically in between. Most fossils were recovered by disaggregating bulk matrix collected at each site, but some specimens were surface collected.

Our fossil vertebrate sample includes several different mosasaurs, a chelonoid turtle, eight osteichthyans and twenty-two elasmobranchs. Some species have previously been reported from the Peedee Formation at Burches Ferry, but most were heretofore not known to occur in South Carolina. New Maastrichtian elasmobranch records for the state include *Lonchidion* sp., *Heterodontus* sp. cf. *H. granti*, *Squatina* sp., *Chiloscyllium* sp., *Cantioscyllium* sp., *Plicatoscyllium derameei*, *Plicatoscyllium antiquum*, *?Pararhincodon* sp., *Carcharias holmdelensis*, *Serratolamna serrata*, *Palaeogaleus* sp., *Squatigaleus sulphurensis*, *Scylliorhinus ivagranae*, *Rhinobatos uvulatus*, *Pseudohypolophus* sp., *Raja farishi*, *Borodinopristis* sp., *Ptychotrygon vermiculata*, *Texatrygon* sp., *Hamrabatis weltoni*, *Texabatis corrugatus*, and *Rhombodus binkhorsti*. The eight osteichthyans represent new records, including *Enchodus gladiolus*, *Enchodus petrosus*, *Paralbula casei*, *Anomoeodus phaseolus*, *Hadrodus* sp., Lepisosteidae indet., and Dercetidae indet. Most of these taxa were originally reported from Texas and have since been identified in North Carolina, so their discovery in SC may therefore not be surprising. However, the SC material provides additional data on the paleoenvironments inhabited by these taxa, as well as the paleobiogeographic distribution of the species.

Each of the exposed beds at Allison's Ferry have been sampled, and further investigation of the Peedee Formation will include systematic sampling of the entire vertical exposure at Burches Ferry and Cains Landing. Comparison of the paleofaunas occurring at each of these sites will provide a better understanding of any changes in marine vertebrate assemblages, laterally (geographic) and vertically (temporal), that occurred during the Maastrichtian.

### Biomechanics & Functional Morphology

#### **WAIR DID FLIGHT COME FROM: ONTOGENIC TRANSITIONS IN BIRDS USING WING-ASSISTED INCLINE RUNNING CAN SHED LIGHT ON THE FLIGHT CAPABILITIES OF EXTINCT SPECIES**

Klein, Stephanie, Chase, Hila Tzipora, Tobalske, Bret W. University of Montana, Madison, Wisconsin, U.S.A.

To understand the evolutionary transitions in form and function that facilitated avian flight, a study of ontogenetic transitions in extant birds can be deeply elucidating. Using this approach, Wing-Assisted Incline Running (WAIR), a new model for avian flight evolution, was developed from observing the development of flight capacity in chukars. This precocial ground bird uses their developing wings to assist the hindlimbs when running up terrain, weeks before they are able to fly. Recent findings on the aerodynamic and kinematic development of flight capacity over ontogenetic stages in the chukar have provided detailed insight into the function of these transitions, showing an increase in lift and flight capacity as the skeleton ossifies, joints become more constrained, and locomotor investment shifts from hindlimbs to forelimbs. However, the structure of these developing joints and how they relate to functional transitions remains unknown. We thus sampled chukars at various age points to investigate the structure of these joints throughout ontogeny, focusing particularly on the trabecular bone within the epiphyses. The trabecular matrix has been shown to structurally adapt to an organism's function throughout its lifetime with high sensitivity, and can thus provide subtle and kinematically-specific functional signals that correlate with behavior at various developmental stages. We collected microCT scans of three humeri and femora at six age points ranging from 2dph to adulthood. Scans showed increasing levels of ossification and a corresponding increase in the presence of trabecular bone throughout ontogeny. Though not fully ossified, a shift in functional signal occurred around the same age as flight capacity becomes more adult-like. In line with our predictions, preliminary analysis of trabecular parameters showed a general increase in trabecular thickness (Tb.Th), while degree of anisotropy gradually decreases as chukars reach adulthood. Ongoing work should be careful to separate developmental signals from functional, but our analysis thus far shows great promise in understanding the relationship between form and function throughout ontogenetic transitions in flight acquisition.

### Mesozoic Herpetology

#### **A NEW SPHENODONTIAN REPTILE WITH PECULIAR MANDIBULAR MORPHOLOGY FROM THE UPPER TRIASSIC OF THE PURGATOIRE RIVER VALLEY, SOUTHEASTERN COLORADO**

Kligman, Ben<sup>1</sup>, McClure, Warren<sup>2</sup>, Korbitz, Mark<sup>2</sup>, Schumacher, Bruce<sup>3</sup>

<sup>1</sup>Department of Geosciences, Virginia Tech, Blacksburg, Virginia, U.S.A., <sup>2</sup>Otero Junior College, La Junta,

Colorado, U.S.A., <sup>3</sup>USDA Forest Service, La Junta, Colorado, U.S.A.

The stratigraphy and paleontology of Upper Triassic rocks from southeast Colorado are little known due to limited exposure and difficult access. However, a sequence of Upper Triassic clastic rocks is exposed in the Purgatoire River valley and its tributaries in Las Animas County due to localized Laramide uplift. These Upper Triassic strata lay between Triassic eolianites of the Jelm Formation, and the Middle Jurassic Ralston Creek Formation. The Upper Triassic rocks are a dominantly red colored sequence of sandstones and siltstones with localized limestone pebble conglomerates deposited in a fluvio-lacustrine setting. Our paleontological investigations reveal a diverse Late Triassic biota of invertebrate and vertebrate ichnofossils, plant megafossils, bony fish, temnospondyl amphibians, and reptiles, sharing many taxonomic elements with other Upper Triassic formations in North America, as well as taxa unique to southeast Colorado. We tested the relative age of these rocks using aetosaur osteoderm biostratigraphy, which allows for correlation to the isotopically dated Chinle Formation, showing that Triassic rocks in the Purgatoire River valley are of mid-late Norian age.

Here we describe a new species of sphenodontian reptile collected from these rocks, represented by an isolated lower jaw with peculiar dental morphology. The presence of a robust dentary, transversely widened teeth, extensive labial wear facets, and a beak like mandibular symphysis suggests a jaw apparatus specialized for herbivory. A tusk-like anterior-most tooth on the lower jaw is unique amongst sphenodontians, and comparisons to extant and extinct taxa with similar morphologies suggests use of these teeth for manipulating plant material. Phylogenetic analyses comparing the new sphenodontian to other lepidosaurs supports its placement within opisthodontian sphenodontians, a group sharing derived cranio-dental morphologies specialized for herbivory. This is the first reported opisthodontian sphenodontian from equatorial Pangea, providing evidence for a global radiation of this clade by the Late Triassic, as well as their importance as small-bodied herbivores in Late Triassic ecosystems across Pangea.

This novel fossil assemblage and its unique geologic context adds to the North American Triassic record, and indicates that the Triassic strata of southwest North America preserves important data on the early evolution of lepidosaurs.

**Funding Sources** Virginia Tech paleobiology group and Otero Junior College.

**Colbert Poster Prize/Cenozoic Herpetology**

## CREATING A 3D MORPHOSPACE OF TURTLE SKULL VARIATION TO FACILITATE THE IDENTIFICATION OF FOSSILS

Kloess, Peter A.

Museum of Paleontology, University of California, Berkeley, California, U.S.A.

Fossil and modern turtles of the genera *Pseudemys*, *Trachemys*, and *Chrysemys* (Family: Emydidae) have been the subject of frequent taxonomic revision for over 150 years. Some resolution has recently been achieved through the application of molecular-based techniques but this leaves the morphological status of the genera, and the position of fossil taxa, unresolved. Only within a comparative morphological framework can bony anatomical differences be revealed that map onto phylogenetic relationships, facilitating the taxonomic identification of fossil specimens. To test the hypothesis that these three genera could be distinguished by morphology and that fossil skulls share similarities with extant analogues, I assembled a dataset of six fossil specimens and 91 skeletonized, modern specimens housed in paleontological and zoological collections across California, Texas, and Florida. These three genera are the focus of my investigation because three-dimensional geometric morphometric studies of turtle skulls have been infrequent and not focused on this part of the clade. Specimens in this dataset were scanned using high resolution computed tomography ( $\mu$ CT) and 3D models generated. I used automated three-dimensional geometric morphometric analysis (auto3dGM) to establish pseudolandmarks, quantify the variation between these specimens using principal components analysis, and develop a turtle skull morphospace. Preliminary results indicate that these genera occupy different regions of the skull morphospace and can be distinguished from each other. Along PC1, *Pseudemys* largely separates from space occupied by *Trachemys* and *Chrysemys*, with this variation driven by changes to the region caudal to the orbits (i.e., the postorbitals, jugals, and squamosals). *Pseudemys* variation is primarily along PC2, whereas the *Trachemys* + *Chrysemys* variation is relatively confined along the PC2 axis. Fossil specimens plotted with their extant congeners with one exception. Fossil *Trachemys* from the Pleistocene of Florida appear at the extreme end of the extant range in morphospace, overlapping with extant *Chrysemys*. For scientists interested in the phylogenetic placement of fossil turtles, this study demonstrates how morphology can be combined with molecular phylogenetics to identify taxonomically relevant cranial variation in turtles.

**Funding Sources** UCMP Graduate Student Research Grant, Integrative Biology Summer Research Grant and GRAC Travel Funds, Berkeley Chapter of Sigma Xi Grants in Aid of Research.

## Symposium: Paleoneurology

### THE BRAIN AND INNER EAR OF DERIVED PTEROSAURS HAVE SIMILAR MORPHOMETRICS TO THOSE OF BIRDS

Knoll, Fabien<sup>2</sup>, Kawabe, Soichiro<sup>1</sup>

<sup>1</sup>Fukui Prefectural University, Eiheijicho, Fukui, Japan,

<sup>2</sup>ARAID-FCPTD, Teruel, Spain

Pterosaurs were the first vertebrates able to sustain powered flight. It has been argued that their brain morphology was fairly similar to that of birds. These two distantly related groups of archosaurs are invaluable to explore the effects of a demanding locomotor mode on the evolution of the central nervous systems and sensory organs. However, information about the brain and inner ear of pterosaurs is scarce. We performed a CT scan of an exquisitely preserved skull of *Tupuxuara* sp., a derived pterodactyloid pterosaur, and investigated its brain and inner ear morphology using both linear measurements and three-dimensional geometric morphometric methods. Our results suggest that the brain of *Tupuxuara* is similar to that of extant birds. In particular, the relative size of the optic lobes is equal to that of extant birds. The cerebellum of *Tupuxuara* is more expanded dorsally than that of basal pterosaurs. The semicircular canals of *Tupuxuara* are extremely well developed. The extent of their development is well within the range of variations seen in extant birds. Although the cochlear duct of *Tupuxuara* is relatively short, it still falls within the range of variations observed across living birds. Thus, the brain and inner ear of *Tupuxuara* are very similar to those of modern birds, indicating parallel evolution of the nervous and sensory systems in the two clades of volant archosaurs.

## Dinosaur Systematics, Diversity & Ecology

### A LARGE NON-CERATOPSID NEOCERATOPSIAN FROM THE UPPER CRETACEOUS BAYANSHIREE FORMATION IN MONGOLIA

Kobayashi, Yoshitsugu<sup>1</sup>, Chiba, Kentaro<sup>2</sup>, Chinzorig, Tsogtbaatar<sup>3</sup>, Ganzorig, Bayasgaa<sup>4</sup>, Tsogtbaatar, Khishigjav<sup>4</sup>

<sup>1</sup>Hokkaido University Museum, Hokkaido University, Sapporo, Hokkaido, Japan, <sup>2</sup>Department of Biosphere-Geosphere Science, Okayama University of Science, Okayama, Japan, <sup>3</sup>Department of Biological Sciences, North Carolina State University, Raleigh, North Carolina, U.S.A., <sup>4</sup>Institute of Paleontology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia

In 2017, the joint expedition of Hokkaido University and the Institute of Paleontology of Mongolian Academy of Sciences discovered an isolated left maxilla and teeth of a neoceratopsian dinosaur from the Bayanshiree Formation at the Baishin Tsav locality in the Gobi Desert of Mongolia. This locality is rich in dinosaur fossils, including the hadrosauroid *Gobihadros*, dromaeosaurids, ornithomimosaurids, and therizinosaurs. This is the second record of a neoceratopsian dinosaur from the formation, following *Graciliceratops* from the Shireegiin Gashuun locality, in Mongolia.

The maxilla preserves its main body and seven alveoli with teeth in place, but all functional teeth are damaged. The anterior-most tooth is the smallest, and tooth size becomes larger posteriorly. The anterodorsal edge of the main body forms a posteroventral rim of the antorbital fenestra. The labial side of the tooth crown is enameled and bears a mesially positioned primary median ridge as well as secondary ridges. A cingulum is pronounced and offset from the base of the primary ridge. Teeth are single rooted. The total length of seven alveoli is 95 mm, which is much larger than the sympatric *Graciliceratops*. It is equivalent to large-sized non-ceratopsid neoceratopsians from the Late Cretaceous (*Udanoceratops* from the Djadokhta Formation in Mongolia, *Protoceratops hellenikorhinus* from the Bayan Mandahu Formation in China, and *Turanoceratops* from the Bissekty Formation in Uzbekistan) from the Asian landmass, separated from Europe by the Turgai Strait. The Bayan Mandahu Formation is correlated with the Djadokhta Formation, dated to the Campanian. A recent geochemical study (U-Pb) on caliches from the Bayanshiree Formation shows an upper Cenomanian to Turonian in age, which is equivalent to the Turonian Bissekty Formation. This line of evidence suggests that there were at least two time-bins, allowing non-ceratopsid neoceratopsians to increase in body size, during the Late Cretaceous in Asia. Paleogeographically, large-sized non-ceratopsid neoceratopsians were present on both the eastern and western sides of the Asian landmass during the Turonian.

## Marine Reptile Diversity & Biology

### A NEW MOSASAURINE (SQUAMATA: MOSASAURIDAE) FROM WESTERN JAPAN WITH UNEXPECTED POSTCRANIAL MORPHOLOGY

Konishi, Takuya<sup>1</sup>, Ohara, Masaaki<sup>2</sup>, Misaki, Akihiro<sup>3</sup>, Matsuoka, Hiroshige<sup>4</sup>, Street, Hallie P.<sup>5</sup>

<sup>1</sup>Biological Sciences, University of Cincinnati, Cincinnati, Ohio, U.S.A., <sup>2</sup>Wakayama Prefectural Museum of Natural History, Kainan, Wakayama, Japan, <sup>3</sup>Kitakyushu Museum of Natural History and Human History, Kitakyushu, Fukuoka, Japan, <sup>4</sup>Geology and Mineralogy, Kyoto

University, Kyoto, Kyoto, Japan, <sup>5</sup>Royal Saskatchewan Museum, Eastend, Saskatchewan, Canada

In 2006, one of us (AM) discovered a caudal vertebra of a mosasaur (Squamata: Mosasauridae) from the upper Campanian Toyajo Formation (c. 72 Ma) cropping out in Wakayama Prefecture, western Japan. Subsequent excavation first led by the Kyoto University and then by the Wakayama Prefectural Museum of Natural History resulted in collection of the most complete mosasaur skeleton to have come from the northwestern Pacific to date. After five years of continuous fossil preparation conducted by the museum, the new mosasaur's osteological and taxonomic significances are documented herein. The specimen, WMNH-Ge-1140240002, is assignable to the subfamily Mosasaurinae, by exhibiting such characteristics as: supraorbital process of prefrontal broad and shelf-like; hemal arches fused to caudal centra; and podial elements well ossified, snugly fitting with one another. Although the mosasaurine affinity of WMNH-Ge-1140240002 is consistent with a global trend of mosasaurine dominance among mosasaurids in the late Campanian and onward, the rest of the postcranial osteology of the new specimen demonstrates that it exhibits a novel body plan hitherto unknown to the subfamily and/or the family, such as: hind flipper longer than front flipper; and both front and hind flippers exceeding the mandible length. The last character is autapomorphic among the entire Mosasauridae, whereas only *Tylosaurus* (Tylosaurinae) are known to possess a hind flipper longer than the front flipper. On the humerus, the glenoid condyle greatly extends mediodistally forming a gentle arc in anteroposterior view, rendering the proximal end of the bone as wide as it is long. The articular surface of the condyle greatly exceeds the latero-medial width of the glenoid fossa, suggesting a great range of humeral adduction and abduction. The robust entepicondyle further indicates the presence of a set of strong muscles to flex the rest of the front flipper. Finally, the tallest neural spines occur on the second to the sixth dorsal vertebrae, which could have increased the range of scapular movement by lengthening of the trapezius and other extrinsic shoulder muscle fibers. Combined together, the preceding suite of characteristics suggests a novel macroevolutionary trajectory concerning mosasaurine postcrania, where some latest Cretaceous mosasaur taxa such as WMNH-Ge-1140240002 may have begun filling a niche left increasingly more vacant by the decline of short-necked plesiosaurs, the paraxial swimmers.

**Funding Sources** Wakayama Prefecture, Japan; Ministry of Health, Labour and Welfare, Government of Japan; The Nippon Foundation.

### **Anatomical & Developmental Explorations of the Mammalian Skull**

## **THE FUNCTIONAL MORPHOLOGY AND COMPARISONS AMONG THE PINNIPED MIDDLE EAR APPARATUSES**

Koper, Lindsey, Koretsky, Irina, Rahmat, Sulman  
Howard University, Washington, District of Columbia, U.S.A.

The mammalian middle ear morphology that evolved about 200 million years ago was a major innovation for terrestrial animals. During the transition from terrestrial to aquatic environments for the ancestors of modern whales and pinnipeds, specializations of the ear continued to occur in the basicranial auditory apparatus. Modern cetacean hearing is well understood, with a rich fossil record of the transitional auditory morphologies from primitive to derived body forms. Pinniped hearing has not been studied in depth, especially because these animals are defined as semiaquatic and require at least two modes of hearing to thrive. The fossil record of pinnipeds is sparse; as a result, the transitional morphologies of the hearing apparatus remain undiagnosed. Previous studies demonstrate lack of clarity regarding osteological and functional morphologies of the auditory system. These earlier studies are limited to the structure of the basicrania and ossicles in pinnipeds, which includes the families: Phocidae (true seals), Otariidae (sea lions and fur seals), and Odobenidae (walruses). In mammals these regions are thought to be more evolutionarily conservative and the hypothesis is that this will remain true for pinnipeds. This preliminary study demonstrates functional comparisons of pinniped ossicle morphology, with special emphasis on phocids. Future analyses will compare modern carnivore basicranial and auditory morphology in relation to hearing and will establish transitional patterns from land to sea in early pinnipeds.

### **Permo-Triassic Tetrapods**

## **FATE MAPPING THE SKULL-NECK BOUNDARY OF MODERN AMPHIBIANS AND IMPLICATIONS FOR NECK DEVELOPMENT IN EARLY TETRAPOD EVOLUTION**

Korneisel, Dana E., Atkins, Jade B., Maddin, Hillary C.  
Earth Science, Carleton University, Ottawa, Ontario, Canada

The diversity of tetrapod body plans, seen both in the fossil record and at present, was facilitated in part by the evolutionary innovation of the neck. Decoupling of the pectoral girdle from the skull allowed independent movement of the head from the trunk and permitted the radiation of tetrapods into diverse terrestrial niches. The neck is an anatomically complex region of an animal, and

throughout evolutionary history tetrapods have developed a variety of specialized structures within the skeletal portion of the neck. Often, the first two cervical vertebrae are highly modified such that they have been termed the atlas and axis, respectively. Our understanding of the origin and homology of these anteriormost vertebral elements of the neck, in particular that of the variably present pro-atlas, remains an open question as new data continue to yield conflicting interpretations. For example, both the proatlas and the odontoid process, when they occur, are considered to derive from the same embryological precursor, the atlas centrum. However, fossil taxa such as sphenacodontids have atlantal centra, intercentra, proatlases, and all axial components. Advances in our understanding of resegmentation reveal that occipital as well as trunk somites may contribute to the atlantal complex and could potentially resolve such inconsistencies. Thus, the fate of somites spanning the skull-neck boundary, may provide novel insights into the homology and thus evolution of these complex cervical structures.

In this study, we performed fluorescent dye fate mapping in the amphibian model species *Ambystoma mexicanum* (axolotl) and *Xenopus laevis* (clawed frog) to establish the developmental origin of the anteriormost cervical vertebral components. Despite differences in the somite position at which the skull-neck boundary occurs, we found that the atlases of these two species develop similarly in terms of somite contribution pattern. We combined these new data with those from the literature on modern amphibian body plan genetics and development and on fossil morphologies of structures at the skull-neck boundary in early and stem tetrapods. This study has implications for the interpretation of early tetrapod cervical anatomy, including unique vertebral morphologies like the axis centrum of albanerpetontids and, later, the complex cervical regions of sphenacodontids. This work lays the foundations for a more extensive assessment of vertebral structure homology across Tetrapoda.

**Funding Sources** NSERC RGPIN-06442.

## **Late Cenozoic Mammalian Macroecology & Macroevolution**

### **QUANTIFYING INDIVIDUAL VARIATION AND WEAR IN THE EXTINCT POCKET GOPHER *ENTOPTYCHUS* (MAMMALIA, RODENTIA)**

Kort, Anne E.<sup>1</sup>, Hicks, Elizabeth J.<sup>2</sup>, Calede, Jonathan<sup>3</sup>, Smiley, Tara M.<sup>4</sup>

<sup>1</sup>Earth and Atmospheric Sciences, Indiana University, Bloomington, Indiana, U.S.A., <sup>2</sup>Department of Biology, Indiana University, Bloomington, Indiana, U.S.A., <sup>3</sup>Evolution, Ecology, and Organismal Biology, The Ohio State University, Columbus, Ohio, U.S.A., <sup>4</sup>Environmental Resilience Institute, Indiana University, Bloomington, Indiana, U.S.A.

As climate cooled and grasslands spread through the Oligocene and Miocene, hypsodont teeth became a widespread trait among mammals, facilitating the processing of more abrasive food and increased exogenous grit in the diet. Increased hypsodonty implies a trend of dietary specialization across lineages, but measuring the extent of specialization requires analysis of individual variation within species and genera. We chose to measure variation in the dental morphology of *Entoptychus*, a hypsodont gopher present in North America 30–15 Ma. To quantify variation within this genus, the impact of multiple factors, including phylogeny, diet, and wear, on dentition needs to be parsed. To investigate the role of wear, specifically, we  $\mu$ CT scanned abundant fossil mandibles of *Entoptychus* from the John Day Formation in Oregon. From these scans, we took linear measurements expected to be either variable or uniform across wear stages. In addition to entire tooth row length, we measured external and internal structures for individual tooth positions: depth below and height above the alveolar margin and depth of the central enamel invagination. Measurements across the premolar and three molars for each individual were standardized by tooth row length. We tested for correlations and performed F-tests between each variable to look for patterns of increased variation that may be indicative of wear. We found positive correlations between all tooth variables (p-value <0.05) and no correlation between tooth row length and single-tooth measurements. Invagination depth varied the most of all measurements and both invagination and root depth show significantly greater variance than tooth height (p-value <0.01). Views of internal dental anatomy show that invagination depth marks the crown of the tooth and is therefore inferred to be a useful indicator of wear. Hypsodont molars erupt over the lifetime of an individual to maintain tooth height as the tooth is abraded. However, this growth is finite, with the invagination depth relative to the alveolar margin changing with wear. In some specimens, the invagination depth extended below the alveolar margin, while in others it was found above. We conclude that all individual tooth metrics were affected by wear, though to varying degrees. By parsing the effects of wear from those of intrinsic variation, we can begin to understand the breadth of *Entoptychus* dietary specialization as reflected by individual-level variation.

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## **Macroecology & Macroevolution**

### **MACROEVOLUTIONARY PATTERNS AND THE APPEARANCE OF THE MODERN-DAY LATITUDINAL BIODIVERSITY GRADIENT IN**

## **SOUTH AMERICAN TERRESTRIAL EUTHERIAN MAMMALS**

Kouvari, Miranta<sup>1</sup>, Mannion, Philip<sup>1</sup>, Goswami, Anjali<sup>2</sup>

<sup>1</sup>Earth Sciences, University College London (UCL), London, U.K., <sup>2</sup>Life Sciences, Natural History Museum, London, U.K.

Current rapid climatic changes are exerting a substantial impact on global biodiversity. The fossil record provides valuable insight on the long-term link between climate and biodiversity, including its underlying mechanisms. One of the most fundamental macroecological patterns today is the latitudinal biodiversity gradient, which describes the increase of biodiversity towards the Equator. However, the timing of its formation and causes remain unclear. Although significant advances have been made to unravel North American spatiotemporal biodiversity patterns, this is not the case for South America. The latter continent provides an excellent case study because of its extended isolation and endemic faunal composition for most of the Cenozoic. We focus on South American terrestrial eutherian mammals, which include the endemic notoungulates. We use a comprehensive dataset built and standardised within the Paleobiology Database, comprising approximately 6200 occurrences of more than 350 genera. We ameliorate the effects of fossil sampling bias using Shareholder Quorum Subsampling and PyRate, as well as a novel approach that integrates ecological niche modelling. We reconstruct Cenozoic paleobiodiversity through time using stage-level bins and calculate origination and extinction rates. We also calculate the spatial evolution of Cenozoic biodiversity using paleolatitudinal bins of 15 degrees for 20, 15, 10, and 5 Ma. Finally, we test the effect of paleoclimatic variables on sample-standardised spatiotemporal biodiversity with regression analyses. Newly observed biodiversity patterns emerge for South American eutherian mammals that can be linked to important climatic and faunal Cenozoic events. However, temporal variation in paleobiodiversity is not correlated with proxies for global paleotemperature fluctuations. Our results suggest that the steep, modern-type latitudinal biodiversity gradient only formed in South America in the last 5 million years, as has also been proposed for North America. By applying a novel combination of methods, our results offer new insights into the understanding of biodiversity shifts and their link to the climatic and environmental changes of the Cenozoic.

**Funding Sources** Funded by The Royal Society.

### **Anatomical & Developmental Explorations of the Mammalian Skull**

## **NEW SKULL MATERIAL OF *TAENIOLABIS TAOENSIS* (MULTITUBERCULATA, TAENIOLABIDIDAE): IMPLICATIONS FOR**

## **TAENIOLABIDID ANATOMY, PALEOBIOLOGY, AND PHYLOGENETIC RELATIONSHIPS**

Krause, David W.<sup>1</sup>, Chester, Stephen G.<sup>2</sup>, Hoffmann, Simone<sup>3</sup>, Lyson, Tyler R.<sup>1</sup>, Dougan, Lindsay G.<sup>1</sup>, Petermann, Holger<sup>1</sup>, Tecza, Adrienne<sup>1</sup>, Miller, Ian M.<sup>1</sup>

<sup>1</sup>Earth Sciences, Denver Museum of Nature & Science, Denver, Colorado, U.S.A., <sup>2</sup>Department of Anthropology and Archaeology, Brooklyn College, Brooklyn, New York, U.S.A., <sup>3</sup>Department of Anatomy, New York Institute of Technology, Old Westbury, New York, U.S.A.

*Taeniolabis taoensis* is an iconic Paleocene mammal from the Western Interior of North America. It is notable in: 1) being the largest known multituberculate (21 kg); 2) possessing the most derived dentition of any known multituberculate; 3) being an index taxon that defines the base of the third Puercan North American Land Mammal Age biochron (Pu3); 4) having been employed to define Multituberculata, Allotheria, and Theriiformes phylogenetically; 5) being the type species of the genus *Taeniolabis*, which is the type genus of Taeniolabidoidea and, in turn, Taeniolabidoidea; and 6) being among the first Cenozoic multituberculates described. Despite its iconic status, *T. taoensis* is not particularly well known, in part because many of the plethora of referred specimens have not been described. Furthermore, as for many fossil mammals, the vast majority of the known specimens of *T. taoensis* are isolated teeth and fragmentary jaws.

Here we report the discovery of significant new skull material (two complete crania, four partial crania, and a nearly complete dentary) of *T. taoensis* in phosphatic concretions from the Corral Bluffs study area, Denver Formation, Denver Basin, Colorado. The new skull material provides the first record of the species from the basin, where it occurs primarily in river channel deposits ~550,000 years after the Cretaceous-Paleogene boundary and roughly coincident with the first appearance of legumes. The new material, in combination with several specimens previously known from the Nacimiento Formation of the San Juan Basin, New Mexico (AMNH 16310, AMNH 16321, UCMP 98083), is the subject of detailed study aided by micro-computed tomography. Our analyses reveal previously unknown aspects of skull anatomy. For instance, DMNH EPV.95284 indicates that the position of the orbit in a previous reconstruction is incorrect and provides the first-ever information on the anatomical structure of the inner ear (cochlear canal elongated and gently curved; vestibule enlarged but to lesser degree than in *Lambdopsalis*), DMNH EPV.130973 reveals that the shape and position of the dentary condyle are also incorrect in previous reconstructions, and UCMP 98083 provides new details to test hypotheses concerning the pattern and sequence of dental eruption. Upon completion of documentation of the anatomical features of this new material, we will reassess the phylogenetic

relationships of *Taeniolabis* relative to other taeniolabidids and other multituberculates.

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### **Mammalian Skeletal Morphology**

#### **ANCESTRAL STATE RECONSTRUCTION OF MAMMALIAN VERTEBRAL COUNTS**

Kubica, Sam, Springer, Mark S.  
Evolution Ecology and Organismal Biology, University of California-Riverside, Riverside, California, U.S.A.

The mammalian vertebral column is both more regionalized and less variable in vertebral number than in other vertebrates. Mammals have five distinct regions: cervical, thoracic, lumbar, sacral, and caudal. Within these five regions, the vertebral counts are more constrained than the same or comparable regions in reptiles, birds, amphibians, or fish. It has been suggested that the first mammals were constrained to a single vertebral count formula. Researchers have sought this pattern. Yuichi Narita and Shigeru Kuratani have proposed that it is seven cervical and 19 thoracolumbar, typically 13 thoracic and six lumbar. Other researchers propose a looser constraint centered around the same formula. However, this pattern has only been investigated in studies with a small sample size and never with counts from every extant mammalian order. I ran a parsimony ancestral state reconstruction to test these claims on 690 mammalian species' vertebral counts. Every extant order of mammals was represented, as were most mammalian families. The reconstruction indicates that the most parsimonious reconstruction for thoracic counts is either 13 or 14, while for lumbar it is four or five. This result is influenced by the diversity in two superorders, Afrotheria and Xenarthra, which show more variation than the superorders Euarchontoglires and Laurasiatheria. Constraints in modern mammals may be due to locomotory adaptations, ecology, or metabolic rate. Using a test of phylogenetic generalized least squares, I have found that all of these factors are correlated with a constrained vertebral count. However, the constraints are not correlated consistently across all mammals. The relationships are limited to smaller clades; for example, locomotory adaptations are correlated with a thoracolumbar constraint in Carnivora and Cetartiodactyla. This suggests that constraints and predictive factors should be considered at lower taxonomic levels in addition to across Mammalia.

### **Permo-Triassic Tetrapods**

#### **BODY SIZE AND PALEOLATITUDE IN *LYSTROSAURUS*: DID BERGMANN'S RULE APPLY DURING THE EARLY TRIASSIC?**

Kulik, Zoe T., Sidor, Christian A.  
Biology, University of Washington, Seattle, Washington, U.S.A.

Bergmann's Rule, which states that high latitude taxa have larger body sizes than their lower latitude relatives, has been studied extensively in modern ecosystems. Mammals, birds, fish, amphibians, turtles, and insects generally show a positive relationship between body size and latitude, whereas snakes and lizards do not. The underlying mechanism driving Bergmann's Rule is hypothesized to relate to food availability and the energy advantages of having a larger body size in harsher, high-latitude environments. While this pattern prevails among many modern vertebrates, few investigations have looked for similar results in the fossil record. Indeed, times in Earth history with a decreased temperate gradient from equator-to-pole may have removed a key factor underlying Bergmann's Rule. One extreme example is the earliest Triassic, where atmospheric CO<sub>2</sub> is estimated to have been four times higher than today. In this hot-house, post-extinction environment, can we expect globally distributed organisms to conform to Bergmann's Rule?

We assessed whether skull size varied predictably with latitude in *Lystroraptor* by measuring 225 skulls from Antarctica, South Africa, India, Russia, and China. Early Triassic *Lystroraptor* localities span a range of paleolatitudes from 82–52° South, and 28–40° North. These ranges are reconstructed from all reported Early Triassic *Lystroraptor* localities but importantly are lacking records from low paleolatitudes. If *Lystroraptor* conforms to Bergmann's Rule, we expect that the highest northern and southern taxa will have larger body sizes than lower latitude *Lystroraptor* assemblages. A failure to detect Bergmann's Rule could imply a previously unrecognized macroevolutionary consequence of climatic warming.

Our preliminary results show that intraspecific average skull size is largest at high northern paleolatitudes. Interestingly, average skull sizes at high northern latitudes is approximately 85% maximum size, compared to 65–70% at southern latitudes. This discrepancy suggests that Bergmann's Rule may not have applied during Early Triassic times. A possible explanation may relate to local environmental conditions that allowed for larger body sizes in northern environments. With continued sampling efforts in China and emerging paleoclimate reconstructions, it may be possible to further refine the possible drivers of *Lystroraptor* body size distribution in the Early Triassic.

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## Colbert Poster Prize/Mesozoic & Early Cenozoic Mammalian Evolution

### THE ANATOMY, PALEOBIOLOGY, AND PHYLOGENY OF THE PALEOCENE TAENIODONT *CONORYCTES*

Kynigopoulou, Zoi<sup>1</sup>, Shelley, Sarah L.<sup>2</sup>, Williamson, Thomas E.<sup>3</sup>, Brusatte, Stephen<sup>1</sup>

<sup>1</sup>School of Geosciences, University of Edinburgh, Edinburgh, U.K., <sup>2</sup>Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A., <sup>3</sup>New Mexico Museum of Natural History, Albuquerque, New Mexico, U.S.A.

*Conoryctes* belongs to the Taeniodonta, a group of Paleogene mammals with unique dentition, suitable for an abrasive diet, and specialized postcranial skeletons. Taeniodonts are among few eutherian clades with fossil evidence indicating they crossed the Cretaceous–Paleogene mass extinction boundary. They are traditionally divided into two families: the more ‘generalist’ Conoryctidae and anatomically derived Stylinodontidae. Here we report new specimens of *Conoryctes* from the Paleocene Nacimiento Formation of the San Juan Basin, New Mexico, U.S.A. These consist of numerous vertebrae, a pelvis, sacrum, partial forelimb and hindlimb, with phalanges and unguals, comprising the first relatively complete associated postcranium of the genus. The new specimens allowed us to add new postcranial characters to a large phylogenetic analysis of early eutherian mammals (622 characters, 125 taxa), which we analysed using parsimony and Bayesian techniques. The results find *Onychodectes* as a basal taeniodont outside of the sister groups Conoryctidae (*Conoryctes*, *Conoryctella*, *Huerfanodon*) and Stylinodontidae (*Wortmania*, *Psittacotherium*, *Ectoganus*, *Stylinodon*). We also examined the anatomy and locomotor adaptations of the hindlimb, using multivariate analysis of 11 linear pes measurements to assess foot posture. Three representative taeniodonts (*Onychodectes*, *Conoryctes*, *Stylinodon*) were compared to a suite of extant mammals with known postural grades of the foot, as well as eight Paleogene taxa. *Onychodectes* and *Conoryctes* exhibit a more plantigrade posture whereas *Stylinodon* is more digitigrade, plotting next to the armadillo (*Oryzomys*). Qualitatively, in *Conoryctes*, the astragalus features a relatively well-developed trochlear surface indicating cruropedal movement was more limited to the parasagittal plane. The articular surfaces on the astragalus and calcaneum with the navicular and cuboid respectively, show a degree of rotational movement within the middle pes suggestive of moderate supination during pedal flexion. The calcaneal tuber is robust indicative of a powerful foot stroke. These features, in combination with other features of the skeleton,

support digging abilities in *Conoryctes*. Our study suggests that a plantigrade foot posture and digging behaviors are ancestral for Conoryctidae and perhaps all taeniodonts. It is likely their ability to burrow, and feed on tough vegetation, was essential to their survival in the early Paleocene and subsequent radiation.

**Funding Sources** European Research Council Starting Grant (ERC StG 2017, 756226, PalM), National Science Foundation (EAR- 1654952).

### Bird Biology & Evolution

### A BAYESIAN REANALYSIS OF PHORUSRHACIDAE AND THE EVOLUTION OF GIGANTISM

LaBarge, Thomas W., Organ, Chris L.  
Earth Science, Montana State University, Syracuse, New York, U.S.A.

Phorusrhacids, commonly referred to as ‘terror birds’, are an extinct group of flightless carnivorous birds. The derived members of this group represent a unique example of predatory birds evolving to gigantic sizes. The evolutionary means by which they achieved these enormous sizes remain largely unstudied. We present a revised evolutionary tree for the family Phorusrhacidae, with analyses on body size evolution. Using past analyses as a framework, we formed a new composite matrix of diagnostic traits and constructed a Bayesian phylogeny. Mass correlated bone measurements were compiled and paired with their respective species, with which we used to test for directionality in body size evolution. We then used the tree to test for variability in the rate of body size evolution and determined whether these rates are associated with species divergence. The new phylogeny indicates that gigantism occurred in multiple lineages within Phorusrhacidae to varying degrees. Extreme examples, however, appear to have solely occurred in the crown group, where the rate of body size evolution was found to be the highest. There is a sharp increase in rates when this clade diverged, indicating that these animals experienced a period of rapid diversification correlated with an overall increase in body size. Notably the largest individual species appear to form a distinct clade and are associated with the overall highest rates of body size evolution within the tree. Lineages which maintained lower body sizes present consistently low rates. There appears to be some decrease in body size evolution rates in the more recently diverging species, but the overall correlation between gigantism and rapid body size evolution is statistically maintained. This revised phorusrhacid tree clarifies how this group evolved and with additional inquiry may have further implications regarding phorusrhacid ecology.

**Funding Sources** Montana State University: Undergraduate Scholars Program.

### **Taphonomy & Stratigraphy**

## **STRONG VARIATION IN DIAGENESIS OF BONES AS A FUNCTION OF SEQUENCE-STRATIGRAPHIC CONTEXT: EOCENE VALLEY OF THE WHALES, EGYPT**

Laker, Rachel<sup>1</sup>, Gingerich, Philip D.<sup>2</sup>, Kidwell, Susan<sup>1</sup>

<sup>1</sup>Geophysical Sciences, University of Chicago, Chicago, Illinois, U.S.A., <sup>2</sup>University of Michigan, Ann Arbor, Michigan, U.S.A.

Bones subjected to significant amounts of reworking, such as those associated with the formation of incised valleys and sequence boundaries, are likely to experience high levels of taphonomic alteration, especially related to erosion (e.g., mechanical abrasion) and subaerial exposure (drying, UV, oxic mineral infill, rooting, and soil formation) prior to re-burial. In contrast, bones that accumulate during the aggradation of system tracts should undergo briefer and rarer events of exposure, reducing the window for taphonomic damage and complex diagenesis. At the other extreme, fossils associated with maximum flooding surfaces (MFS) have potential to experience prolonged exposure but at the sediment-water interface and within the surface mixed layer during times of little to no sedimentation, resulting in maximum opportunity for bioturbation (redox cycling), microbial tunneling, and complex mineralogic infills. The differences in pre-burial trajectories between erosionally reworked, rapidly buried, and slowly buried bone should present as significant differences in preservational quality, implying qualitatively different degrees of time averaging and compositional bias. To test the effect of a bone's likely pre-burial history on preservational quality, bone fragments from the well-studied Birket Qarun and Qasr el-Sagha Formations of Wadi Al-Hitan (Valley of the Whales, Eocene, Egypt) were thin-sectioned and examined for variation in the mineralogic infill of original bone porosity and for the state of bone (apatite) preservation. Previous work found that cetaceans occur as disarticulated bones within the incised valley fill (IVF) of a sequence boundary and as articulated specimens in the underlying falling stage systems tract (FSST). In thin section, IVF bone fragments exhibit abundant micro-fractures, likely from desiccation, and extensive iron oxide-rich infill. Bones from the FSST reveal minimal fracturing and a less complex (single mineral-dominant) infill, and a unique bone from the MFS is highly brecciated, with multi-generational infill showing signs of sidedness. Diagenesis thus varies significantly with stratigraphic context, as expected if it arises from post-mortem and early diagenetic conditions rather than late diagenesis. The stratigraphic context of fossils is thus

an effective predictor of the diagenetic quality of fossil bone and of the scale and nature of time-averaged accumulation.

**Funding Sources** University of Chicago Department of Geophysical Sciences.

### **Mammalian Skeletal Morphology**

## **MORPHOLOGICAL GROUPING AND BODY MASS PREDICTION MODELS**

Lancaster, Terry E.

Basic Sciences, Sherman College of Chiropractic, Spartanburg, South Carolina, U.S.A.

Every facet of an organism's function is affected by its body size, such as heart rate, metabolism, organ size and function, feeding ecology, and locomotion. Using body size to assess the function and size of organs in extant mammals is relatively easy. Estimating the body size and organ function of transitional fossil species, such as the Eocene whales, is difficult. These whales are diverse in body size, structure, and habitat. A single allometric model will not provide the most accurate body size estimation for each fossil whale family and therefore less accurate organ function assessment. My goal is to predict the body size of the Eocene whales using morphological models of extant mammals as guides. Stage 1 is the morphological grouping and body mass prediction models using modern mammal skeletons.

I measured the skull, vertebrae, and appendicular bones of multiple species of modern aquatic, semi-aquatic, and terrestrial mammals. I calculated an average body mass for each species using recorded body weights. Using PCA, I determined morphological groupings for these mammals from the skeletal measurements. For each PCA analysis completed, I created a linear regression equation to predict body size from the skeletal variables used in each analysis and the calculated average body sizes. I tested these prediction models using the measurements from 12 representative skeletons that were not included in the data set used to create the model, specifically *Odocoileus virginianus*, *Tragulus napu*, *Hippopotamus amphibius*, *Tapirus indicus*, *Sus scrofa*, *Canis lupus lycaon*, *Nyctereutes procyonid*, *Ehydra lutris*, *Gulo gulo*, *Neophoca cinerea*, *Lobodon carinophagus*, and *Ursus maritimus*.

From the PCA, I identified five morphological groups for the mammals selected: Aquatic, Semi-aquatic, Semi-terrestrial, Large Terrestrial and Small Terrestrial. For the prediction model using all skeletal variables, the SEE for all 12 test individuals ranged from 0.3359–0.7496. For the skull variables, the SEE ranged from 0.1260–0.3197. For the limb variables, the SEE ranged from 0.1716–0.3964. For the vertebral variables, the SEE ranged from 0.1511–

0.2851. These small SEE values and the large sample size substantiate the accuracy of these predictive models and the reliability of their respective confidence intervals (CI) and prediction intervals (PI) for the models. The results confirm that these linear regression models will be appropriate to predict the body mass of the Eocene whales. **Funding Sources** Kent State University Graduate Student Senate Research Grant, Sigma Xi Grants in Aid of Research.

### **Colbert Poster Prize/Dinosaur Systematics, Diversity & Ecology**

#### **ONTOGENETIC CHANGES IN MANDIBULAR FUNCTION IN *PSITTACOSAURUS***

Landi, Damiano<sup>1</sup>, King, Logan<sup>1</sup>, Qi, Zhao<sup>2</sup>, Rayfield, Emily<sup>1</sup>, Benton, Michael J.<sup>1</sup>

<sup>1</sup>Earth Sciences, University of Bristol, Bristol, U.K.,  
<sup>2</sup>Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China

Many dinosaurs seem to have experienced a major shift function through ontogeny. For example, recent studies on *Psittacosaurus* demonstrated a postural shift from a quadruped to biped at about the age of 3–4 years. Such a shift in posture was probably accompanied by other changes, both behavioral and physiological, one of which might have been a dietary shift, a rare occurrence in extant reptiles.

A shift in diet could affect the shapes of key elements of skull and teeth and their function. We analyzed CT scans of two specimens of *Psittacosaurus lujiatunensis* from IVPP, constituting the endmembers of an ontogenetic series spanning from juvenile to adult. Analysis of the digitally restored mandibles shows allometric scaling in the caudal region of the jaw, with reshaping of the angular and surangular bones, as well as marked growth of the prementary through ontogeny. At the same time, the tooth row moves caudally and dorsally, becoming comparatively shorter in the adult, although the number and size of teeth increase with age.

Despite these changes, there is little change in jaw mechanics between hatchling and adult. Analyzed in two dimensions, the jaw is comparable to a third-class lever system both in the adult and the juvenile, the caudal movement of the tooth row not being sufficient to achieve a second-class status even for the caudalmost teeth. The major components of the lever system change only slightly with age, resulting in overall comparable efficiency estimates for both age classes, with a major gain in mechanical advantage in the adult specimen's caudal tooth row region.

Such a result was unexpected as, with a clear postural shift, equally clear evidence of a dietary shift occurring along with the general rearrangement of the skull were to be expected. However, the similarity between mandibles of hatchling and adult indicate little change in jaw function, at least when considered as a bidimensional system. The only difference lies is increased mechanical efficiency at the back of the tooth row in the adult. While this potentially implies a dietary shift, it indicates a definitely less powerful mandibular build in juveniles, making them comparatively ill-equipped to process fibrous plant material.

### **Marine Mammals**

#### **EVOLUTION OF DENTITION IN THE PHYLOGENY OF BEAKED WHALES (ZIPHIIDAE, ODONTOCETI): THE CASE OF THE TASMAN'S BEAKED WHALE**

Lanzetti, Agnese<sup>1</sup>, Gatesy, John<sup>2</sup>, Meredith, Robert<sup>3</sup>, Springer, Mark<sup>4</sup>, McGowen, Michael R.<sup>5</sup>

<sup>1</sup>Natural History Museum, London, U.K., <sup>2</sup>American Natural History Museum, New York, New York, U.S.A., <sup>3</sup>Montclair State University, Montclair, New Jersey, U.S.A., <sup>4</sup>University of California, Riverside, Riverside, California, U.S.A., <sup>5</sup>Smithsonian National Museum of Natural History, Washington, District of Columbia, U.S.A.

Odontocetes (toothed whales) have acquired extreme feeding adaptations due to their aquatic lifestyle. Members of the family Ziphiidae (beaked whales) have progressively reduced their dentition in response to their highly specialized feeding mode, but one extant taxon (Tasman's beaked whale: *Tasmacetus shepherdi*) still retains complete tooth rows in both jaws, the hypothesized ancestral condition observed in fossil outgroups and other extant odontocetes. *Tasmacetus* is usually placed as the earliest diverging lineage of extant Ziphiidae in morphological phylogenetic analyses, supporting the hypothesis that tooth reduction occurred progressively with the evolution of a more specialized diet. By contrast, many molecular analyses place this genus as nested in the family Ziphiidae, challenging the baseline hypothesis for dental evolution in this family. Here, we use combined analyses of morphological and molecular data including both fossil and living ziphiids to improve the resolution of ziphiid phylogeny and then assess patterns of tooth evolution using ancestral state reconstruction. This work provides a new and more conclusive interpretation of dental evolution in this group, including convergent patterns between extant and extinct beaked whales. We compiled nuclear gene sequences for the six extant genera of Ziphiidae, including new genomic data for *Indopacetus*, and merged these molecular data with a previously published morphological matrix that includes relevant extinct taxa

and outgroups for a total of 33 genera. The combined matrix was analyzed using both parsimony and Bayesian methods; ancestral states were reconstructed using parsimony. Our results position *Tasmacetus* as nested in crown Ziphiidae, in agreement with most molecular analyses. Ancestral state reconstruction suggests that this taxon has independently reacquired full rows of teeth, an event that may have occurred in several fossil lineages as well. This surprising reversal was likely enabled by preservation of the genetic bases for tooth development in crown Ziphiidae. All other extant beaked whale species retain mandibular tusks, and, in some species, vestigial teeth also have been identified in both jaws. The dentition of *Tasmacetus* might also be a plesiomorphic condition, retained from the last common ancestor of crown Ziphiidae. In either case, behavioral and ecological drivers could explain the retention or reacquisition of complete tooth rows in this taxon and in fossils.

### Preparators

#### ULTRAVIOLET INDUCED FLUORESCENCE DIGITAL PHOTOGRAPHY AS A DIAGNOSTIC TOOL FOR DISCOVERY, DIGITAL DOCUMENTATION, ANALYSIS AND CURATION OF PALEONTOLOGICAL SPECIMENS

Lauer, Rene<sup>1</sup>, Lauer, Bruce<sup>1</sup>, Ward, David J.<sup>2</sup>, Ward, Alison<sup>2</sup>, Duffin, Christopher J.<sup>2</sup>

<sup>1</sup>Lauer Foundation for Paleontology, Science and Education, Wheaton, Illinois, U.S.A., <sup>2</sup>Earth Sciences, NHM, London, U.K.

The use of ultraviolet lights to generate Ultraviolet Induced Fluorescence (UVIF) in fossil specimens is well known, but not widely utilized among paleontologists. Unlike many other diagnostic options, UVIF Digital Photography is a non-destructive, cost effective and easy to use tool using standard equipment. It can be performed by anyone to obtain immediate UVIF Digital Photographic images for documentation and analysis of fossil specimens and their enclosing matrix.

UVIF Digital Photography is particularly well suited for use on German Lithographic Limestone fossils which make up most of the Lauer Foundation collection. It helps to reveal rarely seen features such as the soft tissue preservation of muscle and skin. It provides clarity and definition of morphological details such as fine structures, teeth and bones.

UVIF can be used to identify areas where repair has been made and to reveal man-made artifacts of restoration or embellishment. Information obtained utilizing this technique has influenced and improved our fossil preparation practices. It has become part of our standard curation procedure and provides researchers with an

additional diagnostic tool with which to more accurately analyze and measure specimens.

Our preferred UVIF digital photographic system utilizes standard DSLR or mirrorless cameras, without sensor modification, to photograph in the visible spectrum. We developed customized settings and techniques to efficiently capture images which are consistent and reproducible. A lamp equipped with 95-watt ultraviolet UV-A, B and C wavelength bulbs, which are used individually and together, provide the only light source in a darkened room. The UVIF response to specific wavelengths varies from specimen to specimen, therefore each is subjected to the full range of UV frequencies and photographed. A linear polarizing filter and an orange color lens filter provide enhanced clarity and resolution while reducing glare. Safety procedures require protective clothing and UV goggles must be worn to avoid skin and retinal damage.

Refinements include a custom-built light stand, camera stand, motorized table and a tethered 4K monitor. These provide consistent and reproducible results and can be easily modified to accommodate variable sizes and types of fossils.

### Mesozoic Herpetology

#### HISTOLOGICAL ANALYSIS OF THE ARLINGTON ARCHOSAUR SITE FOSSILS SUPPORTS NICHE PARTITIONING AND ENVIRONMENTAL STABILITY AS DRIVERS OF BIODIVERSITY IN THE WOODBINE GROUP

Lee, Andrew H.<sup>1</sup>, Noto, Christopher R.<sup>2</sup>

<sup>1</sup>Anatomy, Midwestern University, Glendale, Arizona, U.S.A., <sup>2</sup>University of Wisconsin–Parkside, Kenosha, Wisconsin, U.S.A.

The Arlington Archosaur Site (AAS) in north-central Texas preserves a rare record of the terrestrial ecosystem from the middle–late Cenomanian (95–100 mya) Woodbine Group. At least 37 vertebrate taxa have been recovered thus far. Herbivorous taxa are represented only by the large-bodied hadrosauroid *Protohadros* and an early trionychid turtle. Predatory taxa, however, are quite diverse, including a large size range of theropods, several aquatic turtles representing multiple ecomorphs, and four crocodyliforms, of which *Deltasuchus* is the most abundant and represented by numerous individuals from a range of body sizes. The assemblage likely reflects a time-averaged accumulation, thereby mixing the isolated skeletal remains of juveniles and adults from taxa large and small. In order to assess how common small specimens represent juvenile stages from large-bodied taxa, we performed paleohistology on a selection of 12 specimens, mainly humeri and femora with additional rib and cortical

fragments. At least three crocodyliform specimens (one humerus and two femora) show evidence of growth-maturation, namely the presence of a continuous external fundamental system (EFS). Interestingly, an EFS is present in small and large specimens, consistent with previous work suggesting that size variation reflects specialization and niche partitioning. Secondary osteons are abundant in three specimens: a small crocodyliform femur with an EFS, a large turtle humerus possibly from *Naomichelys*, and rib likely from *Protohadros*. Although secondary osteons are not exclusive to somatically mature individuals, co-occurrence with an EFS (at least in the crocodyliform femur) is consistent with late ontogeny. Put together, the results suggest that fully-grown individuals of small- and large-bodied taxa are relatively common at the AAS. The relative abundance of adults from taxa of various sizes supports the interpretation of niche partitioning and specializations possibly due to relatively stable environmental conditions. Future directions involve expanding the breadth of histological sampling to compare the histo-ontogenetic responses of several coeval taxa to prevailing environmental conditions.

**Funding Sources** Funded in part by the National Geographic Society, grant #C325-16.

## Quantitative Methods

### PHYLOGENETIC AND ONTOGENETIC CHANGES OF THE ANATOMICAL ORGANIZATION AND MODULARITY IN THE SKULL OF ARCHOSAURS

Lee, Hui Wai<sup>1</sup>, Esteve-Altava, Borja<sup>2</sup>, Abzhanov, Arkhat<sup>1</sup>  
<sup>1</sup>Life Science, Imperial College London, London, U.K.,  
<sup>2</sup>Department of Experimental and Health Sciences, Institute of Evolutionary Biology (UPF-CSIC), Pompeu Fabra University, Barcelona, Spain

Comparative anatomy studies of the skull of archosaurs provide insights on the mechanisms of evolution for the morphologically and functionally diverse species of crocodiles and birds. One of the key attributes of skull evolution is the anatomical changes associated with the physical arrangement of cranial bones. Here, we compare the changes in anatomical organization and modularity of the skull of extinct and extant archosaurs using an Anatomical Network Analysis approach. We show that the number of bones, their topological arrangement, and modular organization can discriminate between birds, non-avian dinosaurs, and crurotarsans, and between extant and extinct species. By comparing within the same framework juveniles and adults for crown birds and alligator (*Alligator mississippiensis*), we find that adult and juvenile alligator skulls are topologically similar, whereas juvenile bird skulls have a morphological complexity and anisomerism more similar to that of non-avian dinosaurs and

crurotarsans than to their adult forms. Clade-specific ontogenetic differences in skull organization, such as extensive postnatal fusion of cranial bones in crown birds, can explain this pattern. The fact that juvenile and adult skulls in birds do share a similar anatomical integration suggests the presence of specific constraint in their ontogenetic growth.

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## Symposium: Dietary Reconstruction

### MEASURING NITROGEN ISOTOPES IN TOOTH ENAMEL: A NOVEL METHOD FOR CHARACTERIZING TROPHIC POSITION IN FOSSIL ECOSYSTEMS

Leichtler, Jennifer N.<sup>1</sup>, Luedecke, Tina<sup>2</sup>, Duprey, Nicolas<sup>2</sup>, Winkler, Daniela E.<sup>1</sup>, Clauss, Marcus<sup>3</sup>, Tütken, Thomas<sup>1</sup>, Martínez-García, Alfredo<sup>2</sup>

<sup>1</sup>Institute of Geosciences, Johannes Gutenberg University, Mainz, Rheinland-Pfalz, Germany, <sup>2</sup>Climate Geochemistry Department, Max Planck Institute for Chemistry, Mainz, Rheinland-Pfalz, Germany, <sup>3</sup>Clinic for Zoo Animals, Exotic Pets and Wildlife, University of Zurich, Zurich, Switzerland

Paleontologists have long sought a reliable geochemical proxy for inferring the diet and trophic position of fossil organisms. Stable carbon and oxygen isotope analyses of tooth enamel have greatly enhanced our understanding of the dietary ecology of fossil taxa, but they reveal relatively little about trophic position. In contrast, nitrogen isotope ratios (<sup>15</sup>N/<sup>14</sup>N, expressed as  $\delta^{15}\text{N}$ ) are widely used as trophic indicators in modern ecosystems. Measurement of  $\delta^{15}\text{N}$  in the fossil record, however, is limited to relatively young (<120 ka), well-preserved collagen extracted from bone or dentine. While tooth enamel is far less susceptible to diagenetic alteration than bone and can therefore preserve dietary information into deep time,  $\delta^{15}\text{N}$  analysis of enamel has long been hindered by enamel's low nitrogen content.

Here, we present a novel analytical technique for measuring  $\delta^{15}\text{N}$  values in modern and fossil enamel ( $\delta^{15}\text{N}_{\text{enamel}}$ ) that permits analyses of sample sizes of  $\leq 5$  mg. This method, referred to as the oxidation-denitrification method, involves the conversion of nitrogen in enamel-bound organic matter to nitrate (oxidation) followed by bacterial conversion of nitrate to N<sub>2</sub>O (denitrification). It is routinely used for determining  $\delta^{15}\text{N}$  of mineral-bound organic matter from the hard parts of modern and fossil invertebrates (e.g., foraminifera, diatoms and corals) and is  $\geq 100$ -fold more sensitive than traditional combustion methods.

We demonstrate the robusticity of this new proxy in both experimental settings and natural ecosystems by analyzing  $\delta^{15}\text{N}_{\text{enamel}}$  of animals that consumed different diets, and cross validating these measurements using  $\delta^{15}\text{N}$  data (e.g., soft tissue, collagen) from the same individuals. We establish that  $\delta^{15}\text{N}_{\text{enamel}}$  reflects the isotopic composition of diet plus an enrichment of ca. 2-4‰ and is positively correlated with tissue  $\delta^{15}\text{N}$  values. Further, animals which consumed plant-based diets exhibit significantly lower  $\delta^{15}\text{N}_{\text{enamel}}$  than animals which consumed meat-based diets. Next, we present data from fossil enamel of up to 150-million-year-old fauna from a variety of depositional contexts and phylogenetic groups (e.g., mammals, fish, and dinosaurs), which belong to different trophic levels. In all fossil datasets, we observe the same pattern of trophic enrichment (2–3‰) in  $\delta^{15}\text{N}_{\text{enamel}}$  that is observed in modern systems. This novel method represents a powerful new tool for reconstructing dietary evolution, trophic niche, and (paleo-)food webs.

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### Dinosaur Systematics, Diversity & Ecology

#### METACARPUS EVOLUTION IN NON-AVIAN DINOSAURS

Leite, João V.<sup>1</sup>, Goswami, Anjali<sup>2</sup>, Barrett, Paul M.<sup>1</sup>

<sup>1</sup>Earth Sciences, The Natural History Museum, London, U.K., <sup>2</sup>Life Sciences, The Natural History Museum, London, U.K.

The manus is one of the most important and adaptable skeletal structures in terrestrial tetrapods, not only in terms of locomotion but also for its overall interactions with the environment, suggesting that complex selective pressures would have acted upon its morphology. Non-avian dinosaurs provide an excellent opportunity to study manus shape evolution, due to their wide range of body sizes, stances, ecological niches, and putative behaviors. Their ancestral bipedal bauplan allowed diverse morphologies and inferred hand functions to evolve, but multiple independent reversions to quadrupedality imposed some shared mechanical constraints.

Here, I present the first study on metacarpus morphospace evolution in non-avian dinosaurs using two-dimensional geometric morphometrics. Photographs and published figures of metacarpals in dorsal view were obtained for 92 taxa, representing all major non-avian dinosaur lineages including early diverging and deeply nested examples from Sauropodomorpha, Theropoda, and Ornithischia. Shape variation of the individual metacarpals was quantified using a combination of four landmarks and four curves of 50 sliding semilandmarks along the medial, lateral,

proximal, and distal surfaces. Generalised Procrustes Analysis and phylogenetically informed Principal Component Analysis (PCA), MANOVA, and analyses of disparity and evolutionary rates were conducted in R using the packages *geomorph*, and *phytools*.

The first axis of the PCA explained over 74% of the variation, separating taxa with longer and more slender metacarpals from those with shorter shafts and proportionally wider proximal and distal ends. PCA indicates some clustering between clades, as well as identifying extreme morphologies, such as the reduced metacarpals in derived abelisaurids (e.g., *Majungasaurus*). Each major clade occupies distinct areas of morphospace, with some overlap between basal sauropodomorphs, thyreophorans, and ceratopsians. Surprisingly, we did not observe substantial differentiation between bipedal and quadrupedal taxa. However, our results suggest two quadrupedal morphotypes, in the form of the stout metacarpals in thyreophorans, ceratopsians, and some basal sauropodomorphs (e.g., *Ingentia*), compared to longer, slender elements in sauropods and hadrosaurs. In the evolution of both sauropodomorphs and ornithopods there is a clear progressive development and convergence toward a more ‘columnar’ manus structure.

**Funding Sources** Natural Environment Research Council Doctoral Training Partnership (London NERC DTP) grant NE/L002485/1, UCL Bogue Fellowship, Jurassic Foundation grant.

### Paleozoic Tetrapods & Lissamphibians

#### TOMOGRAPHY OF A TANTALIZINGLY TINY TIKTAALIK-LIKE TAXON

Lemberg, Justin B.<sup>1</sup>, Stewart, Thomas A.<sup>1</sup>, Daeschler, Edward B.<sup>2</sup>, Shubin, Neil H.<sup>1</sup>

<sup>1</sup>Department of Organismal Biology and Anatomy, University of Chicago, Chicago, Illinois, U.S.A., <sup>2</sup>Department of Vertebrate Zoology, Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania, U.S.A.

The elpistostegalian stem-tetrapod *Tiktaalik roseae* is known from a single locality (NV2K17) within the Fram Formation of Ellesmere Island, Nunavut Territory, Canada. Specimens from this locality represent subadult to adult specimens, including specimens up to 61% larger than the holotype specimen (NUFV 108) and reaching an estimated 3 meters in length. Here we present fossil material of a much smaller elpistostegalian specimen (NUFV 137) from a second, slightly older locality within the Fram Formation on Ellesmere Island (NV0401), possibly representing a juvenile *T. roseae* specimen or a new taxon. Preserved remains of NUFV 137 include fragmentary lower and upper jaws, gular plates, fragments of the rostrum, articulated body scales, articulated pectoral fin elements, and several other currently unidentified endoskeletal

pieces. Micro-computed tomography ( $\mu$ CT) data of the lower jaws enable precise anatomical reconstruction and morphometric comparison of the anterior portion of the character-rich lower jaws. Linear proportions between homologous landmarks of lower jaws of NUFV 137 and NUFV 108 suggest an animal approximately 61% smaller than the holotype of *T. roseae*, and, with a reconstructed total jaw length of approximately 12.4 cm, NUFV 137 is similar in size to one of the smallest known elpistostegalian taxa (*Rubrognathus kuleshovi*). If NUFV 137 represents a juvenile *T. roseae* individual, it would expand the known size range of *T. roseae* specimens, with implications for understanding allometric growth in a tetrapodomorph taxon. While lower jaw characters appear to be similar to those in *T. roseae*, it is uncertain if some features, such as a posteriorly displaced postsplenial pit line, reduced adsymphyseal dentition, and varying postcranial proportions, are the result of differences in ontogeny or warrant a separate taxonomic grouping. These differences, and the presence of a potential operculum, indicate NUFV 137 might represent a distinct but similar, *Tiktaalik*-like taxon.

**Funding Sources** Funding for this project comes from The Brinson Foundation, the Academy of Natural Sciences, The University of Chicago, and The National Science Foundation.

## Education & Outreach

### ACTIVE LEARNING AND STEAM IN PALEONTOLOGY: CASE STUDIES WITH NEURODIVERSE ADULTS AND FEMALE-IDENTIFYING K–12 STUDENTS

Lepore, Taormina J.<sup>1</sup>, Lepore, Katrina<sup>2</sup>, Taylor, Larry<sup>1</sup>, Scharnagl, Anna<sup>3</sup>, Muskelly, Cameron<sup>4</sup>

<sup>1</sup>Museum of Paleontology, University of California Berkeley, Berkeley, California, U.S.A., <sup>2</sup>Communitas, Woburn, Massachusetts, U.S.A., <sup>3</sup>Integrative Biology, University of California Berkeley, Berkeley, California, U.S.A., <sup>4</sup>Paleontology Association of Georgia, Duluth, Georgia, U.S.A.

Active learning places the student at the center of the learning process, emphasizes student choice, and allows learner agency in determining learning goals as well as learning methodologies. As K–12 classrooms, museums, and university lecture halls continue to champion active learning, paleontology education provides an accessible window into hands-on science education and inquiry-based learning that has the potential to reach underserved audiences with strong science interests. Here we highlight two case studies utilizing art and hands-on creation of fossil educational materials by the learners, with best practices for implementing self-advocacy and active

learning techniques. In case study 1, neurodiverse adults at a life skills day program assisted in the curation of a small in-house museum exhibit with fossil casts and exhibit tags, and produced plaster cast pieces during an additional project activity. Augmented reality was also utilized to enhance exhibit accessibility for non-verbal and reading impaired individuals, and participant feedback was elicited to determine best practices for effective museum environmental conditions that can assist these learners, such as low ambient lighting and touch displays. In case study 2, female-identifying K–12 students attended a one-day workshop on the intersection of art and paleontology, where participants examined fossil specimens and produced canvas art pieces of the fossil material. Learners here were guided in open-ended inquiry to step into the role of a paleontologist and create a record of their learning they could take home with them, to continue inspiring their pursuit of science. In both case studies, active learning pedagogy and self-advocacy was emphasized. With simple, adaptable steps, these techniques can be implemented in a wide variety of paleontology education environments, from the online to the hands-on classroom, and can ultimately foster greater inclusion for diverse audiences in our field.

**Funding Sources** Funded by Associated Students of the University of California (ASUC) via the Expanding Your Horizons program; gender-inclusion training provided by TechBridge Girls, Inc.

## Symposium: Paleoneurology

### TRIGEMINAL NERVE BRANCHING PATTERNS REVEAL DIVERSITY AND EVOLUTION OF FACIAL SENSITIVITY AMONG ARCHOSAURS

Lessner, Emily, Holliday, Casey  
University of Missouri, Columbia, Missouri, U.S.A.

Vertebrates evolved numerous types of integumentary sensory systems, many of which enhance facial somatosensation. Species with sensitive faces exhibit high densities of trigeminal nerve-innervated receptors at the ends of nerve branches that course through bony canals and foramina in the face and mandibles. These bony features of the trigeminal system are often used to infer facial sensation in extinct vertebrates. However, the form and function of the trigeminal system are diverse in extant reptiles, and its physiological significance and phylogenetic patterns are unclear. Extant reptiles display morphological diversity in proximal (i.e., trigeminal fossa contents and trigeminal division pathways), intermediate (i.e., inferior alveolar canal neurovasculature and its relation to teeth and integument), and distal structures (i.e., symphyseal neurovasculature and bill-tip-organs). These structural differences are reflected in the behavioral

diversity (e.g., lingual vs. jaw prehension in squamates, tactile-feeding in birds) across Sauropsida. Using CT data, we performed morphometric analyses of the inferior alveolar canal of several extant sauropsids to build a robust phylogenetic bracket for extinct archosaurs. We employed a novel quantitative method to compare inferior alveolar canal branching patterns and found a more complex arrangement in crocodylian inferior alveolar canals in comparison to most other reptiles, suggesting reduced ability for mandibular sensation in non-crocodylian taxa. By employing the same techniques to investigate extinct taxa including pseudosuchians (*Araripesuchus*, *Simosuchus*, *Junggarsuchus*) and non-avian dinosaurs (*Tyrannosaurus*, *Majungasaurus*, *Acristavus*), we reveal significant diversity in trigeminal nerve distribution and thus facial sensation in extinct archosaurs. Comparisons show similar branching patterns between dinosaurs and terrestrial pseudosuchians indicating similarity in sensory behaviors in these taxa. Additionally, there is an increase in branching complexity along the pseudosuchian line, corresponding with a transition from terrestrial to semi-aquatic environments and the appearance of tactile-feeding in the clade. Overall, these findings assist in reconstruction of soft tissues from osteological correlates in fossil taxa and will help uncover patterns of reptilian somatosensory ecology and evolution.

**Funding Sources** Life Sciences Fellowship Program, National Science Foundation; Jurassic Foundation; Evolving Earth; Animal Behavior Society; American Ornithological Society; Paleontological Society.

### **Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

#### **THE FIRST RECORD OF *HOMOTHERIUM* FROM MCFADDIN BEACH, TEXAS**

Lewis, Patrick J.<sup>1</sup>, Moretti, John<sup>3</sup>, Flores, Mary D.<sup>1</sup>, Godwin, William<sup>4</sup>, Bell, Christopher J.<sup>3</sup>, Dickinson, Edwin<sup>2</sup>, Hartstone-Rose, Adam<sup>2</sup>

<sup>1</sup>Biological Sciences, Sam Houston State University, Huntsville, Texas, U.S.A., <sup>2</sup>Department of Biological Sciences, North Carolina State University, Raleigh, North Carolina, U.S.A., <sup>3</sup>Jackson School of Geosciences, The University of Texas, Austin, Texas, U.S.A., <sup>4</sup>Sam Houston State University Natural Science and Art Research Center, Sam Houston State University, Huntsville, Texas, U.S.A.

The McFaddin Beach locality (MB) spans about 20 miles of the Texas Gulf Coast in Jefferson County. Remains of Pleistocene vertebrates accumulate on MB from submerged but unknown primary depositional settings on the continental shelf. Those deposits formed part of a poorly known, broad extension of the Gulf Coastal Plain during periods of lower sea level in the Pleistocene. The

fauna that washes ashore at MB includes *Bison*, *Canis dirus*, *Equus*, *Camelops*, *Mammut*, and *Mammuthus*, supporting assignment to the Rancholabrean mammal age, which maximally extends from approximately 200 to 9.5 ka. *Panthera onca* and *Smilodon fatalis* also are documented at MB, although other felids are absent. Although the fauna has been documented since the 1970s, recent work on the collection housed at Sam Houston State University, including specimens donated from private collectors, added to the known taxonomic list for the locality. Here we present a specimen preliminarily identified as a subadult *Homotherium* (SHSU-1-00155). The specimen consists of several fragmentary incisors and a portion of the right canine embedded in fragments of the premaxilla and maxilla. Although the teeth are adult, the degree of their eruption suggests the specimen is a subadult. The tip of the canine is missing, with the rest of the crown unerupted and completely within the alveolus. Although a surface examination of the fossil itself did not detect any diagnostic characters, a microCT scan of the specimen revealed diagnostic anatomical details of the canine. The size and sharp taper of the canine are similar to *Homotherium* and distinguish the MB specimen from other Rancholabrean felids. The specimen of *Homotherium* from MB extends the range for this taxon in Texas, where it is primarily known from localities in central and western parts of the state. The presence of *Homotherium* at MB also adds another apex predator to the Pleistocene coastal plain of Texas, refining our understanding of this ecosystem. Continued comparison of the specimen with other known taxa should provide greater confidence in its identification.

### **Fishes & Chondrichthyans: Evolution & Distribution**

#### **A NEW CHONDRICHTHYAN FAUNA FROM THE ZHUGANPO MEMBER OF THE FALANG FORMATION AT NIMAIGU SECTION, GUIZHOU PROVINCE, SOUTH CHINA**

Li, Jiachun<sup>1</sup>, Sun, Zuoyu<sup>1</sup>, Gilles, Cuny<sup>2</sup>, Jiang, Dayong<sup>1</sup>  
<sup>1</sup>earth and space sciences, Peking university, Beijing, China, <sup>2</sup>Laboratoire d'Ecologie des Hydrosystèmes Naturels et Anthropisés, University Claude Bernard Lyon 1, Lyon, France

The Middle-Late Triassic succession of the Nimaigu Section (Wusha area, Xingyi City, Guizhou Province, South China) has yielded two exceptionally well-preserved marine vertebrate faunas, i.e., the Middle-Late Ladinian Xingyi Fauna and the overlying younger Carnian Guanling Biota, of which the former shows turnover of marine reptiles from coastal to oceanic environments. Herein, we report a newly discovered chondrichthyan fauna strata intermediate between the above-mentioned vertebrate faunas. This chondrichthyan assemblage consists of one new genus of stem Synchodonyiformes (neoselachian),

one new genus closed to *Omanoselache* (hybodont shark), aff. *Arctacanthus* (chimaeroids?), and some shark genera showing Paleozoic affinities.

The new genus of stem Synchodonyiformes possesses a double-layered enameloid made of Single Crystallite Enameloid (SCE) and Parallel-Bundled Enameloid (PBE) and represents the first definitive record of a neoselachian shark from the Chinese Mesozoic so far. Another species is similar to *Acrodus* aff. *spitzbergensis* that was previously recorded from the Triassic of Japan, and which is certainly related to *Omanoselache*. The classification of *Arctacanthus* is still problematic because of its peculiar morphology. Several teeth display a cladodont crown with intermediate lateral cusplets and outermost accessory cusplet, which would suggest affinities with Paleozoic genera although this needs further investigation.

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### Dinosaur Systematics, Diversity & Ecology

#### A NEW EARLY-BRANCHING TITANOSAURIFORM (DINOSAURIA, SAUROPODA) FROM THE MID-CRETACEOUS OF NORTHEASTERN CHINA

Liao, Chun-Chi<sup>1</sup>, Xu, Xing<sup>1</sup>, Yang, Tzu-Reui<sup>2</sup>

<sup>1</sup>Department of Paleoichthyology and Paleoherpetology, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China, <sup>2</sup>National Museum of Natural Science, Taichung, Taiwan

Titanosauriformes is the largest subgroup of sauropod dinosaurs, which was the most geographically widespread clade that survived to the end of Cretaceous. Despite the abundance of postcranial remains, cranial elements are rarely preserved and thus hinder our further understanding of the titanosauriform evolution. Here we describe a new early-branching titanosauriform dinosaur from the mid-Cretaceous of northeastern China. It resembles brachiosaurid sauropods in the following features: the length of jugal process accounting approximately for one-third of the maxilla, the preantorbital foramen anterior to the antorbital fenestra, the vascular grooves presenting above the alveoli, the alveoli and teeth perpendicular to the ventral margin of the maxilla, and moderate robust maxillary teeth crown; it is similar to somphospondylan sauropods in step-wise transition of the main body of maxilla and the anterior margin of the internal antorbital fossa extending over half of the tooth row. Additionally, it also displays some unique features among sauropods (e.g., sharp transition to internal antorbital fossa and elongated and large subnarial foramen). This new specimen adds to the mid-Cretaceous dinosaur fauna of northeastern China,

and more importantly, provides significant information on the cranial evolution of Titanosauriformes.

### Mesozoic Herpetology

#### A TESTUDINOID TURTLE FROM THE UPPER CRETACEOUS OF NEW MEXICO

Lichtig, Asher J., Lucas, Spencer G.  
New Mexico Museum of Natural History and Science,  
Albuquerque, New Mexico, U.S.A.

A new fossil turtle taxon from the Upper Cretaceous (upper Campanian, ~ 74–75 Ma) Fruitland Formation of the San Juan Basin, northwestern New Mexico, is represented by more than half of the carapace and plastron as well as parts of the limb girdles, cervical vertebrae and maxillary bone. This turtle is distinguished by the lack of a costiform process, significant overlap of the scutes on the visceral side, lack of dorsal ridges, and smaller size (carapace length = 256 mm) than co-occurring baenids. These baenids form the distal portions of their costals late in ontogeny relative to extant turtles, and, at this small size, would still have had large costal fontanelles. The overall shell of the new taxon has a low dome, with the posterior margin of the carapace slightly scalloped. The nuchal is significantly longer than wide, with no costiform process. There is no cervical scute in this individual. A small cephalic emargination of the carapace is present. This turtle has a neural formula of 4-6-6-6-6-6, with the more posterior neural sutures unclear. The peripherals show a musk duct groove on peripheral 2 and possibly on peripheral 7. The plastron is only preserved on the left side, but the anterior and posterior lobes appear to be of similar width. The posterior lobe has an angular end, with a deep caudal emargination. The anal scutes are short, with a posteriorly concave curve near the lateral margin. All of the plastral scutes have a significant lip on the dorsal side of the anterior and posterior lobes. This new turtle does not match any species previously known from the Cretaceous of New Mexico or, to our knowledge, from anywhere else. The testudinoid identity of this material is indicated by the lack of a mesoplastron and costiform process. These missing features suggest the turtle is not a pleurodire, paracryptodire or chelydroid. Furthermore, the overlap of the plastral scutes on the visceral surface of the plastron is typical of testudinoids. This is a significant discovery, as no testudinoids were previously known in strata older than the K-Pa boundary in North America. The new turtle taxon thus suggests that, contrary to previous hypotheses, testudinoids entered North America before the K-Pa boundary.

### Marine Reptile Diversity & Biology

**PHYLOGENY OF THE EOSAUROPTERYGIA  
(DIAPSIDA: SAUROPTERYGIA)  
INCORPORATING RECENT DISCOVERIES FROM  
SOUTH CHINA**

Lin, Wenbin<sup>1</sup>, Jiang, Dayong<sup>2</sup>, Rieppel, Olivier<sup>3</sup>, Motani, Ryosuke<sup>4</sup>, Tintori, Andrea<sup>5</sup>, Sun, Zuoyu<sup>2</sup>, Zhou, Min<sup>2</sup>

<sup>1</sup>Fujian University of Technology, Fuzhou, China, <sup>2</sup>Peking University, Beijing, China, <sup>3</sup>The Field Museum, Chicago, Illinois, U.S.A., <sup>4</sup>University of California, Davis, California, U.S.A., <sup>5</sup>Università degli Studi di Milano, Milan, Italy

During the last two decades, abundant Triassic sauropterygians have been reported from Europe and southwestern China, which greatly improve our understanding of the diversity and stratigraphic, as well as paleogeographic, distribution of Triassic sauropterygians. The phylogeny of Sauropterygia was also repeatedly analyzed with the description of each new species. Except for Placodontia, however, various analyses of sauropterygian interrelationships have yielded incongruent results, especially with regards to the monophyly of Pachypleurosauridae and Eusauroptrygia, which were alternatively supported or rejected by different analyses. The incongruent results of these analyses were probably caused by the implementation of different character codings, based primarily on the same data matrix taken from a global parsimony analysis by Rieppel about 20 years ago, which was based almost exclusively on European material. Since we have a large number of new specimens from the rest of the world, it is high time to reexamine the phylogeny of the entire group, or at least of the eosauroptrygians, in order to assess whether and how the newly described taxa affect overall tree topology.

Given that the ingroup relationships of Placodontia is well established, we herein focus on reanalyzing the interrelationships of Eosauroptrygia, which is the sister clade of the Placodontia within the Sauropterygia. We present a comprehensive phylogenetic hypothesis for Eosauroptrygia based on a cladistic analysis of 137 characters coded for four outgroup and 49 ingroup taxa, including nearly all currently recognized Triassic eosauroptrygian genera. This is the most inclusive phylogenetic analysis of Eosauroptrygia to date.

The new phylogenetic hypothesis of Eosauroptrygia suggests that Pachypleurosauridae is the sister taxon of Eusauroptrygia, and their monophyly as traditionally upheld is reestablished. Furthermore, the monophyly of the genus *Nothosaurus* as traditionally conceived is not supported, whereas the monophyly of *Lariosaurus* is obtained if the lariosaurian affinity of *N. juvenilis*, *N. youngi*, and *N. winkelhorsti* is accepted. In this study, the monophyletic Pistosauroidea excludes *Corosaurus* and *Cymatosaurus*. The latter two genera are found to form a clade that represents the basal-most members of

Eusauroptrygia. The new phylogenetic hypothesis is mostly in good accordance with the stratigraphic distribution of the genera.

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**Fishes & Chondrichthyans: Evolution & Distribution**

**DUE NORTH: NORTHERN EXPOSURES OF  
PACHYCORMIDS EXTEND THE  
BIOGEOGRAPHICAL RANGE OF  
PACHYCORMIDS IN THE LOWER JURASSIC  
AND UPPER CRETACEOUS**

Liston, Jeff<sup>1</sup>, Maltese, Anthony E.<sup>2</sup>

<sup>1</sup>Preservation & Research, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada, <sup>2</sup>Damage, Rocky Mountain Dinosaur Resource Center, Woodland Park, Colorado, U.S.A.

Occupying a key-position within Actinopterygii as part of the Holostei-Teleostei Transition, pachycormids are critical to understanding teleost origins. Arising in an explosive diversification in the Toarcian, pachycormids developed into two recognized tribes of ‘toothless’ (suspension-feeding) and ‘tusked’ (carnivorous) forms, persisting until the end of the Cretaceous. As a group they range greatly in size, across three orders of magnitude, exhibiting a trend of reduced ossification for the skeleton with the increasing adult size of a given pachycormid taxon. One of the consequences of this has been the collection of large numbers of isolated pectoral and caudal fins, particularly in the early nineteenth century by researchers such as Gideon Mantell, working on specimens of *Protosphyraena* in the chalk of the south coast of England. Currently, such specimens tend to be largely ignored in favour of more complete material recovered from deposits of the Upper Cretaceous Western Interior Seaway in the U.S.A., even in review literature.

In spite of this, recent discoveries of similar isolated material have served to extend the northern limit of the range of discoveries. Cretaceous specimens of *Protosphyraena* and *Bonnerichthys* have been found from the Turonian-Santonian of the Canadian Provinces of Alberta, Saskatchewan and Manitoba, as well as the Maastrichtian of Denmark. In addition, a three-dimensionally preserved Toarcian specimen from the Isle of Skye, in Scotland, has produced the most northerly-discovered pachycormid thus far described, as well as expanding the geographic extent of pachycormids during the earliest stage of their fossil record.

Together with the new Upper Cretaceous examples, these specimens serve to expand our understanding of the cosmopolitan dispersal of a group that enjoyed a global

distribution, at the beginning and the end of their stratigraphic range.

### **Fishes & Chondrichthyans: Evolution & Distribution**

#### **POTENTIAL UTILITY OF QUANTITATIVE BODY SHAPE ANALYSIS IN TAXONOMY OF EOCENE CYPRINIFORMS AND IMPLICATIONS FOR EVOLUTION**

Liu, Juan

Integrative Biology, University of California, Berkeley, Berkeley, California, U.S.A.

The oldest skeleton-based fossil cypriniforms (Teleost: Ostariophysii: Cypriniformes) recovered from the Eocene sediments of North America (NA) and East Asia (EA) belong to families Cyprinidae, Catostomidae, and Jianghanichthyidae. They are the principal sources for understanding the early diversity and divergence of the Cypriniformes. However, relatively conserved overall body plan has caused confusion for confident taxonomic assignment. To better understand the early morphological disparity, I conducted body shape analysis on all available Eocene cypriniform specimens. Ninety complete and undeformed specimens (three families, four genera, and 10 species) were captured with scale using surface scanners. Fourteen homologous anatomical landmarks were digitized in TPS dig2, and analyses were performed in R using the *geomorph* package with customized script. First, in the morphospace of PC1 (34.1%) and PC2 (26.6%) from Principal Component Analysis (PCA) on Procrustes shape, members of the three families and taxa from NA and EA occupy different regions with minimum overlap. Second, PCA on Procrustes shape and appended size found similar pattern (PC1 99.66%, PC2 0.11%). Also, Procrustes ANOVA found significant body shape differences between above groups with and without accounting for body size. Third, allometry visualization using common allometric component suggested that growth trajectories of the three families are divergent. Fourth, in the body shape morphospace accounted for phylogeny, projection of the phylogenetic tree shows species of each family are clustered without crossing over, and phylogenetic signal is statistically significant ( $K = 0.7431$ ,  $P = 0.006$ ). Last but not least, Procrustes ANOVA on *Amyzon aggregatum* and *Amyzon gosiutense* show no significant difference on shape only variables, but significant differences after accounting for covariation of shape and size. This finding explains the confusion resulted in their synonymization by using linear measurement and meristic counts only, and support both should be species of themselves. To conclude, quantified and calibrated body shape data are able to identify major groups of Eocene cypriniforms and even some closely related species. The distinctiveness of these three families

in overall body shape, ontogeny trajectories, and significant correlated with phylogeny suggests that there was few homoplasy in body shape characteristics during the early divergence of cypriniforms.

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### **Marine Reptile Diversity & Biology**

#### **DISPARITY OF MOSASAURS IN THE WESTERN INTERIOR SEAWAY AND THE IMPORTANCE OF VARIABILITY TO THE DIVERSIFICATION OF MOSASAURINAE**

Lively, Joshua R.

Environmental Studies, University of Illinois Springfield, Springfield, Illinois, U.S.A.

Filling numerous predatory niches throughout their evolutionary history, mosasaurs were important components to marine ecosystems during the Late Cretaceous. Owing to large sample sizes and high diversity, they are an exceptional system for examining macroevolutionary patterns. In particular, the well-sampled deposits of the Western Interior Seaway (WIS) provide one of the best regional case studies for evolutionary and ecological dynamics within a Cretaceous marine ecosystem. The nature of the mosasaur fossil record here lends itself to the integration disparity and intraspecific variation analyses into a phylogenetic framework.

I examined anatomical diversity for members of the Mosasauridae by building a novel matrix of morphological features, focused on taxa collected from deposits of the WIS. I augmented taxon-character matrices used for phylogenetic analyses with autapomorphic and variable features to more completely quantify changes in disparity through time. I ran principal coordinates analyses and calculated mean pairwise dissimilarity using the R package Claddis. I calculated dissimilarity and 95% confidence intervals in equal-length time bins through the Late Cretaceous for all mosasaurs and for individual sub-familial clades. I used the same metrics to examine intraspecific variation in two particularly abundant taxa from the WIS.

Individual clades of mosasaurs showed statistically significant changes in disparity. Plioplatecarpines exhibited an early peak during the Santonian to earliest Campanian, followed by a significant decrease throughout the rest of the Cretaceous. Within the Mosasaurinae, low disparity through their early evolution was followed by a significant increase during the Campanian, associated with increased taxonomic diversity.

Early members of those two clades exhibited similar levels of intraspecific variation across the entire skeleton. However, the early mosasaurine *Clidastes propython* exhibited significantly higher variation within tooth-bearing elements. Temporally and phylogenetically, that homoplasy preceded an increase in disparity in those elements in later mosasaurines with the origin of taxa such as *Mosasaurus*, *Globidens*, and *Prognathodon*. Variability in the anatomical system associated with prey capture was likely associated with an increased propensity for the Mosasaurinae to diversify taxonomically, morphologically, and ecologically during the last 15 Ma of the Cretaceous compared to other mosasaur clades.

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### Symposium: Dietary Reconstruction

#### APPLYING REFINED CLUMPED AND OXYGEN ISOTOPE TEMPERATURE CALIBRATIONS TO TEETH FROM *T. REX* AND *C. MEGALODON*

Löffler, Niklas<sup>1</sup>, Fiebig, Jens<sup>2</sup>, Mulch, Andreas<sup>1</sup>, Tütken, Thomas<sup>3</sup>, Schmidt, Burkhard C.<sup>4</sup>, Conrad, Anika C.<sup>5</sup>, Wacker, Ulrike<sup>6</sup>, Schulp, Anne S.<sup>7</sup>, Böttcher, Michael E.<sup>5</sup>  
<sup>1</sup>Senckenberg Biodiversity and Climate Research Center, Frankfurt (Main), Germany, <sup>2</sup>Goethe University Frankfurt, Frankfurt (Main), Germany, <sup>3</sup>Johannes Gutenberg University Mainz, Mainz, Germany, <sup>4</sup>Georg-August-University Goettingen, Goettingen, Germany, <sup>5</sup>Leibniz Institute for Baltic Sea Research (IOW), Warnemuende, Germany, <sup>6</sup>Thermo Fisher Scientific GmbH, Bremen, Germany, <sup>7</sup>Naturalis Biodiversity Center, Leiden, Netherlands

Clumped isotope analysis of carbonates has been shown to be a reliable tool for reconstructing marine and terrestrial temperatures with a precision of a few degrees centigrade, independent from the oxygen isotopic composition of the mineralizing fluid. Preliminary results suggested that this thermometer may also be applied to bioapatites to determine body temperatures of extinct vertebrates, even though discrepant  $\Delta_{47}$ - $1/T^2$  relationships were ascertained. The existing (bio)apatite  $\Delta_{47}$  record has therefore been extended ultimately resulting in  $\Delta_{47}$  and  $\delta^{18}\text{O}$  temperature calibrations for (bio)apatite that range from 1 to 80 °C, which facilitates quantitative thermophysiological and paleoenvironmental studies on vertebrates. Here, we present results from applying these calibrations to fossil tooth enamel(oid) from a *T. rex* (66.75 ± 0.75 Ma) and a *Carcharodon megalodon* shark (5.75 ± 0.06 Ma) yielding temperatures and  $\delta^{18}\text{O}_{\text{H}_2\text{O}}$  values that are well in agreement with previous studies. The reconstructed body temperature of the adult *T. rex* specimen (RGM 792.000) falls within the

range of modern endothermic vertebrates of 34 to 44 °C, while the calculated  $\delta^{18}\text{O}_{\text{H}_2\text{O}}$  of the body fluid is in line with previously reported mean surface water  $\delta^{18}\text{O}_{\text{H}_2\text{O}}$  values calculated from Late Cretaceous North American foreland basin sediments.

The reconstructed habitat temperature of *C. megalodon* agrees with previously published mean annual ocean temperatures derived from ecological niche models and furthermore matches the preferred habitat temperature range of its modern analogue, the lamniform great white shark (*Carcharodon carcharias*), of 16 to 22 °C. Additionally, the oxygen isotopic composition of the seawater surrounding the *C. megalodon* is, within error, indistinguishable from Miocene to Pliocene seawater- $\delta^{18}\text{O}$ . The fact that consistent and reasonable temperatures and  $\delta^{18}\text{O}_{\text{H}_2\text{O}}$  values can be reconstructed on fossil tooth enamel(oid) from the Miocene and Cretaceous corroborates the potential of coupled oxygen and clumped isotope analyses on tooth enamel(oid) for paleontological studies on vertebrates.

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### Late Cenozoic Mammalian Macroecology & Macroevolution

#### NEW INSIGHTS INTO THE PHYLOGENY OF EARLY MUROID RODENTS

López-Antoñanzas, Raquel<sup>1</sup>, Peláez-Campomanes, Pablo<sup>2</sup>, Prieto-Marquez, Albert<sup>3</sup>  
<sup>1</sup>FORME, Université de Montpellier-CNRS, Montpellier, France, <sup>2</sup>Palaeobiology, Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain, <sup>3</sup>Paleobiology, Instituto Catalán de Paleontología Miguel Crusafont, Cerdanyola del Vallés, Spain

Muroid rodents are one of the most evolutionarily successful clades of mammals. Increasing interest in muroids has resulted in the publication of molecular phylogenies of living species. However, no attempt has been made to build phylogenies using characters of extinct representatives. We performed a cladistic analysis to shed light into the interrelationships of extinct species of murid and cricetid rodents. Preliminary results recover two large clades corresponding to Muridae and Cricetidae (mainly Cricetodontinae). The basalmost murid is '*Myocricetodon sivalensis*' from the middle Miocene of Pakistan. Further from the base of Muridae are the two species of *Dakkamyoidea*, which form together the sister group to the clade that includes all the remaining murids. The latter is composed of two speciose lineages: *Mellalomys-Zramys-Aisamys* on one side and a clade that comprises the Myocricetodontinae, *Dakkamys*, *Paradakkamys*,

*Progonomys*, and *Antemus* on the other. The latter lineage, which would eventually give rise to gerbillines and murines, divides into two clades: *Myocricetodon*, *Abudhabia bayunensis*, '*Paradakkamys*' *ouaichi* and *Dakkamys*, *Paradakkamys*, *Potwarmus*, *Progonomys*, *Antemus*. Gerbillines would originate from the first clade, which is fully African, whereas murines root in the second one, the most derived species of which are Asian. In Cricetodontinae, the basalmost taxon is *Cricetodon versteegi* from the lower Miocene of Turkey. *C. goklerensis* is one node up in the clade. It is sister species to a large group that includes *Deperetomys* at the base and an array of more derived cricetodontines. The latter presents two main branches. One is mostly represented by plesiomorphic species of *Cricetodon* from Asia, which provide evidence for an early Miocene dispersal from China towards Turkey and Greece. The other branch is constituted by all the more derived species of *Cricetodon*, which are mostly European. This lineage splits to give rise to *Byzantinia* and *Hispanomys* during the middle Miocene. The bifurcation in which *Hispanomys* originated includes the late middle Miocene species of '*Cricetodon*' from Central Europe ('*C.*' *fandli*, '*C.*' *klariankae*, and '*C.*' *venczeli*), which should be considered as belonging to *Hispanomys*. Similarly, the bifurcation from which *Byzantinia* evolved contains the middle Miocene '*Cricetodon*' *hungaricus*, '*C.*' *cariensis*, '*C.*' *candirensis*, and '*C.*' *pasalarensis* basally, which are reinterpreted as plesiomorphic representatives of *Byzantinia*.

## Fishes & Chondrichthyans: Evolution & Distribution

### REGIONALIZATION OF THE VERTEBRAL COLUMN IN RAY-FINNED FISHES

López-Arbarello, Adriana<sup>1</sup>, Maxwell, Erin E.<sup>2</sup>

<sup>1</sup>Department of Earth- and Environmental Sciences, Paleontology & Geobiology, Ludwig-Maximilians-University, Munich, Germany, <sup>2</sup>Staatliches Museum fuer Naturkunde Stuttgart, Stuttgart, Germany

The differentiation of five morphofunctionally distinct regions in the vertebral column has been considered to be exclusive to tetrapods; only abdominal and caudal regions have been widely acknowledged in actinopterygian fishes. However, defining these regions has been problematic. Many authors interpret the first caudal vertebra to be the first vertebra with an ossified hemal arch, while others consider the first caudal vertebra to be the first vertebra bearing a hemal spine. The first hemal arch and spine occur in the same vertebra in many actinopterygians, but this is not always the case: in many groups, the distinction between abdominal and caudal regions is blurred by the presence of one or more vertebrae with mosaic or

transitional morphologies. The recognition of these transitional vertebrae, as well as of specializations such as the Weberian vertebrae in ostariophysans, has led to the identification of three to six morphologically distinct regions in different teleost groups. However, little has been done to understand patterns of regionalization in the various actinopterygian lineages and their evolutionary implications.

We explored patterns of regionalization in fossil ray-finned fishes, and distinguished six to eight vertebral regions in early teleosts, holosteans, and some non-neopterygian actinopterygians (*Pteronisculus*, *Australosomus*, *Birgeria*, saurichthyids, coccolepidids, acipenseriforms). Our survey recognizes emergent morphological traits that define a basic pattern of six vertebral regions in the axial skeleton of ray-finned fishes: a postoccipital region with morphologically distinct neural arches and/or spines and lacking the hemal canal; an abdominal region with ribs and lacking the hemal canal; a transitional region in which an open or closed hemal canal, ribs, or infrahemals are present; a caudal region in which a closed hemal canal and hemal spines are present; and two regions associated with the caudal fin, a preural region with a closed hemal canal, and hemal and neural spines modified to stiffen the tail, and a ural region in which the neural arches and/or spines are modified or absent. Both additional differentiation and de-differentiation occurred in different lineages, most likely in response to different selective pressures. The enormous plasticity of the axial skeleton in actinopterygians is probably underpinned by the conserved capacity to generate morphologically disparate regions in Osteichthyes.

**Funding Sources** The research is supported by the German Research Foundation (DFG).

## Symposium: Dietary Reconstruction

### DISCRIMINATING DENTAL MICROWEAR TEXTURES OF DIFFERENT SEED EATERS: PERSPECTIVES FROM A CONTROLLED FEEDING STUDY WITH PIGS

Louail, Margot<sup>1</sup>, Ferchaud, Stéphane<sup>3</sup>, Souron, Antoine<sup>2</sup>, Walker, Axelle E.<sup>1</sup>, Merceron, Gildas<sup>1</sup>

<sup>1</sup>PALEVOPRIM UMR 7262, CNRS and University of Poitiers, Poitiers, France, <sup>2</sup>PACEA UMR 5199, CNRS and University of Bordeaux, Pessac, France, <sup>3</sup>GenESI UE1372, INRAE, Rouillé, France

The thick enameled, bunodont tooth morphology shared by most early hominins has traditionally been interpreted as an adaptation to durophagy, especially in the cranio-dentally robust genus *Paranthropus*. However, subsequent work using dental microwear textures (DMT) and isotope compositions have challenged this hypothesis,

demonstrating contrasting patterns between eastern and southern African *Paranthropus*. Among various hypotheses proposed to explain these contrasting patterns, the ingestion of dust with food and the occasional consumption of hard seeds have received considerable attention. However, without an experimental baseline using taxa with bunodont, thick-enameled cheek teeth, it has proven difficult to interpret DMT of early hominins.

In recent years, studies have shown that DMT can reflect subtle dietary differences in extant taxa, and controlled-feeding experiments permit investigation of the effects of specific resources on DMT. Here, we investigate whether variations in DMT reflect the consumption of different types of seeds in bunodont mammals with similar overall diets. Seeds differ in terms of physical and mechanical properties, and consumption of different seeds may lead to different DMT patterns. Therefore, we conducted trials at the experimental unit GenESI from the INRAE (Vienne, France) on domestic pigs (*Sus scrofa*). We studied four groups: one fed with 100% wheat and soy flours (n = 6), and three fed the same flours supplemented with either 30% barley seeds (n = 5), 20% maize kernels (n = 6) or 10 unshelled hazelnuts per day (n = 6). Pigs were fed daily from about 2 to 8 months of age and received their dedicated diet for at least 75 days before death, except pigs fed with hazelnuts who received them only the last month. We analyzed DMT on crushing and shearing facets of upper/lower first molars, and on upper fourth deciduous premolars. Using a standardized surface sampling strategy, we performed PCA and ANOVAs to detect significant differences between dietary groups. Although it has recently been argued that microwear textures are barely influenced by the hard tissues of plants, our results show that the groups exhibit significant variations in DMT depending on the type of seeds consumed. Moreover, although crushing facets are mostly considered in DMT analyses on hominins because they are thought to be more discriminant, we show that combining both types of facets improves the dietary discrimination on molars, but not on upper deciduous premolars.

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## **Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

### **COMPARING THE FUNCTIONAL ECOLOGY AND TAPHONOMIC DIFFERENCES BETWEEN HOLOCENE AND MODERN NORTH AMERICAN MAMMALIAN COMMUNITIES ACROSS THE TRANSITION BETWEEN FOREST AND PRAIRIE BIOMES**

Loughlin, Nora, Fox, David L.

Department of Earth and Environmental Sciences, University of Minnesota, Minneapolis, Minnesota, U.S.A.

We compare fossil mammalian communities in the midwestern U.S.A. to modern counterparts to examine differences in functional ecology between Holocene and modern ecosystems. This functional approach may provide a more nuanced understanding of changes in mammalian communities since the last glacial maximum than a strictly taxonomic approach. We used correspondence analysis (CA) to compare three functional variables of fossil mammalian communities to those of modern ones in the same region. Our dataset consists of 72 Holocene sites that span the transition between forest and prairie biomes. These sites were selected because their taxonomic structure analyzed in a previous study suggested taphonomic size bias may obscure ecological differences in ordinations of the data. Taxon lists for each site were aggregated into 100 km<sup>2</sup> grid cells to compare with corresponding lists of modern species in each of the 25 grid cells. We then performed CA in R to ordinate the modern species frequencies in each grid cell in three categorical functional variables: body size (categorized by log<sub>10</sub> of body mass in grams, ranging from sizes 1 to 6), diet (carnivores, herbivores, granivores, omnivores, terrestrial insectivores, aerial insectivores, and aquatic faunivores), and locomotor mode (terrestrial, scansorial, arboreal, flying, semifossorial, fossorial, and semiaquatic); fossil sites were projected into this ordination. Controlling for taphonomic differences in the abundance of small mammals (specifically bats) in fossil and modern grid cells, the fossil grid cells are distinct from the modern grid cells in the ordination space due to a higher proportion of larger body size categories in the fossil sites. Although the majority of the mammal species in the fossil dataset also occur in the corresponding modern dataset, those absent from the modern grid cells tend to be relatively large, such as *Taxidea taxus* (size 4) or *Cervus elaphus* (size 6). This suggests potential ecological differences between the fossil and modern communities, as well as a possible taphonomic size bias. Grid cells in modern forest and prairie biomes are distinct in the ordination based on locomotor mode (forest communities have a higher proportion of arboreal and scansorial species), and savanna grid cells are intermediate. Our results suggest ecological differences may lurk in taxonomically similar Holocene faunas and that these differences may reflect subtle changes in habitats through time.

## **Late Cenozoic Mammalian Macroecology & Macroevolution**

### **MAMMAL RICHNESS AND TECTONIC HISTORY OF THE BASIN AND RANGE SINCE 36 MA**

Loughney, Katharine M.<sup>1</sup>, Badgley, Catherine<sup>1</sup>, Bahadori, Alireza<sup>2</sup>, Holt, William E.<sup>2</sup>, Rasbury, E. Troy<sup>2</sup>  
<sup>1</sup>Ecology & Evolutionary Biology, University of Michigan, Ann Arbor, Michigan, U.S.A., <sup>2</sup>Geosciences, Stony Brook University, Stony Brook, New York, U.S.A.

The fossil record of western North America is marked by high mammal-species richness during the Neogene and coincided with significant tectonic activity in the region. Widespread extension in western North America since the Oligocene created the numerous basins of the Basin and Range physiographic province. The fossil record from many of these basins shows high mammal richness over an interval of rapid areal extension, including a peak in species richness at ~16 Ma. A possible scenario contributing to high richness is that high rates of extension led to increased sediment accumulation, thick stratigraphic sequences, and increased fossil burial. Thus, the observed patterns of mammal richness may be the result of increased sediment and fossil accumulation over broad areas of high accommodation due to regional extension.

In order to test whether mammal richness is linked to the timing of basin development, we compiled records of 161 mammal-bearing lithostratigraphic units deposited in western North America since 36 Ma from the Macrostrat database and literature sources. For the Basin and Range region, we calculated mammal-species richness per 0.5 million-year intervals and compared it to changes in stratigraphic thickness, sediment-accumulation rate, and extensional deformation rates. We found that mammal richness patterns are correlated with the number and thickness of lithostratigraphic units, but deformation rate and deposition of the fossil record are decoupled. Average deformation rates in the Basin and Range increase substantially after 30 Ma but decline prior to the mid-Miocene peak in mammal richness. The number and thickness of fossiliferous lithostratigraphic units increase after deformation rates decline. An ~8 million year offset between intervals of high deformation and increased richness may relate to the type of sedimentary environments forming in extensional basins: syn-extensional deposits typically do not preserve mammal remains, whereas post-extensional deposits have high preservation potential. This regional pattern is similar to the pattern of fossil occurrence documented for individual extensional basins. Regional patterns of Neogene mammal richness in the Basin and Range are linked to its tectonic history and may stem from the history of deposition and fossil preservation occurring in individual basins.

**Funding Sources** This work was funded by National Science Foundation Integrated Earth Systems grant No. 1814051.

## Cenozoic Herpetology

## **CARDICHELYON SP., A NEW TESTUDINOID MORPHOTYPE FROM THE PALEOCENE (PUERCAN–TORREJONIAN) OF NEW MEXICO**

Lucas, Spencer G., Lichtig, Asher J.  
New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, U.S.A.

Several new specimens of *Cardichelyon* from the Nacimiento Formation of the San Juna Basin, northwestern New Mexico, demonstrate the presence of this taxon in the earliest Paleocene (Puercan-Torrejonian) of New Mexico. Two of these specimens (NMMNH [New Mexico Museum of Natural History and Science] P-44640 and P-44641) were found articulated, one on top of the other, and differ slightly in their morphology. The concave plastron of the upper shell can be explained two ways, either as sexual dimorphism or (less likely) as a diagenetic feature of the upper shell. This may indicate that a pronounced sexual dimorphism was present in this species. These specimens also include a fragmented specimen with most of the cervical vertebrae and limb bones intact. This specimen has a femur of morphology similar to that associated with an aquatic habitus in past studies. Another specimen (NMMNH P-54991) includes an articulated skull with an associated shell and other postcrania, which reinforces the testudinoid affinities of this turtle. Thus, this skull has reduced frontals and enlarged prefrontals and parietals similar to those of *Platysternon*. The premaxilla has a pronounced hook, and the triturating surfaces are broad. Finally, a juvenile specimen (NMMNH P-54625) with a morphology similar to the adult specimens and a nearly complete plastron demonstrates that the *Platysternon*-like shape of the plastron persists through ontogeny. Together, these specimens significantly add to our knowledge of the morphology of these early testudinoids. They also indicate that the original suggestion of emydid or platysternid affinities of *Cardichelyon* is well supported.

## **Symposium: Dietary Reconstruction**

### **FIRST ENAMEL NITROGEN ISOTOPE DATA OF EARLY HOMININS: TROPHIC LEVEL RECONSTRUCTION OF AUSTRALOPITHECUS IN THE EARLY PLEISTOCENE (STERKFORTEIN MEMBER 4, SOUTH AFRICA)**

Luedecke, Tina<sup>1</sup>, Leichter, Jennifer N.<sup>2</sup>, Duprey, Nicolas<sup>1</sup>, Stratford, Dominic<sup>3</sup>, Vonhof, Hubert<sup>1</sup>, Bamford, Marion<sup>4</sup>, Haug, Gerald<sup>1</sup>, Martínez-García, Alfredo<sup>1</sup>  
<sup>1</sup>Climate Geochemistry, Max Planck Institute for Chemistry, Mainz, Germany, <sup>2</sup>Institute of Geosciences, Johannes Gutenberg University, Mainz, Germany, <sup>3</sup>School of Geography, Archaeology and Environmental Studies, University of the Witwatersrand, Johannesburg, South

Africa, <sup>4</sup>Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa

Dietary change, specifically the incorporation of animal resources, played a major role in the evolution of the hominin lineage, as they are calorie-dense, high-quality foods and their consumption has been linked to brain expansion and other significant adaptations. However, direct evidence for the trophic behavior of our hominin ancestors remains elusive. The earliest signs of meat consumption include crude stone tools and possible cut marks on fossil bones (3.4 to 3.3 Ma). However, their origin and the assumption that *Australopithecus* shaped and used tools prior to the emergence of *Homo* are heavily debated. A better understanding of animal resource consumption by early hominins, such as in the genus *Australopithecus*, is crucial to reconstruct the timing of changes in hominin dietary behavior and to evaluate their position in (paleo) food webs.

Nitrogen isotope (<sup>15</sup>N/<sup>14</sup>N ratio expressed as  $\delta^{15}\text{N}$  value) data reveal information about an individual's position in the food web and is frequently used in conjunction with carbon isotopes (<sup>13</sup>C/<sup>12</sup>C ratio expressed as  $\delta^{13}\text{C}$  value) to reconstruct diet.  $\delta^{15}\text{N}$  values measured in collagen from fossil bone and dentin provide insight into the dietary behavior of species in modern ecosystems and the recent geological past (<120 kyr). However, due to diagenetic alteration, such analyses have been limited to sites with exceptional preservation. Unlike bone or dentin, organic matter in tooth enamel is protected from alteration by its highly mineralized structure, potentially preserving isotopic signals over millions of years, but low organic matter content in enamel has so far prevented N isotope analysis.

Here, we utilize a novel biogeochemical method that allows us to perform high precision  $\delta^{15}\text{N}$  measurements of diagenetically resistant tooth enamel. We present  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  data for ca. 2.6 to 2.2 million year old *Australopithecus* (n = 7) from southern Africa, which represent the first  $\delta^{15}\text{N}$  data measured in any early hominin. Our data indicate a large variation in  $\delta^{15}\text{N}$  values between *Australopithecus* individuals, larger than in the other primate taxa analyzed from Sterkfontein Member 4. The values do not, however, overlap with carnivore  $\delta^{15}\text{N}$  data, pointing to a plant-based diet for these early Pleistocene hominins. These data provide a first glimpse into the trophic behavior of *Australopithecus* and thereby significantly enhance our understanding of hominin dietary diversity.

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### Symposium: Dietary Reconstruction

## DETECTING THE INTRODUCTION OF NON-BREASTMILK FOOD IN INFANTS' DIET THROUGH HISTOLOGICALLY-DEFINED LA-(MC)-ICPMS ANALYSES OF DECIDUOUS DENTAL ENAMEL

Lugli, Federico<sup>1</sup>, Nava, Alessia<sup>2</sup>, Bondioli, Luca<sup>3</sup>, Dean, Christopher<sup>4</sup>, Benazzi, Stefano<sup>1</sup>, Müller, Wolfgang<sup>5</sup>

<sup>1</sup>Department of Cultural Heritage, University of Bologna, Ravenna, Italy, <sup>2</sup>Department of Maxillo-Facial Sciences, Sapienza University of Rome, Rome, Italy, <sup>3</sup>Department of Cultural Heritage, University of Padua, Padua, Italy, <sup>4</sup>Department of Earth Sciences, Natural History Museum, London, U.K., <sup>5</sup>Department of Geosciences, Goethe University Frankfurt, Frankfurt, Germany

The timing and mode of weaning onset have profound implications for fertility rates, maternal energetic investment, immune development, and infant health. Humans wean their offspring before they are able to forage for food by themselves, which is significantly earlier than other primates. It has been suggested that such an early weaning onset results from the high nutritional demand of human brain development during the first years of life.

Such dietary shifts during infancy are recorded within tooth enamel, a rhythmically-growing highly-mineralized tissue that incorporates the chemical and physiological history of an individual. Previous work suggested that enamel registers time-resolved elemental and isotopic data as indicators for diet, mobility, or environmental exposure, besides being relatively resistant to post-mortem diagenetic alteration due to its highly mineralized nature. In particular, due to the passive transport across biological barriers (e.g., mammary gland and placenta), Sr/Ca demonstrated its usefulness as an early dietary transition marker, with human breastmilk representing the lowest accessible Sr/Ca endmember.

Here we showcase how high spatial-resolution elemental and isotopic analysis through laser ablation (multi-collector) inductively-coupled-plasma mass spectrometry (LA-(MC-)ICPMS) is capable of reconstructing both nursing history and first introduction of non-breastmilk foodstuff of an individual at better than weekly time-resolution. After preparing thin ground sections of deciduous teeth, dental enamel Sr/Ca and Ba/Ca ratios in modern and fossil human specimens are measured along the enamel-dentine junction, following enamel growth. In turn, laser tracks can precisely be chronologized through dental histomorphometry by optical microscopy. Moreover, diagenetic proxies (U, REE, Al, Mn) are collected to understand the post-depositional compositional alteration and spatially-resolved <sup>87</sup>Sr/<sup>86</sup>Sr profiles are measured to detect potential mobility of the individual. We will present results of contemporary children with known feeding histories, as well as those of

a unique set of late Neanderthals and Upper Paleolithic modern humans from northern Italy.

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### **Anatomical & Developmental Explorations of the Mammalian Skull**

#### **USING CT SCAN DATA TO DESCRIBE THE WELL-PRESERVED TURBINALS OF THE ADAPIFORM PRIMATE *LEPTADAPIS LEENHARDTI***

Lundeen, Ingrid K.

Department of Anthropology, University of Texas at Austin, Austin, Texas, U.S.A.

Turbinals, small scrolls of bone housed in the nasal fossa, exhibit high degrees of morphological variability among extant primate lineages. Derived increases in ethmoturbinal and frontoturbinal numbers among extant strepsirrhines make it difficult to determine the primitive number of turbinals in crown primates. Furthermore, turbinals rarely fossilize, making establishing the primitive condition by examining fossil data difficult. As such, there is debate over whether four or five ethmoturbinals and one or two frontoturbinals is the primitive condition for primates. To date, fossil primate turbinals have only been reported and described in omomyoid euprimates and stem platyrrhines. Here, I report the first known preservation of turbinates in an adapiform euprimate, *Leptadapis leenhardti* (YPM-011481) from the Eocene Quercy phosphorites of southwestern France. In each nasal fossa, this specimen preserves a nasoturbinal and four well-developed ethmoturbinals with a small fifth ethmoturbinal posteriorly located in the olfactory recess. Sequestered posterolaterally in the frontal recess are two frontoturbinals. The primitive turbinal configuration for crown primates has been argued to be four or five ethmoturbinals and only one frontoturbinal. The configuration of turbinals in *Leptadapis* is then significant first because of the presence of a fifth ethmoturbinal, a condition seen in dermopterans and some extant strepsirrhines but has never before been seen in a fossil primate. Secondly, two frontoturbinals are commonly present amongst extant rodents and non-primate euarchontans but are only present in a few species of extant strepsirrhine primates. The anatomy in *Leptadapis* then corroborates the hypothesis that five ethmoturbinals and two frontoturbinals is the primitive condition in crown primates and was independently lost along multiple primate lineages.

### **Romer Prize**

#### **EVOLUTIONARY RATE ANALYSIS REVEALS DYNAMIC AND VARIABLE PATTERNING OF FORELIMB EVOLUTION ACROSS THE DEEP HISTORY OF SYNAPSIDA**

Lungmus, Jacqueline K.

Univ of Chicago, Chicago, Illinois, U.S.A.

Mammals are noteworthy for their striking ecomorphological diversity in comparison to their non-mammalian synapsid ancestors. However, the lack of a large phenotypic sample coupled with a phylogeny has hindered examination of this characteristic's acquisition. Did this diversity accumulate at a constant pace, or did evolutionary rate vary between clades and elements? Here I present an analysis of phenotypic evolutionary rate for synapsid forelimbs using 2D geometric morphometric data of 1279 fossil elements, and a time-calibrated composite tree of 160 genera. Rate comparisons were made for five radiations ('pelycosaurs', non-cynodont therapsids, non-mammalian cynodonts, Mammaliaformes, Mammalia), and three functional subunits of the forelimb (proximal humerus, distal humerus, ulna). Mammaliaforms were characterized by the highest evolutionary rates for all functional units, followed by therapsids. Both of these groups underwent major ecomorphological diversifications, and the highest rates are found in taxa characterized by specialized forelimb ecologies, such as fossorial dicynodonts (Therapsida) or the semi-aquatic *Haldanodon* (Mammaliaformes).

In all groups the proximal humerus displayed higher rates than the distal humerus, with the highest found in mammaliaforms and therapsids. These groups underwent dramatic morphological change, especially in the glenohumeral joint. Critically though, the ulna displays the highest evolutionary rates across all groups, highlighting the underappreciated role the ulna played in the morphological and functional transformations of the synapsid forelimb. The simplification of the structure likely increased the possibility for expansion into new morphologies and played a key role in facilitating ecomorphological diversification. Overall, therapsids and mammaliaforms can both be characterized by important functional changes to the forelimb that likely played a role in this dynamic.

Phylogenetic signal also varied across the sample, with Pelycosaurs and non-mammalian cynodonts displaying the lowest levels. This in turn reflects these groups' conservative forelimb morphologies, especially compared with other synapsid clades. Together, these results demonstrate that synapsid forelimb evolution should be characterized as a dynamic and complex accumulation of 'mammalian' morphologies. Evolutionary rates varied across taxa and elements as clades adapted their forelimbs

in particular ways to accommodate novel ecologies and functions.

**Funding Sources** NSF DEB-1754502, Field Museum Women-in-Science Graduate Fellowship.

### **Biomechanics & Functional Morphology**

#### **MANDIBULAR ADAPTATIONS IN THE DIETARY DIVERSIFICATION OF THEROPOD DINOSAURS**

Ma, Waisum<sup>1</sup>, Lautenschlager, Stephan<sup>1</sup>, Pittman, Michael<sup>2</sup>, Butler, Richard J.<sup>1</sup>

<sup>1</sup>School of Geography, Earth and Environmental Sciences, University of Birmingham, Hong Kong, Hong Kong, <sup>2</sup>Vertebrate Palaeontology Laboratory, Division of Earth and Planetary Science, The University of Hong Kong, Hong Kong, Hong Kong

The diets of vertebrate animals are known to have changed multiple times across their evolution. Among these, theropod dinosaurs underwent some of the most remarkable dietary shifts in vertebrate evolutionary history. They shifted from ancestral carnivory to more specialized carnivory and to omnivore and herbivory, and even reversed back to omnivory and carnivory in some cases. The mandible serves an important role in food acquisition and likely reflects adaptations to respective feeding modes. However, the functional adaptations of the mandible that accompany theropod dietary shifts remain unclear. Here, we conducted the first comprehensive study on the feeding mechanics of 46 non-avian coelurosaurian theropods using 2D finite element analysis.

We find that carnivorous theropods like dromaeosaurids and tyrannosauroids are less adapted to biting at the anterior tip of the mandible compared to herbivorous theropods like ornithomimosaurians, therizinosaurs, and oviraptorosaurians, as reflected by their less stress-resistant and less bite-efficient mandibles. An overall reduction in feeding-induced stress is identified along all theropod lineages, suggesting a common tendency for structural strengthening of the mandible regardless of diet. Although carnivorous and herbivorous theropod lineages demonstrate post-dentary expansion of the mandible for stress dissipation, different evolutionary pathways are identified in the dentary. Convergent evolution of a more downturned dentary to enhance mandibular stability is observed in derived herbivorous taxa. This is not observed in carnivores, which instead evolved a more speed-efficient mandible with a wavy occlusal margin for predation. Deformation simulations of mandibles from lineages of known herbivorous theropods show that the mandibles of earlier-diverging forms generate 'more downturned mandibles' resembling the mandibles of later-diverging forms in these lineages. This is possibly because the

simulated deformed mandibles tend to be more stress-resistant than the original mandibles.

Our study uncovers the pattern of mandibular adaptations accompanying large-scale dietary shifts in non-avian theropods, which represents a powerful case study for understanding the dietary evolution in other vertebrates.

**Funding Sources** The Paleontological Society; The University of Hong Kong.

### **Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

#### **TOOTH MORPHOMETRIC ANALYSIS CONFIRMS STASIS IN LATE PLEISTOCENE HORSES FROM RANCHO LA BREA**

Machado, Helena

Earth Sciences, University of Oregon, Eugene, Oregon, U.S.A.

The Rancho La Brea tar pits are a well-studied late Pleistocene site with a large abundance of well-preserved fossils, including a great number of horse specimens. The site contains a single equid species, *Equus occidentalis* (sensu Merriam). As each pit corresponds to a distinct time period spanning the different climatic fluctuations of the last glacial-interglacial cycle, several studies have aimed to understand the morphometric responses of different mammals to this climatic change. The felid *Smilodon fatalis* showed static limb bone size, but had different jaw sizes in different pits. The dire wolf *Canis dirus* also had variation in jaw sizes, which correlated with levels of primary productivity. Prior work with limb bones of the *Equus* from La Brea revealed no variation in size among the pits, although a few cases showed significant changes which the authors attributed to a 'random walk' pattern. Within horse evolution, tooth morphology and complexity appear to be related to different feeding strategies, so if there were variation in the teeth of the La Brea *Equus*, it could indicate changes in diet. This work, then, aims to investigate whether the teeth of Rancho La Brea horses remained unchanged like the limb bones or varied among the pits. In addition, this work analyzes a larger number of pits than the prior limb bone analyses which, apart from the analysis of patellae, only included five pits. The current analysis takes into consideration all molars and premolars except third molars and second premolars. It includes 193 lower and 188 upper teeth from 15 and 11 pits, respectively. The analyses consisted of Multivariate Analysis of Variance (MANOVA), Discriminant Function Analysis (DFA) and Cluster Analysis (CA). Results from MANOVA of both upper and lower teeth showed no significant differences among pits. DFA of upper teeth can only correctly identify the pit of 26% of the total horses analyzed, while DFA of lower teeth yields only 21%. CA

analyses for both sets of dentitions indicated no differentiation nor correlation with the pits. The results of this tooth analysis are in accordance with the results of limb bones analyses and showed no differentiation among the pits. *Equus occidentalis*, from Rancho La Brea, appears to show general stasis through the last glacial-interglacial cycle.

**Funding Sources** University of Oregon Baldwin Award and The Functional Trait Resource for Environmental Studies (FuTRES) project.

### **Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

#### **LESTODON DOESN'T WANT YOUR AVOCADO TOAST: DEBUNKING THE DIETARY MYTHS OF THE LATE PLEISTOCENE SLOTHS (MAMMALIA, PILOSA)**

Macias, Melissa A.<sup>2</sup>, McAfee, Robert K.<sup>1</sup>

<sup>1</sup>Biomedical Sciences, PCOM-GA, Lawrenceville, Georgia, U.S.A., <sup>2</sup>Applied EarthWorks, Pasadena, California, U.S.A.

Recent popular press items have claimed a dietary link and historical dispersal of avocados (*Persea*) by the Pleistocene ground sloth *Lestodon*, but with little supporting evidence. A review of those claims and their source demonstrates that the original concept was related to exploring anachronistic flora and the potential megafauna that could have acted as dispersal units, albeit in a vague and hypothetical manner. Ground sloths were never explicitly tied to ingesting avocados, except via a quote from a magazine interview that specifically stated *Lestodon*, which is contrary to the author's original publication. Analysis of the geographic distribution and environment that *Lestodon* occupied shows a preference for high latitudes with cooler and drier climates that are not favorable for *Persea* spp. The *Lestodon* locality data was combined with *Persea* spp. distributions in GIS, and analyzed using potential geographic range predicting software MAXENT. Paleohistory of *Persea* reveals a migration towards lower latitudes as climates cooled, and by the Pleistocene was restricted to the tropical regions, which is far removed from the range of *Lestodon*. The lack of biogeographic overlap between the species, in addition to the feeding ecology that points towards bulk ingestion of grasses by *Lestodon*, makes the likelihood of *Lestodon* being the anachronistic disperser of avocados very unlikely. An analysis of known coprolites from other sloth species shows no evidence of avocado ingestion. Coprolite data for those sloths (e.g., *Nothrotheriops*, *Megalocnus*, *Megatherium*) occurring in the potential overlapping ranges with *Persea* reveal a varied diet, consisting primarily of grasses with the occasional legume or fruit. The dietary range of these

sloths would also seem to exclude avocados as a part of their diet, implying that the role of an anachronistic disperser of *Persea* would have to be filled by some other megafaunal taxon.

### **Symposium: Dietary Reconstruction**

#### **EXQUISITE COMPLEXITIES: RADIOCARBON BOMB-PULSE CHRONOMETRY OF ENAMEL MINERALIZATION AND TOOTH WEAR RATE VARIATION IN INSULAR OVICAPRINES FROM THE SOUTH PACIFIC**

Madden, Richard H.<sup>1</sup>, Buchholz, Bruce A.<sup>2</sup>, Lemberg, Justin B.<sup>1</sup>, Parkes, John P.<sup>3</sup>, Dunn, Regan E.<sup>4</sup>

<sup>1</sup>Organismal Biology & Anatomy, University of Chicago, Chicago, Illinois, U.S.A., <sup>2</sup>Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory, Lawrence, California, U.S.A., <sup>3</sup>Karahapu Consulting, Christchurch, New Zealand, <sup>4</sup>La Brea Tar Pits & Museum, Natural History Museums of Los Angeles County, Los Angeles, California, U.S.A.

Much of the evolution of mammalian tooth shape involves the acquisition of structures to prolong functional longevity and confront abrasive tooth wear. Current theories about the dominant cause of dental wear (mechanical properties of plant foods, concentration of silica phytoliths, amount of ingested soil, or features of gross habitat that relate to rainfall) predict geographic variation in rates of tooth wear. For example, mountain, glacial, and volcanic settings exert a positive influence on the prevalence of hypsodonty among mammals globally, and this prevalence is coincident with the intensity of surface processes that entrain and transport mineral particles into and through the animal's environment.

Here we report progress toward development of a volumetric and chronometric measure of tooth wear rates and its application to feral populations of ovicaprines on islands, where selection pressures are unavoidable (there is no escape) and where variation in tooth wear rates appears to reflect the type and extent of soil exposed at the surface and the intensity of surface processes (including animal behavior) that mobilize and deliver soil into the oral cavity. Daily and annual molar wear rates obtained using 3D volume segmentation of dentine and enamel in microCT image stacks and registration-subtraction of worn on unworn crowns, coupled with AMS <sup>14</sup>C bomb-spike calibration of enamel mineralization at the m1 crown neck (coincident with the onset of wear), are applied to feral goats (*Capra hircus*) on Raoul, Macauley, and Arapawa islands, and sheep (*Ovis aries*) on Campbell Island. Chronometric calibration using bomb-spike radiocarbon help resolve the cause of population differences in rates of linear and volumetric loss of tooth mineral substance and

crown functional life, but interpretation is made difficult by the complexities of the carbon cycle and radiocarbon concentrations peculiar to each island. For example, atmospheric radiocarbon concentrations are believed uniform throughout the southern hemisphere (from local station records and tree-rings), but the contribution of organic carbon from diverse island soils, foliar carbon intake from young and old leaves, and the dissolved organic carbon content of sea-spray blowing onto islands at different latitudes are all potential sources of radiocarbon variation that impact calendar date age calibration of enamel mineralization.

## Mesozoic Herpetology

### ONTOGENY OF *DELTASUCHUS MOTHERALI* (NEOSUCHIA, CROCODYLIFORMES): IMPLICATIONS FOR PALEOECOLOGY AND NICHE PARTITIONING

Maddox, Hannah M.<sup>4</sup>, Drumheller, Stephanie K.<sup>3</sup>, Adams, Thomas L.<sup>1</sup>, Noto, Christopher R.<sup>2</sup>

<sup>1</sup>Witte Museum, San Antonio, Texas, U.S.A., <sup>2</sup>Department of Biological Sciences, University of Wisconsin-Parkside, Kenosha, Wisconsin, U.S.A., <sup>3</sup>Department of Earth and Planetary Sciences, University of Tennessee, Knoxville, Tennessee, U.S.A., <sup>4</sup>Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee, U.S.A.

In crocodyliforms, snout shape and dentition often correlate with different feeding strategies. Broad snout shapes imply a more generalist strategy, where the animal can feed on larger-bodied or hard-shelled prey, blunter snouts are often partnered with anvil-shaped dentition, often associated with durophagy, and narrower snout shapes reflect a feeding strategy focusing on smaller, softer prey items. Snout shape also changes throughout the growth and development of the animal, and therefore, when partnered with accompanying changes in body mass, the niche of a crocodyliform has the ability to shift across its lifetime. The recent identification of at least fifteen individuals attributable to the neosuchian *Deltasuchus motherali*, representing a range of sizes and therefore ages, provides a rare opportunity to explore the shifting dietary niche through growth and development in an extinct crocodyliform taxon. Adult specimens of *Deltasuchus* have a broad, triangular snout paired with sturdy conical teeth, indicative of a generalist feeding strategy. However, juvenile material from *Deltasuchus* has a dental and skull morphology that is less well-suited to this niche. Measurements indicate that the smallest juvenile *Deltasuchus* had a dentary angle of about 20° that widens to around 30° as an adult, and associated juvenile and subadult teeth are notably more slender than those of adult

specimens. This suggests that the juvenile's ecomorphotype was best suited for hunting smaller, softer-bodied prey, such as fish and amphibians, a tendency that is seen in modern groups where rostral and dental shape changes significantly throughout development. This shift in niche has implications for the paleoecology of the Woodbine ecosystem, as *Deltasuchus* shared its habitat with at least three other crocodyliforms that all have different ecomorphotypes. The gracile snout of juvenile *Deltasuchus* would have removed it from direct competition with the small-bodied, blunt snouted crocodyliform *Scolomastax*. With growth and development, the widening snout of *Deltasuchus* transitioned it out of a smaller-bodied niche and into the role of a generalist, apex predator. This differentiated adults of this taxon from other large-bodied, sympatric crocodyliforms: the slender-snouted *Woodbinesuchus* and *Terminonaris*. These findings reveal a complexity to ontogenetic niche partitioning within crocodyliforms that can be masked when only adult morphotypes are taken into account.

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## Macroecology & Macroevolution

### BIODIVERSITY PATTERNS, FAUNAL ENDEMISM, AND THE DINOSAURIAN FOSSIL RECORD IN THE LATE CRETACEOUS WESTERN INTERIOR, U.S.A.

Maidment, Susannah<sup>1</sup>, Mansergh, Robert I.<sup>2</sup>, Dean, Christopher D.<sup>3</sup>, Butler, Richard J.<sup>3</sup>

<sup>1</sup>Department of Earth Sciences, Natural History Museum, London, U.K., <sup>2</sup>Faculty of Health & Medical Sciences, University of Surrey, Guildford, U.K., <sup>3</sup>School of Geography, Earth and Environmental Sciences, University of Birmingham, Birmingham, U.K.

During the Late Cretaceous, the Western Interior, U.S.A., was divided into two landmasses, Laramidia and Appalachia, by the Western Interior Seaway. On Laramidia, large-bodied herbivorous niches were dominated by hadrosaur and ceratopsid dinosaurs. Numerous studies have argued for strong faunal provinciality on Laramidia, particularly in the Campanian, and this endemism is thought to have underpinned ornithischian radiations. However, studies of faunal provinciality have generally been qualitative. We used phylogenetically-corrected Biogeographic Connectedness (pBC), a quantitative method that uses a network approach to assess phylogenetic distances between taxa in different geographic areas, to quantify the degree of faunal provinciality across Laramidia during the Campanian and Maastrichtian. pBC is statistically significantly lower than

randomized datasets for both ceratopsids and hadrosaurs in the Campanian and Maastrichtian, and Campanian pBC is lower than Maastrichtian values, supporting high levels of endemism in the Campanian and slightly lower levels of endemism in the Maastrichtian. However, curves of raw occurrences with latitude for both the Campanian and Maastrichtian correlate strongly and statistically significantly with dinosaur-bearing collections, indicating that faunal endemism is a sampling artifact. Campanian sampling is focused on two latitudes: 51 degrees north, corresponding with the Dinosaur Park Formation of Alberta, and 36–37 degrees north, corresponding with the Fruitland/Kirtland Formation and New Mexico. These two areas have been sampled orders of magnitude better than the surroundings. This sampling bias is caused by higher outcrop area, increased suitability of rock for fossilization, and the possible effects of climate, topography and historical sampling practises that are hard to quantify. The Late Cretaceous Western Interior region represents probably the best-sampled Late Cretaceous ecosystem on Earth, but even in this intensively-sampled area, it is not possible to reconstruct diversity patterns. In order for paleontologists to make a meaningful contribution to ecological hypotheses about the causes of biodiversity patterns, we must focus our efforts on smaller-scale case studies, where temporal resolution is high, stratigraphic correlation is well-established, and where sampling biases can be more easily quantified.

### Fishes & Chondrichthyans: Evolution & Distribution

#### CHONDRICHTHYANS AND OSTEICHTHYANS FROM A TURONIAN–CONIACIAN LAG DEPOSIT BETWEEN THE TOCITO SANDSTONE AND MULATTO TONGUE (MANCOS SHALE), SANDOVAL COUNTY, NEW MEXICO, U.S.A. WITH COMMENTS ON CORRELATIVE LAGS IN THE WESTERN INTERIOR SEAWAY

Maisch, Harry<sup>1</sup>, Becker, Martin A.<sup>1</sup>, Shimada, Kenshu<sup>2</sup>  
<sup>1</sup>Environmental Science, William Paterson University of New Jersey, Wayne, New Jersey, U.S.A., <sup>2</sup>Environmental Science and Studies and Biology, DePaul University, Chicago, Illinois, U.S.A.

A lag deposit between the Tocito Sandstone and Mulatto Tongue of the Upper Cretaceous Mancos Shale in Sandoval County, New Mexico, U.S.A., contains an assemblage of late Turonian–early Coniacian chondrichthyans and osteichthyans. This assemblage consists primarily of isolated teeth that derive from at least 24 taxa including: *Meristodonoides* sp.; *Ptychodus mortoni*; *Ptychodus mammillaris*; *Scapanorhynchus raphiodon*; *Protolamna* sp.; *Cretodus* cf. *C. semiplicatus*; *Cretodus* sp.; *Cretalamna* ‘*appendiculata*’; *Archaeolamna*

cf. *A. kopingensis*; *Squalicorax* cf. *S. falcatus*; *Squalicorax deckeri*; *Squalicorax* sp.; cf. *Paranomotodon* sp.; *Rhinobatos lobatus*; *Ptychotrygon triangularis*; *Pseudohypolophus mcultyi*; *Ischyrhiza mira*; Chondrichthyes indet.; *Micropycnodon* cf. *M. kansasensis*; Pycnodontiformes indet.; Asphidorhynchidae indet.; *Protosphyraena* sp.; and *Enchodus* cf. *E. gladiolus*. The Tocito Sandstone–Mulatto Tongue lag was deposited along a series of outer shoreface and discontinuous sandbars in the southeastern corner of the San Juan Basin during eustatic sea-level fluctuation in the late Turonian–early Coniacian. This sea-level event and the concentration of chondrichthyans and osteichthyans into a lag deposit is also recorded at several other states within the Western Interior Seaway. These stratigraphic properties have correlative potential across basins and states and provide a framework by which regional and eustatic sea-level events can be interpreted. Differences in coeval faunas found within these Turonian–Coniacian lags are bathymetrically controlled, related to the degree of taphonomic reworking, and proximity of the ancestral shoreline.

### Dinosaur Systematics, Diversity & Ecology

#### NEW SPECIMENS OF THE BASAL HADROSAUROID, *PARROSAURUS MISSOURIENSIS*, FROM THE LATE CRETACEOUS OF MISSOURI, U.S.A.

Makovicky, Peter J.<sup>1</sup>, Darrough, Guy<sup>2</sup>, Cullen, Thomas M.<sup>3</sup>, Fix, Michael<sup>4</sup>, Gorscak, Eric<sup>5</sup>, McDonald, Andrew<sup>6</sup>, Saitta, Evan T.<sup>7</sup>, Shinya, Akiko<sup>7</sup>, Stinchcomb, Bruce<sup>8</sup>, Wiersma, Jelle<sup>9</sup>

<sup>1</sup>Dept. of Earth & Environmental Sciences, University of Minnesota, Twin Cities, Minneapolis, Minnesota, U.S.A., <sup>2</sup>Lost World Studios, Cadet, Missouri, U.S.A., <sup>3</sup>Paleontology, North Carolina Museum of Natural Sciences, Raleigh, North Carolina, U.S.A., <sup>4</sup>Physics, University of Missouri–St Louis, St Louis, Missouri, U.S.A., <sup>5</sup>Department of Anatomy, Midwestern University, Downers Grove, Illinois, U.S.A., <sup>6</sup>Western Science Center, Hemet, California, U.S.A., <sup>7</sup>Integrated Research Center, Field Museum of Natural History, Chicago, Illinois, U.S.A., <sup>8</sup>St Louis Community College – Florissant Valley, Florissant, Missouri, U.S.A., <sup>9</sup>Department of Geosciences, James Cook University, Townsville, Queensland, Australia

An articulated tail section of a dinosaur recovered by the Chronister family in 1940 during cistern excavation near Glen Allen, Missouri, was described by C.W. Gilmore and D. Stewart as *Neosaurus missouriense*. Later renamed as *Parrosaurus*, it was subsequently synonymized with *Hypsibema*, a Late Cretaceous hadrosauroid from North Carolina, based on plesiomorphic similarities in caudal

proportions. Bruce Stinchcomb later acquired the Chronister property in order to protect and develop its paleontological significance. Excavations by local volunteers led by Guy Darrough led to the recovery of a partial juvenile skeleton, followed by three excavations in 2017–2018 by the Field Museum, which recovered the skull, forelimbs, and tail of an adult-sized animal. The site, which also preserves abundant turtle and microvertebrate remains, is interpreted as a graben and has been referred to the upper Campanian–lower Maastrichtian Ripley Formation. Although this age is broadly consistent with recovered microvertebrates, more precise chronological controls are needed.

The new material exhibits numerous traits distinguishing it from other Late Cretaceous hadrosauroids, justifying resurrection of the name *Parrosaurus*. A complement of plesiomorphic traits are manifest in the new material relative to other putatively co-eval hadrosauroids, including: small naris; low number of broad dentary teeth with coarse denticles and faint secondary distal ridges; fused carpals; robust metacarpals; and large thumb spikes. A preliminary phylogenetic analysis indicates that *Parrosaurus* represents a non-hadrosaurid hadrosauroid that diverged earlier than the stratigraphically older Appalachian hadrosauroids *Eotrachodon* and *Lophorhothon*, lending support to the prevailing hypothesis that Appalachian dinosaur faunas are assemblages of mostly archaic, endemic lineages evolving in relative isolation from other continental regions. The co-existence of multiple long-lived, distinct lineages of non-hadrosaurid hadrosauroids in the Late Cretaceous of Appalachia stands in marked contrast to the high evolutionary rates and turnover among saurolophine and lambeosaurine hadrosaurids in Laramidia. Whereas the latter diversification pattern among hadrosaurids has been interpreted as driven by major tectonic activity in Laramidia during the Late Cretaceous, the former biogeographic pattern could be characteristic of a combination of isolation and tectonic quiescence.

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### **Biomechanics & Functional Morphology**

#### **FROM BONES TO MOBILITY TO LOCOMOTION: RECONSTRUCTING HIND LIMB POSES IN EXTANT ARCHOSAURS**

Manafzadeh, Armita R., Gatesy, Stephen M.  
Department of Ecology and Evolutionary Biology, Brown  
University, Providence, Rhode Island, U.S.A.

Paleontologists have traditionally reconstructed the locomotion of extinct animals by manipulating their fossil

bones and inferring the mobilities of their limb joints. These range of motion (ROM; i.e., mobility) estimates are most commonly used to eliminate impossible joint poses from potential locomotor sequences. But how well do our best paleontological estimates of ROM actually reflect true joint mobilities? And if we could estimate ROM perfectly, might hindlimb joint mobility be a helpful predictor of locomotor poses?

To address these questions within a comparative framework, we collected data from the hindlimb joints of two living archosaurs: the helmeted guineafowl (*Numida meleagris*) and the American alligator (*Alligator mississippiensis*). Following methods currently used in 3-D virtual estimations of ROM, we estimated the mobility of each joint using CT-derived bone models. Then, we determined each joint's true ROM from marker-based X-Ray Reconstruction of Moving Morphology (XROMM) analyses of manipulations of fully intact cadavers ( $n = 3-4$  for each joint). Finally, we used XROMM to measure thousands of joint poses used during locomotion ( $n = 4-7$  for each joint). We plotted the resulting mobilities and poses for each joint on a 3-D ROM map in cosine-corrected Euler space.

In agreement with previous studies, we found that estimates of ROM based on bones alone substantially overpredict true mobilities. However, even with a generous cartilage allowance, our paleontological estimates failed to include all cadaveric poses for four of the five joints studied. This discrepancy reveals that digitally-derived estimates of ROM do not simply suffer from a lack of soft tissue constraints. Instead, their over-simplified motion assumptions could benefit from an improved methodology that can account for interactions among articular translations and rotations.

Our comparison between cadavers and live animals found that although the true ROM is a poor predictor of the degree of abduction-adduction assumed during locomotion, it is a strong predictor of locomotor excursions in the other two rotational degrees of freedom. Thus, as paleontological estimations of ROM improve and are able to more closely approximate true hindlimb joint mobility, these data have the potential to serve as a valuable line of evidence, rather than just a constraint, in reconstructions of locomotion for extinct ornithomirans.

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### **Evolution & Biology of Non-Avian Theropods**

#### **DETAILED MORPHOLOGY OF THE SKULL AND DENTITION IN A NEW, EXCEPTIONALLY PRESERVED SPECIMEN OF *MICRORAPTOR* (THEROPODA: DROMAEOSAURIDAE) FROM THE EARLY CRETACEOUS OF CHINA**

Maranga, Denise Coleen<sup>1</sup>, Reisz, Robert<sup>3</sup>, Evans, David<sup>2</sup>

<sup>1</sup>Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario, Canada, <sup>2</sup>Royal Ontario Museum, Toronto, Ontario, Canada, <sup>3</sup>Biology, University of Toronto Mississauga, Mississauga, Ontario, Canada

*Microraptor* is a small, four-winged dromaeosaurid known only from the Early Cretaceous deposits of Liaoning, China. *Microraptor* is well-represented in these deposits; however, well preserved craniodental material in *Microraptor* has been lacking. Small dromaeosaurids are commonly represented in microfossil assemblages by isolated bones and teeth because of size-based taphonomic biases. Theropod teeth can be diagnostic; however, due to the lack of high-quality microraptorine tooth-bearing specimens, identification of isolated teeth in microsites is difficult. Here we describe a complete and exceptionally preserved skull of *Microraptor* that includes pristine dentition in both the upper and lower jaws. The recently discovered specimen was collected from the Jiufotang Formation of the Sihedang locality in the western area of Liaoning Province, China. The specimen was completely unexposed in situ and was professionally prepared and documented; as a result, an incredible detail of the cranial anatomy can be observed. The delicate cranial bones retain their shape and are only slightly disarticulated, allowing for the first detailed description of cranial anatomy that is otherwise poorly preserved in the holotype and in other specimens of *Microraptor*. This new specimen preserves a complete dentition, which allows for the analysis of the positional variation of dental morphology within an individual. The premaxillary teeth, of which the second is largest in size, bear no serrations. The maxillary teeth show denticles on the distal carinae and are largest in the middle of the maxilla. The anterior dentary teeth exhibit no serrations. Examination of the posterior dentary dentition reveals the presence of denticles on both the mesial and distal carinae of the posterior dentary teeth, a characteristic that has never been observed in *Microraptor* to date, likely due to poor preservation of the available material. All teeth exhibit a straight crown to root transition, except for the posterior dentary teeth, which show the constriction between crown and root that is typical of *Microraptor*. This newly established range of dental variation in a microraptorine skull helps establish a framework for identifying microraptorine teeth in highly diverse microfossil assemblages in the latest Cretaceous of North America, where skeletons are absent, and will contribute to our knowledge of the presence and diversity of this group leading up to the end Cretaceous extinction event.

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### Permo-Triassic Tetrapods

## NEOMORPHIC OSSIFICATIONS: HISTOLOGICAL INSIGHT INTO THE PREPARIETAL OF DICYNODONT THERAPSID

Marilao, Lianna M.<sup>2</sup>, Kulik, Zoe T.<sup>1</sup>, Sidor, Christian A.<sup>1</sup>  
<sup>1</sup>University of Washington, Seattle, Washington, U.S.A.,  
<sup>2</sup>Oklahoma State University Center for Health Sciences, Tulsa, Oklahoma, U.S.A.

Neomorphic skull bones are rare among tetrapods, appearing only a handful of times. One notable example is the preparietal, which is thought to have evolved three times in therapsids within dicynodonts, biarmosuchians, and gorgonopsians. However, its development and homology are poorly understood. Here, we histologically describe the preparietal in specimens of two dicynodonts: *Diictodon feliceps* and an indeterminate species of *Lystrosaurus*. For both, we made coronal thin sections through the skull roof in the region containing the frontal, the preparietal, and the parietal foramen. It has been noted that the preparietal shape varies substantially in dorsal view, and we found a similar pattern in thin-section. In the *Diictodon* specimen, which likely represents a mature individual, the anterior thin-sections show that the preparietal forms fan-like prongs that embed themselves entirely within the frontal bone. Additionally, there is evidence of an anterior midline suture. In the *Lystrosaurus* specimen, which shows evidence of being a juvenile, there is a well-defined midline suture in the posterior section of the preparietal, but the prongs and midline suture were not present anteriorly. In both taxa, there is an interdigitated suture that is formed between the anterior portion of the preparietal and the underlying frontal and parietal bones. We also found highly vascularized fibrolamellar bone in the posterior sections of the preparietal in both taxa, suggesting rapid growth in the posteroventral direction. Because our data shows these two features present in both taxa, we believe that these are characteristics of the dicynodont preparietal. More histological work will need to be done on gorgonopsians and biarmosuchians to determine if the histological features characterizing dicynodonts are also found in the other groups of therapsids that evolved a preparietal. This future histological work will hopefully be able to test whether these neomorphic ossifications are homologous. The therapsid preparietal can help shed light on the development and evolution of a neomorphic cranial element in the vertebrate fossil record.

### Paleozoic Tetrapods & Lissamphibians

## A COMPLETE, THREE-DIMENSIONAL EARLY PERMIAN ANISTOPOD (TETRAPODOMORPHA) ILLUMINATES THE PHYLOGENY, ONTOGENY AND TERRESTRIALIZATION OF EARLY LIMBED AND LIMBLESS VERTEBRATES

Marjanović, David, Jansen, Maren  
Evolutionary Morphology, Museum für Naturkunde,  
Berlin, Berlin, Germany

A complete, articulated, three-dimensional, and stunningly well-prepared skeleton from the Saar-Nahe basin (western Germany) phenetically resembles *Oestocephalus*, but achieves a lower head-to-body length ratio by possessing more elongate and more numerous vertebrae. Despite the rather young ontogenetic age indicated by size and skull proportions, the shape range of the dorsal scales is that of *Colosteus*, including rhombic scales around the dorsal midline. As in the ‘nectridean’ *Keraterpeton*, the dorsal scales bear microscopic honeycombed sculpture; we also report this in *Oestocephalus*. Such sculpture is also seen on the ventral scales of the new specimen, which are nonetheless as narrow as in other aïstopods. The presence of the braincase and the first complete, undistorted aïstopod palate is confirmed by  $\mu$ CT; hyobranchial bones, endochondral girdles or a tail-fin skeleton are absent. The tail tapers to a point, is not laterally flattened, and the scales do not leave room for a soft-tissue tail fin; no gill slit is apparent in the scale cover behind the head. These indicators of terrestrial life contrast with the mandibular lateral-line canal previously identified in *Coloraderpeton* and suggest that the new specimen, together with the phlegethontiids from the contemporaneous fossil forest floor of Chemnitz (eastern Germany), represents a transition to terrestrial life independent from any crown-group tetrapods. Yet, despite the stem-tetrapodomorph plesiomorphies in the braincase, lower jaw and scales of Aïstopoda, a preliminary phylogenetic analysis of an improved and greatly enlarged dataset finds no support for a whatcheeriid-grade position, and less support for a more crownward colosteid-grade position (as recently proposed) than for an amphibian one. Only *Andersonerpeton*, an isolated lower jaw described as an aïstopod, joins *Densignathus* in the whatcheeriid grade. Redescriptions of additional ‘nectrideans’ and other supposed ‘lepospondyls’ will be needed to resolve this conundrum.

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### Permo-Triassic Tetrapods

### APOMORPHY-BASED IDENTIFICATION OF RECENTLY COLLECTED DINOSAUFOMORPH FOSSILS FROM PETRIFIED FOREST NATIONAL PARK (UPPER TRIASSIC, CHINLE FORMATION)

Marsh, Adam D.<sup>1</sup>, Parker, William<sup>1</sup>, Beightol, Charles V.<sup>2</sup>, Sidor, Christian A.<sup>3</sup>

<sup>1</sup>Science and Resource Management, Petrified Forest National Park, Petrified Forest, Arizona, U.S.A., <sup>2</sup>Vicksburg National Military Park, Vicksburg, Mississippi, U.S.A., <sup>3</sup>Biology and Burke Museum, University of Washington, Seattle, Washington, U.S.A.

The historic interpretation of the dinosauriform record from the Chinle Formation included partial and complete skeletons of coelophysid and herrerasaurid theropods and isolated teeth of ‘fabrosaurid’ ornithischians. Ongoing research occurring in Europe, southern Africa, and North and South America over the last 20+ years has shown that dinosaurs and their closest dinosauriform relatives co-occurred in many places across Pangea for most of the Late Triassic. This includes western North America, where ornithischians and sauropodomorphs were primitively absent but diverse dinosauriform faunas comprised lagerpetids, silesaurids, basal theropods, and coelophysids. Petrified Forest National Park (PEFO) preserves one of the most complete stratigraphic sections of the Chinle Formation, including three fossiliferous members: the Blue Mesa Member, the Sonsela Member, and the Petrified Forest Member. Most of the research interest on dinosauriforms at PEFO has focused on the early theropods, including *Chindesaurus bryansmalli*, but here we report more than 20 new dinosauriform specimens recovered as part of various collecting efforts in the park, including within a recent expansion of park lands. We use synapomorphies of ornithodiran groups to identify each specimen to its least inclusive clade, which include a non-dinosauriform dinosauriform, silesaurid dinosauriforms, non-herrerasaurid basal theropods, and neotheropods. A proximal end of a neotheropod tibia from PEFO and a lagerpetid astragalus from the Navajo Nation represent the oldest and youngest dinosauriforms from the Chinle Formation in Arizona, respectively. A neotheropod tibia from the Blue Mesa Member may represent the oldest record of a dinosaur in North America. Along with a robust lithostratigraphic framework and high-precision radiometric ages, these specimens support the hypothesis that dinosaurs and their closest ornithodiran relatives coexisted for more than 10 million years in the western portion of the Chinle Formation paleobasin during the Late Triassic.

**Funding Sources** Petrified Forest Museum Association; Friends of Petrified Forest National Park.

### Education & Outreach

### INTERACTING WITH THE UNTOUCHABLE: UTILIZING MULTIMEDIA-BASED VISUAL CONTENTS FOR THE JAPANESE NATIONAL MONUMENT, THE *TANIWHASAUROS MIKASAENSIS* (MOSASAURIDAE)

Matsui, Kumiko<sup>1</sup>, Karasawa, Tomoki<sup>2</sup>

<sup>1</sup>The Kyushu University Museum, Kyushu University, Fukuoka, Japan, <sup>2</sup>Mikasa City Museum, Mikasa, Hokkaido, Japan

The holotype of *Taniwhasaurus mikasaensis* (Squamata: Mosasauria) (MCM-M0009) comprises a partial skull and is registered as a Japanese National Monument (JNM). Although this specimen is among the most famous vertebrate fossils in Japan, it is very difficult to be handled by researchers, let alone museum visitors, owing to its JNM status.

In recent years, because ‘heritage tourism’ in museum activities has attracted attention, we have worked to utilize multimedia data relating to MCM-M0009 as a new method for introducing this iconic specimen to the public in a considerably enhanced interactive setting.

The production cost of such multimedia data is particularly important to consider because local museums generally operate on a small budget. Accordingly, this project was conducted using low-cost, readily available tools. First, the digital 3D model of MCM-M0009 was generated using a smartphone-based movie application. The resultant digital 3D model facilitated the production of two downsized plastic models using a 3D printer for hands-on activities. Finally, an augmented reality (AR) system was developed. Users with a smartphone and/or an electronic tablet can use this system by connecting their device to a dedicated HTML website.

Further, the educational effect of the new multimedia components of *T. mikasaensis* was accessed during a workshop in July 2019. Questionnaire results gathered from 11 examinees related to hands-on models and AR viewing of *T. mikasaensis* indicated that the new multimedia applications garnered the users’ interest in both paleontological aspects of the specimen and advanced imaging technology. Thus, results revealed that the incorporation of multimedia technologies in the museum activities has an unexpected interdisciplinary effect.

Digital 3D data are deemed crucial to prevent the total loss of valuable specimens owing to disasters, such as the locality of *Utatusaurus hataii*, another JNM, damaged during the 2011 Tohoku earthquake and tsunami. More recently, the global COVID-19 pandemic has forced many museums to temporarily shut down. To reduce the risk of spreading COVID-19 infection via contact in museum exhibitions, discontinuing hands-on activities in museums is vital for the foreseeable future. Under such a circumstance, it is expected that exhibitions will be enriched by interweaving AR into conventional exhibitions without losing the ‘experience’ of the museum setting.

#### Mesozoic & Early Cenozoic Mammalian Evolution

#### A NEW BASAL CARNIVORAFORM FROM THE EARLY OLIGOCENE OF LIBYA: OLDEST KNOWN RECORD OF CARNIVORAMORPHA IN AFRICA

Mattingly, Spencer G.<sup>1</sup>, Beard, K. Christopher<sup>1</sup>, Coster, Pauline<sup>2</sup>, Salem, Mustafa<sup>3</sup>, Chaimanee, Yaowalak<sup>4</sup>, Jaeger, Jean-Jacques<sup>4</sup>

<sup>1</sup>Ecology and Evolutionary Biology, University of Kansas, Lawrence, Kansas, U.S.A., <sup>2</sup>Reserve Naturelle Nationale Géologique du Luberon, Luberon, France, <sup>3</sup>Geology, Tripoli University, Tripoli, Libya, <sup>4</sup>Université de Poitiers, Poitiers, France

Carnivoraformes is a clade comprised of members of the Carnivora, as well as the paraphyletic assemblage of stem taxa previously united under the ‘Miacidae’. ‘Miacids’, herein referred to as ‘basal carnivoraforms’, have been well-documented on all Laurasian continents, and range temporally from the latest Paleocene to the end of the Eocene. Here we describe the first and only known African occurrence of a basal carnivoraform from the early Oligocene Zallah Incision locality in the Sirt Basin of central Libya. The new taxon is represented by three isolated teeth: m1, P4, and dP3, all of which are carnassial loci diagnostic of the Carnivoraformes. Despite its meager anatomical representation, the new Libyan carnivoraform possesses numerous characters that distinguish it from contemporaneous African hyaenodontans, including the retention of a large m1 metaconid, an enlarged and transversely oriented P4 metastyle, and the absence of a metacone on dP3, among other features. The new Libyan carnivoraform is the earliest known occurrence of a carnivoramorphan in Africa, providing the first empirical evidence that members of this clade were present in Africa during the Oligocene. All other known basal carnivoraforms were extirpated by the end of the Eocene in Laurasia, implying that the new taxon is a late-surviving relict. The new carnivoraform further augments the record of interchange between Eurasia and Africa prior to the closure of the Tethys Sea.

**Funding Sources** We gratefully acknowledge financial support from the U.S. National Science Foundation (BCS 1157142 and BCS 1441585) and the David B. Jones Foundation.

#### Anatomical & Developmental Explorations of the Mammalian Skull

#### EVOLUTION OF ENDOCAST MORPHOLOGY IN THE SUBORDER YINPTEROCHIROPTERA (CHIROPTERA): MORPHOLOGICAL SIGNAL AND ENCEPHALIZATION EVOLUTION IN A CLADE REGROUPING ECHOLOCATING AND NON-ECHOLOCATING BATS

Maugoust, Jacob, Orliac, Maëva J.  
ISEM, Montpellier, Occitanie, France

Chiroptera exhibit among the most spectacular morpho-anatomical modifications in mammalian history, most notably the modifications to their perception organs and their sensory integration in relation to the physical constraints of the aerial environment. During the 20th century, morphological studies divided this order into two suborders: Megachiroptera ('fruit bats' or 'megabats'), the mostly diurnal, rather big, and non-echolocating bats, and Microchiroptera ('microbats'), the more nocturnal, smaller, echolocating bats. However, several recent molecular studies demonstrated that bats are composed of two main clades: the Yangochiroptera, echolocating-bats, and the Yinpterochiroptera, comprising echolocating (Rhinolophoidea) and non-echolocating (Pteropodidae) bats. Inclusion of Pteropodidae in the paraphyletic 'microbats' raises issues regarding the evolutionary history of the order, notably regarding the acquisition of echolocation. To date, no extensive study, including fossils, has been done regarding the evolution of brain morphology in Yinpterochiroptera. Only quantitative studies regarding encephalization have been performed based on extant taxa only. These studies indicated a decrease in encephalization through time in some families (in apical rhinolophoid families Hipposideridae and Rhinolophidae, and in some Pteropodidae), which is quite unique in mammals.

In this work, we reconstructed the endocasts of 55 Yinpterochiroptera taxa, representing the seven families of the suborder, including eight fossil taxa, in order to investigate the evolutionary history of the external features of the brain at the level of suborder. We followed the evolution of 40 morphological characters to provide a first qualitative overview of the morphological evolution of yinpterochiropteran brains and tested the previous assumptions about encephalization evolution by adding fossil data. Our results highlight the potential phylogenetic significance of morphological characters of the endocast and propose a more complicated picture of encephalization increase and decrease in Yinpterochiroptera. Finally, inclusion of fossils allows for reducing the morphological gap between pteropodid and rhinolophoid bats.

#### **Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

#### **A NEW SPECIES OF THE GROUND SLOTH *PAROCNUS* (MAMMALIA, PILOSA, MEGALONYCHOIDEA) FROM THE LATE PLEISTOCENE–EARLY HOLOCENE OF THE DOMINICAN REPUBLIC**

McAfee, Robert K.<sup>1</sup>, Beery, Sophia M.<sup>2</sup>, Cooke, Siobhan<sup>3</sup>, Rimoli, Renato<sup>4</sup>, Almonte, Juan<sup>5</sup>, Lehman, Phillip<sup>6</sup>

<sup>1</sup>Biomedical Sciences, PCOM-GA, Lawrenceville, Georgia, U.S.A., <sup>2</sup>Ohio University, Athens, Ohio, U.S.A.,

<sup>3</sup>Johns Hopkins University, Baltimore, Maryland, U.S.A.,

<sup>4</sup>Museo del Hombre Dominicano, Santo Domingo, Dominican Republic, <sup>5</sup>Museo Nacional de Historia Natural

“Prof. Eugenio de Jesús Marcano”, Santo Domingo, Dominican Republic, <sup>6</sup>Dominican Republic Speleological Society, Cabarete, Dominican Republic

Fossil remains of the ground sloth *Parocnus* are restricted to just two islands of the Greater Antilles (Cuba, Hispaniola), and the overall recovery of specimens on each island has been sparse. The karstic landscape of portions of Hispaniola has produced numerous caves, and underwater exploration of submerged caves on the eastern side of the island has yielded extensive, well-preserved fossils of sloths as well as birds, bats, rodents, primates, insectivores, crocodylians, turtles, and invertebrates. Of particular note are the caves of Parque Nacional del Este (National Park of the East) in the southeastern Dominican Republic. These sites have produced numerous sloth specimens, including a nearly complete skeleton from Padre Nuestro cavern, which represents a new species of *Parocnus*. The new species, *Parocnus* nov. sp., is about 15% smaller in body size than the other Hispaniolan species, *P. serus*. *Parocnus* nov. sp. also exhibits a distinct suite of morphological characters that further distinguish it, and which are not size-related. Geographically, there is no overlap between the Hispaniolan *Parocnus* species, with *Parocnus* nov. sp. so far restricted to Parque Nacional del Este. As multiple individuals were recovered at each site, it is evident that the localized populations exhibited a slight sexual dimorphism in the overall length of their limb elements, which matches similar patterns displayed by *P. serus* bearing localities. Archaeological specimens related to the Archaic (ca. 6000–500 BC) and Taino (1000–1500 AD) cultures that settled Hispaniola have also been recovered from the type locality, and it is possible there were interactions between the early humans and the sloths, which may have further contributed to their extinction.

#### **Mesozoic Herpetology**

#### **NEW MARINE REPTILES FROM THE LATE CRETACEOUS OF SOUTH CAROLINA, INCLUDING FIRST OCCURRENCES OF ELASMOSAURIDAE, *CLIDASTES*, *MOSASAURUS*, AND ‘*LIODON*’**

McCuen, William

Geology and Environmental Geosciences, College of Charleston, Aiken, South Carolina, U.S.A.

A new collection of marine reptile fossils (chiefly teeth) from the Late Cretaceous Donoho Creek and Peedee Formations near Myrtle Beach, South Carolina (donated to CCNHM by the late Mrs. Rita McDaniel) expands our knowledge of marine vertebrate diversity on the southern Atlantic Coastal Plain. Prior reports documented only *Tylosaurus* sp. and *Prognathodon* sp., but were hindered by small sample sizes. This new collection adds many taxa to the assemblage, including the region's first *Mosasaurus* (*M.* sp. cf. *M. hoffmanni*, identified from three teeth and *M. missouriensis*, one tooth) and *Clidastes propython* (one tooth). The *Mosasaurus missouriensis* specimen constitutes the easternmost occurrence of the species yet known and represents its only known occurrence on the Atlantic coast. We also report elasmosaurid teeth, the first plesiosaur material from the state diagnostic below ordinal level. The collection additionally included crocodylian material, as well as invertebrates and selachians assignable to *Sphenodiscus*, *Cucullaea gigantea*, *Belemnitella americana*, *Exogyra*, *Cretalamna*, *Squalicorax*, and *Ischyrhiza*. Cryptic mosasaur specimens resembling '*Liodon*' (one tooth) and *Prognathodon* (three teeth), and well as fragmentary sea turtle remains, hint at further diversity to be uncovered in the region. This collection dramatically increases our knowledge of Late Cretaceous marine reptile diversity in South Carolina.

### Mammalian Skeletal Morphology

#### PHYLOGENETIC AND ECOMORPHOLOGICAL SIGNAL IN NOTOUNGULATE AND LITOPTERN (MAMMALIA) TARSALS FROM THE EARLY MIOCENE SANTA CRUZ FORMATION (ARGENTINA)

McGrath, Andrew, Wyss, André  
Earth Science, University of California, Santa Barbara,  
Santa Barbara, California, U.S.A.

Ecomorphological analyses of tarsal bones are widely used to reconstruct the locomotor behavior of ancient mammal species and inform community-level paleoenvironmental reconstructions. Here, for the first time, we use multivariate methods to investigate the tarsal morphology of South American native ungulates (SANUs), a wholly extinct group whose paleobiology is thus challenging to study. We examined astragali and calcanei from four of five notoungulate and two of three litoptern 'families' recorded in the early Miocene Santa Cruz Formation (SCF) of southern Argentina. The present study assesses the morphological disparity of SCF SANU tarsals and its phylogenetic and ecological causes.

We collected 16 linear and four angular measurements for each astragalus ( $n = 62$ ), and 14 linear and two angular measurements for each calcaneus ( $n = 75$ ), all normalized

to the proximodistal length of the element. Linear discriminant analysis (LDA) correctly assigned 98.4% of astragali and 93.3% of calcanei to 'family.' Due to small sample size, the efficacy of LDA in distinguishing SANU tarsals at the genus level could not be tested. Litoptern tarsals strongly cluster in Principal Components Analysis (PCA), these elements being nearly indistinguishable in *Theosodon* (Macraucheniiidae) and proterotheriids. The tarsals of tyotheres (small-bodied notoungulates) are notable in that the two hegetotheriid genera plot in distinct regions of the morphospace, particularly their astragali. *Pachyrhkos* plots near *Interatherium* and *Protypotherium* (Interatheriidae), whereas *Hegetotherium* falls in an isolated position. The same pattern arises from a tyotheres-only analysis. Santacrucian tyotheres are commonly interpreted to have been generalized locomotors, perhaps with cursorial tendencies. Our results strongly suggest that *Hegetotherium* was distinct from other tyotheres in its locomotion.

Most SCF SANU 'families' are distinctive and conservative in their tarsal morphology, hegetotheriids being unusual for their intra-'family' disparity. Future comparisons of the tarsals in SANUs and extant mammals (which may provide modern analogs) will enhance our understanding of SANU locomotion and refine associations between the SCF fauna and modern herbivore communities. Expansion of the SANU tarsal dataset temporally and geographically will provide a broader view of the 'family'-level disparity observed here.

**Funding Sources** This project was funded by a Geological Society of America Graduate Research Grant.

### Taphonomy & Stratigraphy

#### INVERTEBRATE-MODIFIED DINOSAUR FOSSILS FROM THE MYGATT-MOORE QUARRY IN WESTERN COLORADO REVEAL NEW INSIGHTS INTO DECAY AND DECOMPOSITION IN THE LATE JURASSIC PERIOD

McHugh, Julia<sup>1</sup>, Drumheller, Stephanie K.<sup>2</sup>, Riedel, Anja<sup>3</sup>, Kane, Miriam<sup>3</sup>

<sup>1</sup>Museums of Western Colorado, Grand Junction, Colorado, U.S.A., <sup>2</sup>Department of Earth and Planetary Sciences, University of Tennessee, Knoxville, Knoxville, Tennessee, U.S.A., <sup>3</sup>Department of Geology, Colorado Mesa University, Grand Junction, Colorado, U.S.A.

A survey of 2,368 vertebrate fossils from the Upper Jurassic Mygatt-Moore Quarry (Morrison Formation, Brushy Basin Member) in western Colorado revealed over 2,100 individual bone surface modifications. This is the largest, site-wide bone surface modification survey of any Jurassic fossil locality. Traces made by invertebrate actors were common in the assemblage, second in observed

frequency after vertebrate bite marks, and are found on 16.174% of the surveyed material. Six distinct invertebrate trace types were identified, including pits and furrows, rosettes, two types of bioglyph scrapes, bore holes, and chambers. A minimum of four trace makers are indicated by the types, sizes, and morphologies of the traces. Potential trace makers are inferred to be dermestid or clerid beetles, gastropods, an unknown necrophagous insect, and an unknown osteophagus insect. Of these, only gastropods are preserved at the site as body fossils. The remaining potential trace makers are part of the hidden paleodiversity from the North American Late Jurassic Period, revealed only through this ichnologic and taphonomic analysis. Site taphonomy suggests variable, but generally slow burial rates that range from months up to six years, while invertebrate traces on exposed elements indicate a minimum residence time of five months for elements with even just a few preserved invertebrate traces. These traces provide insight into the paleoecology, paleoclimate, and site formation of the Mygatt-Moore Quarry, especially with regards to residence times of the skeletal remains on the paleolandscape. Comprehensive taphonomic studies, like this survey, are useful in exploring patterns of paleoecology and site formation, but they are also rare in Mesozoic assemblages. Additional work is required to determine if results found here are typical of bulk-collected fossils from Jurassic ecosystems in North America, or if the Mygatt-Moore Quarry represents an exemplar locality for the preservation of modified bone surfaces.

**Funding Sources** David B. Jones Foundation.

### **Mammalian Skeletal Morphology**

#### **STATISTICAL CLUSTERING ANALYSIS OF MAMMALIAN POSTCRANIAL MORPHOLOGY REVEALS POSSIBLE SEXUAL DIMORPHISM RATHER THAN SPECIES-LEVEL DIVERSITY IN THE PALAEOMERYCIDAE**

McLaughlin, Win N.<sup>1</sup>, Weldon, Nicholas<sup>3</sup>, Davis, Edward B.<sup>2</sup>

<sup>1</sup>Geology, Pomona College, Santa Monica, California, U.S.A., <sup>2</sup>Earth Sciences, University of Oregon, Eugene, Oregon, U.S.A., <sup>3</sup>No Institution, Santa Monica, California, U.S.A.

Vertebrate paleontology often concentrates on craniodental material, but postcranial material can be more common and often represents the only evidence of taxonomic membership. We utilize a statistical approach to parse species membership and sexual dimorphism in known modern taxa, to then attempt to answer questions about range and source of variance in the extinct family Palaeomerycidae. Previous work demonstrates that statistical analysis of 2-D and 3-D morphometrics

differentiates taxa, but shape differences arise from more than just species- or genus-level differences. In this study, we examine statistical distributions of linear measurements of postcrania to identify how the shapes of these structures cluster or diverge in closely related species and within sexually dimorphic species. The order Artiodactyla includes families such as the camels, where the size and shape of postcranial structures reliably differentiate species, and families where sexual dimorphism is more important, such as deer. We use measurements of the astragali, as this durable ankle bone is common enough in the Cenozoic fossil record to be compared in detail with modern assemblages. A Principal Component Analysis of eight standardized measurements on the astragalus reveals clustering of these morphological proxies at a family level; however, it does not allow for assignment to particular families or genera and is most impacted by size differences. We therefore applied a novel statistical approach of calculated k-means to remove overall body size as a variance factor and then ran a cluster analysis on the standardized measurements. Distinct clusters emerge for all families included (bovids, cervids, antilocaprids, camelids, giraffids, and palaeomerycids); however, within-family analyses produce different results by family. Antilocaprids show no sexual dimorphism, while cervids show little species-level difference, but maintain a strong signal of sexual. Giraffid and bovid taxa typically cluster by both size-corrected species and by sex. Camelids do not show size dimorphism and leave few distinguishable species. While clusters did not emerge for palaeomerycids, their variance is most similar to that of strongly sexually dimorphic taxa, like cervids. However, initial results do suggest overinflated taxonomic diversity in palaeomerycids, as no compared modern species or genera span as great a range of size and morphological variation without significant sexual dimorphism.

**Funding Sources** T. Roosevelt Grant for the study of understudied North American taxa, AMNH 2014.

### **Marine Mammals**

#### **A FOSSIL RIGHT WHALE FROM THE LATE MIOCENE MARINE DIATOMITES NEAR LOMPOC, SANTA BARBARA COUNTY, CALIFORNIA, U.S.A.**

McLeod, Samuel, Hook, Juliet  
Vertebrate Paleontology, LACM Natural History, Los Angeles, California, U.S.A.

Fossils of the right whale family Balaenidae are uncommon to rare, especially of elements other than the dense otic bones. An unusual specimen of a fossil right whale was collected in a large indurated concretion from within the diatomaceous deposits near Lompoc, Santa Barbara

County, California, U.S.A. The thick marine deposits of diatomaceous earth near Lompoc have been commercially mined for more than a century. Fossil fish specimens are relatively common from these deposits, but specimens of other marine vertebrates are not. Occasionally, concretions containing well preserved larger vertebrates are encountered within the diatomaceous deposits. One such concretion nearly two meters long, containing a partial right whale cranium and jaw, has been laboriously prepared by volunteer effort for almost a decade and is still being worked on. This specimen preserved the distinctive highly arched narrow rostrum of right whales including the skull vertex with both nasal bones. The most posterior portion of the cranium is missing but an impression of part of the occipital shield is preserved. Impressions of the baleen plates are even preserved next to the right side of the skull. Whether the right whale specimen came from the Siquoc Formation or the underlying Monterey Formation is unknown, but regardless the age is 9–12 Ma.

### **Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

#### **FROZEN IN TIME: THE TALE OF A PLEISTOCENE WOLF PUP FROM THE YUKON TERRITORY**

Meachen, Julie<sup>1</sup>, Wooller, Matthew J.<sup>2</sup>, Barst, Benjamin D.<sup>2</sup>, Funck, Juliette<sup>2</sup>, Crann, Carly<sup>3</sup>, Cassatt-Johnstone, Molly<sup>4</sup>, Shapiro, Beth<sup>4</sup>, Hall, Elizabeth<sup>5</sup>, Hewitson, Susan<sup>5</sup>, Zazula, Grant<sup>5</sup>

<sup>1</sup>Anatomy Department, Des Moines University, Des Moines, Iowa, U.S.A., <sup>2</sup>Alaska Stable Isotope Facility, Water and Environmental Research Center, University of Alaska, Fairbanks, Fairbanks, Alaska, U.S.A., <sup>3</sup>A.E. Lalonde AMS Laboratory, University of Ottawa, Ottawa, Ontario, Canada, <sup>4</sup>Ecology and Evolutionary Biology, UC Santa Cruz, Santa Cruz, California, U.S.A., <sup>5</sup>Yukon Palaeontology Program, Government of Yukon, Department of Tourism and Culture, Whitehorse, Yukon, Canada

In July 2016, a gold miner named Neil Loveless uncovered an incredible find from the permafrost: a frozen, ancient wolf pup from Pleistocene sediments exposed along Last Chance Creek in the Klondike goldfields, near Dawson City, Yukon, Canada. In the Hän language of the local Tr'ondëk Hwëch'in First Nation, the pup was named 'Zhur' and is among the most complete and best-preserved fossil mummified carcasses ever found in the region. Since then, our team has been studying the pup to learn more about her life and how she died. To this end, we conducted morphological measurements, radiocarbon dating, stable isotope analyses, radiographic imaging, and ancient DNA analyses. Radiocarbon dating (<sup>14</sup>C) revealed that this wolf

pup died >50,000 years before present. Morphological analyses reveal a near completely intact specimen measuring 417 mm in length (nose to tail base), and weighing 670 g; which includes fur, skin, and soft tissues (including female external genitalia), and X-rays reveal the persistent presence of a digestive tract. The pup had almost all of her deciduous teeth at the time of her death. X-ray results revealed unfused vertebral plates and centers of ossification forming in the distal ulna, indicating the pup was approximately 7 weeks of age when she died. Stable carbon isotope fingerprinting of the essential amino acids (EAA) in the pup's claws reveal that her diet (and her mother's) was not unusual for a wolf from interior Beringia and that the EAAs in the pup were primarily derived from a terrestrial plant-based food web. Stable nitrogen isotope analyses of the phenylalanine and glutamic acid from sequential samples from along a claw were used to estimate the trophic position and examine whether it changed over her short life. Very little change was observed from a trophic position of  $\approx 3$ . Phylogenetic analyses of mitochondrial DNA isolated from the pup confirm her as *Canis lupus*. Her haplotype clusters into a clade with other ancient Eurasian wolves that is basal to extant wolf and dog mitochondrial diversity with the exception of high-altitude wolves. The exceptional preservation of this pup suggests that she was buried rapidly directly after her death or coincident with it, likely while she was still in her den. This small mummified pup from the Yukon is the oldest, best preserved, late Pleistocene wolf specimen known at this time.

**Funding Sources** NSF DEB-1754451 to B. Shapiro and MJ Murdock Charitable Trust (Grant ID# SR-201811010) to M. Wooller.

### **Symposium: Dietary Reconstruction**

#### **DENTAL MICROWEAR ANALYSIS OF TWO NEW SPECIES OF TRILOPHOSAURID FROM THE CHINLE FORMATION (ARIZONA) REVEALS DIVERSITY OF HERBIVOROUS DIETS WITHIN THE CLADE**

Mellett, Michael P.<sup>1</sup>, Kligman, Ben<sup>1</sup>, Marsh, Adam D.<sup>2</sup>, Parker, William<sup>2</sup>, Nesbitt, Sterling J.<sup>1</sup>, Stocker, Michelle R.<sup>1</sup>

<sup>1</sup>Virginia Polytechnic Institute and State University, Arlington, Virginia, U.S.A., <sup>2</sup>Division of Science and Resource Management, Petrified Forest National Park, Holbrook, Arizona, U.S.A.

Determining specific diets of Triassic vertebrates is crucial to understanding the stability of ecosystems during concurrent changes in the Earth system at this time. Herbivores are an important element of these ecosystems,

but little is known about tetrapod herbivory in the Late Triassic beyond broad categorizations.

Trilophosaurids are a group of Late Triassic archosauromorph reptiles commonly found in what is now western North America and are named for their three-cusped teeth. Beyond suggestions of herbivory for this group, little research has been done to estimate their diets. In many herbivores the teeth wear against each other and their food as they chew, making diet a major influence on the patterning of wear surfaces and texture on teeth. Measuring the patterning of scratches and pits on the teeth (= microwear analysis) is an effective way to clarify diets of extinct and extant taxa with burgeoning applicability for reptiles. Here we quantify microwear from two specimens of trilophosaurids, the unnamed PEFO 43837 (lower jaw with teeth) and (PEFO 42082; isolated tooth of *Trilophosaurus phasmalophos*), representing two new species of trilophosaurids from the Upper Triassic Chinle Formation, Arizona. PEFO 43837 is unique in having more bulbous teeth than those of other trilophosaurids, whereas PEFO 42082 uniquely possesses two, rather than three, cusps per tooth. We analyzed relative abundance of scratches to pits using data collected from SEM images to determine approximate diet, taken at a magnification of 1200x for PEFO 43837 and 600x for PEFO 42082. Microwear structures are nested within their visible range, making results comparable despite different scales of image.

Our analysis found PEFO 43837 to have a higher proportion of pits to scratches, indicating a diet of tough plants. PEFO 42082 was found to have a higher proportion of scratches to pits and indicates a diet of softer plants. Plant assemblages including ferns, horsetails, and diverse gymnosperms are found in horizons stratigraphically equivalent to the trilophosaurid-bearing sites, indicating possible source diets which produced the distinct microwear textures seen in the analyzed trilophosaurids. We show that for the Chinle Formation, the 'herbivorous' dietary categorization does not sufficiently reflect the possible range of diets animals can have and reveal new levels of complexity for herbivorous trophic interactions in Late Triassic ecosystems.

### **Macroecology & Macroevolution**

#### **THE INFLUENCE OF ECOLOGY ON CROCODYLOMORPH SUCCESS THROUGH MASS EXTINCTIONS**

Melstrom, Keegan

Research and Collections, Natural History Museum of Los Angeles County, Los Angeles, California, U.S.A.

Crocodylomorph reptiles have survived two mass extinctions since their appearance >230 million years ago,

but their responses to these biotic crises varied markedly. Their exceptional fossil record presents an opportunity to investigate macroevolutionary drivers to these responses in an ecological disparate and species-rich clade. Here, I test the hypothesis that ecology plays an important role in crocodylomorph responses to mass extinctions. I did this by employing independent methods of shape quantification: orientation patch count rotated to measure dental complexity and geometric morphometrics on skull morphology. I first assessed the relationship between feeding ecology and skull shape morphospace in a dataset that encompasses a wide phylogenetic breadth of extant amniotes to then compare with extinct crocodylomorphs.

I find that the skull shape of 156 living amniotes is related to both phylogeny and feeding ecology. The three major amniote clades (Mammalia, Lepidosauria, Crocodylia) plot in distinct regions of morphospace. Within these groups, however, feeding ecology exerts significant influence on morphology, suggesting that skull shape may be a useful indicator of dietary ecology. When 97 extinct crocodylomorphs are included, they cover a larger morphological range than their living relatives, including overlap with mammals and lepidosaurs. This result, when combined with dental complexity data, suggests a greater ecological range was occupied by extinct crocodylomorphs. Early crocodylomorphs appear to be terrestrial generalists, occupying a morphological region not observed in sampled living amniotes, and successfully radiate following the end-Triassic mass extinction. By the end-Cretaceous mass extinction, which did not result in a major crocodylomorph radiation, this range is no longer occupied, implying the loss of terrestrial generalists. Statistical tests show that dietary ecology played a role in mass extinction response, with ecological generalists preferentially surviving these events. Crocodylomorph resilience to biotic crises may be related to their repeated occupation of a generalist role and their failure to ecologically diversify following the end-Cretaceous mass extinction may be attributable to the loss of terrestrial members of this ecology. These results reinforce similar observations in mammals and suggest that this pattern may be applicable to other amniote groups through biotic crises. **Funding Sources** This project was supported by the NSF Graduate Research Fellowship Program, Palaeontological Association, AMNH, and Natural History Museum LA County.

### **Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

#### **THE LATITUDINAL DIVERSITY GRADIENT OF MODERN NORTH AMERICAN MAMMALS MASKS MULTIPLE ORDINAL LEVEL PATTERNS: IMPLICATIONS FOR THE ORIGIN OF THE MAMMALIAN DIVERSITY GRADIENT IN THE LATE CENOZOIC FOSSIL RECORD**

Meltesen, Kirsten M.<sup>1</sup>, Whiting, Evan<sup>2</sup>, Fox, David L.<sup>2</sup>  
<sup>1</sup>Ecology, Evolution, and Behavior, University of Minnesota, Minneapolis, Minnesota, U.S.A., <sup>2</sup>Earth & Environmental Sciences, University of Minnesota, Minneapolis, Minnesota, U.S.A.

Extant North American mammals exhibit the canonical latitudinal gradient in species richness. However, total species richness varies substantially among the nominal orders of North American mammals; Rodentia (384 spp.) and Chiroptera (180 spp.) comprise ca. 75% of modern North American mammal species. To determine the degree to which these two clades control the latitudinal diversity gradient of all North American mammals, we analyzed the relationship between species richness and latitude for the ten orders of North American terrestrial mammals.

The latitudinal diversity gradient for bats is exceptionally strong and accounts for most of the pattern observed for all mammals. However, the relationship between species richness and latitude is non-monotonic or is weak to nonexistent for the remaining orders. For example, rodents have a mid-latitude peak in richness, and eulipotyphlans have richness peaks in the Pacific northwest and in northeastern North America. Thus, the latitudinal diversity gradient for all North American mammals is the result of many diverse biogeographic patterns at the ordinal level. However, the suite of climatic and topographic variables that best explains species richness at the continental scale does not differ much between each mammalian order.

These results have important implications for understanding the history and dynamics of the latitudinal diversity gradient of North American mammals through time. Previous studies recovered weak to even reversed gradients for North American mammals for most of the Cenozoic and indicated that the modern pattern was only established after ca. 4 Ma. Our results indicate that, without bats, the modern gradient is not very strong, which is broadly similar to reconstructions of past patterns. Bats have a very poor fossil record, but molecular phylogenies of some currently speciose clades of bats indicate major radiations only in the Neogene or Quaternary. Thus, bats may not have contributed to the gradient in the past as they do to the modern North American gradient. Our work, in concert with the results of previous studies, implies that there is not and never was a strong latitudinal diversity gradient for North American mammals excluding bats. Future studies could investigate latitudinal diversity gradients through time within and among mammalian orders to deconstruct the larger, total mammal pattern and evaluate the responses of individual clades to climatic changes throughout the Cenozoic.

**Symposium: Dietary Reconstruction**

## GROUND TRUTHING DENTAL ECOLOGICAL PROXIES ON A MODERN ALPINE COMMUNITY OF SYMPATRIC RUMINANTS

Merceron, Gildas<sup>1</sup>, Berlioz, Emilie<sup>2</sup>, Vonhof, Hubert<sup>3</sup>, Green, Daniel R.<sup>4</sup>, Garel, Mathieu<sup>5</sup>, Bourgon, Nicolas<sup>6</sup>, Tütken, Thomas<sup>7</sup>

<sup>1</sup>Paleovprim Lab, CNRS, Poitiers, France, <sup>2</sup>TRACES, CNRS, Toulouse, France, <sup>3</sup>Department of Climate Geochemistry, Max Planck Institute for Chemistry, Mainz, Germany, <sup>4</sup>Department of Human Evolutionary Biology, Harvard University, Cambridge, Massachusetts, U.S.A., <sup>5</sup>Direction de la Recherche et Appui Scientifique, Unité Ongulés Sauvages, Office français de la biodiversité, Gières, France, <sup>6</sup>Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany, <sup>7</sup>Institute of Geosciences, Johannes Gutenberg University, Mainz, Germany

Ecological information from fossilized hard tissues is often difficult to interpret, because links between environment, diet, and hard tissue biology are insufficiently studied in modern communities. To address this dilemma, we investigate dietary proxies in a four-ruminant community from the French Alps, for which most of the vegetation cover is characterized on terrain up to 500 m from the very place where the animals were shot. Molar microwear textural analyses are applied to 82 specimens of roe deer (n = 18), red deer (n = 21), chamois (n = 21), and mouflons (n = 22). Intra-tooth serial enamel stable carbon and oxygen isotope analyses of the structurally bound carbonate were made on 11 specimens to assess the seasonality of diet and drinking water.

Both inter-individual dispersion and heterogeneity of complexity together with the anisotropy track dietary differences. The red deer are likely more engaged in grazing than the two bovids, which both plot as mixed feeders. When combined, dental microwear and carbon stable isotope analyses accurately reflect known ecological separation between the chamois and the roe deer. Carbon and oxygen isotopes suggest niche separation by increasing enrichment from roe deer, to red deer, to chamois; mouflons appear to feed as generalists. In roe deer, which show the highest enamel oxygen isotope range (5.7‰), variation is nevertheless constrained compared to  $\delta^{18}\text{O}$  ranges observed in regional precipitation, where mean annual range reaches 9.9‰. However, through inverse modeling we estimate seasonal input ranges that average 9.7‰, a result strikingly similar to regional values.

A preliminary analysis of correlation based on microwear textures with habitat type (open, mixed, and forested habitats) detect significant correlations. Dental microwear anisotropy is positively correlated with the mixed vegetation cover and negatively correlated with open vegetation cover. Given that anisotropy is expected to be higher for the most grazing species in open habitats, such

results are at first glance surprising. Our results reflect the fact that the most open habitat dwelling species are not grazers but rather mixed feeders and that the cervids, both occupying the most forested zones, display contrasted feeding preferences.

Altogether, our data demonstrate that given appropriate sampling strategies and modeling approaches, microwear and isotopic data can be effective tools for demonstrating niche separation among sympatric ungulates.

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## Cenozoic Herpetology

### THE FIRST COMPLETE SPECIMEN OF THE OLIGOCENE ANGUID *PAROPHISAURUS PAWNEENSIS* WITH IMPLICATIONS FOR THE PHYLOGENY OF ANGUIDAE

Meyer, Dalton, Bhullar, Bhart-Anjan S., Gauthier, Jacques A.

Earth and Planetary Sciences, Yale University, New Haven, Connecticut, U.S.A.

We describe a new specimen of the anguid lizard *Parophisaurus pawneensis* from the lower Oligocene Brule formation of Converse County, Wyoming, housed at the Yale Peabody Museum (YPM 060609). CT scanning has revealed that YPM 060609 is an articulated and nearly complete specimen consisting of a skull and mandibles, lacking only the snout tip; a nearly complete vertebral column with the entire cervical series, and much of the dorsal and caudal series; the pectoral girdle including both coracoids, scapulae, clavicles, and the interclavicle; both for the forelimbs including the humeri, radii and ulnae, as well as disarticulated carpals and manual phalanges; an ilium, ischium, and pubis; and one hindlimb including the femur, tibia, fibula, tarsals, metatarsals and disarticulated pedal phalanges. *P. pawneensis* has previously been known from partial cranial specimens of varying degrees of completeness and partly obscured by osteoderms, and scant, fragmentary postcrania; YPM 060609 is the first specimen of *P. pawneensis* to preserve the entire animal.

Examination of the CT data has given new insight into previously obscured anatomy such as details of the palate and braincase, and has allowed for the exploration of the previously unknown postcrania. This has revealed, in addition to the previously recognized recurved and non-striated dentition, a novel combination of diagnostic characters for *Parophisaurus pawneensis*. These include a maxillary superior alveolar foramen which runs in an open channel on the supradental shelf before becoming enclosed; a prefrontal that extends posteriorly to the

midorbit; a supratemporal that extends anteriorly to the parietal notch; a weakly developed prootic trigeminal process; a concave margin of the occipital condyle in ventral view; a splenial that does not extend posteriorly past the apex of the coronoid; the presence of a prearticular crest; and the presence of a tubercle on the ilium.

We analyzed *Parophisaurus pawneensis* (537 out of 791 characters) in a large morphological phylogenetic dataset of squamates (207 species). Unconstrained maximum parsimony, Bayesian, and implied weights parsimony analyses all recover *P. pawneensis* as sister to a clade consisting of the diploglossines and gerrhonotines, supporting the existence of a North American clade of anguids. While maximum parsimony analyses constrained to recent molecular topologies find *P. pawneensis* nested in an anguine clade sister to the diploglossines.

## Fishes & Chondrichthyans: Evolution & Distribution

### BABY MEGASHARK DO DO DO DO: AN OLIGOCENE *CARCHAROCLES ANGUSTIDENS* NURSERY FROM SOUTH CAROLINA

Miller, Addison, Boessenecker, Robert

Department of Geology and Environmental Geosciences, College of Charleston, Mount Pleasant, South Carolina, U.S.A.

Many extant sharks are cosmopolitan as adults but inhabit nursery areas as youngsters - often shallow, dynamic ecosystems. Megatoothed sharks (Otodontidae) were the largest sharks of all time, and nursery areas have been demonstrated for *Carcharocles megalodon* in the Miocene of Panama. We present evidence of an ancient *Carcharocles angustidens* nursery from the Oligocene of Charleston, South Carolina, consisting of two collections dominated by neonatal and juvenile teeth ( $n = 97$ ) of *C. angustidens* from the Oligocene of South Carolina (Chandler Bridge Formation). Correcting for tooth position, published body length estimation equation yielded body lengths of 1.5–6.5 meters for most individuals. This assemblage is dominated by juvenile and neonatal *C. angustidens*, with few adults. The Oligocene Charleston embayment therefore represents the first documented paleo-nursery area for *Carcharocles angustidens*. Oligocene strata of the Charleston embayment preserve an unusually rich assemblage of marine vertebrates including a plethora of suitable prey items for a growing megatoothed shark: billfish, tuna, mackerel, cheloniid sea turtles, leatherback sea turtles, dolphins, baleen whales, sea cows, and other sharks and rays. This assemblage further sheds light on the identity of late Oligocene *Carcharocles*: while some specimens resemble early Miocene *C. chubutensis* by lacking a notch between the main cusp and lateral cusplet, most possess a

notch. These teeth also possess narrower crowns than *C. chubutensis*, and along with the Oligocene age, argue for placement in the Oligocene chronospecies *C. angustidens*.

## Bird Biology & Evolution

### **PRESERVED DISASSOCIATED RHAMPHOTHECA OF THE CRETACEOUS EARLY BIRD *CONFUCIUSORNIS* AND ITS IMPLICATIONS FOR RECONSTRUCTION AND EVOLUTIONARY DEVELOPMENT OF AVIALAN BEAKS**

Miller, Case V.<sup>1</sup>, Pittman, Michael<sup>1</sup>, Kaye, Thomas G.<sup>2</sup>, Wang, Xiaolin<sup>4</sup>, Zheng, Xiaoting<sup>3</sup>

<sup>1</sup>Vertebrate Palaeontology Laboratory, Division of Earth and Planetary Science., University of Hong Kong, Hong Kong, Hong Kong, <sup>2</sup>Foundation for Scientific Advancement, Sierra Vista, Arizona, U.S.A., <sup>3</sup>Shandong Tianyu Museum of Nature, Pingyi, Shandong, China, <sup>4</sup>Institute of Geology and Paleontology, Linyi University, Linyi City, Shandong, China

*Confuciusornis* is the earliest known avialan to have a fully edentulous beak that evolved convergently to that in crown birds. We report a new specimen of *Confuciusornis sanctus* whose rhamphotheca (the horny covering of the beak) is visibly detached, separated from the skull, and imaged using Laser-Stimulated Fluorescence (LSF). In addition to an undescribed specimen previously imaged with UV light, a total of two confuciusornithid rhamphothecae are preserved disassociated from the skull, while the skull remains attached to the body. Two additional confuciusornithid rhamphothecae are preserved *in situ*, with another of debatable association. Taken together, roughly half of known confuciusornithid rhamphothecae are preserved detached from the skull. Separation of the rhamphotheca from the skull has not been reported in decay studies of crown bird corpses. However, these same studies find birds' heads to separate from the body easily, suggesting the aforementioned specimens are in an early state of decay. Together, these suggest that confuciusornithid rhamphothecae were less firmly attached to the underlying bone than in crown birds. Reconstructing the rhamphotheca position in the new specimen allows us to confirm the previous diagnoses of the *in vivo* position of the rhamphotheca, and to comment on broad trends of extent and shape of the rhamphotheca across Avialae. Cranial extent of the confuciusornithid rhamphotheca is similar to most crown birds. However, the confuciusornithid rhamphotheca projects less beyond the premaxilla than in a crown bird with the same amount of rostral vascularity. Rhamphotheca curvature relative to the underlying bone is similar to that of crown birds in *C. sanctus* and *Eopengornis zhengi*, but more similar to that

of some turtles in *Confuciusornis dui*. Together, this evidence paints a picture of the confuciusornithid beak being a structure reminiscent of that in crown birds, but distinct in several ways likely related to different developmental pathways formed by the groups' distinct evolutionary histories.

## Fishes & Chondrichthyans: Evolution & Distribution

### **DENTAL PATHOLOGY IN CHONDRICHTHYES REPRESENTS FIRST DOCUMENTATION OF GEMINATION OUTSIDE MAMMALIA**

Miller, Harrison S.<sup>1</sup>, Avrahami, Haviv M.<sup>2</sup>, Zanno, Lindsay E.<sup>2</sup>

<sup>1</sup>Marine, Earth, and Atmospheric Sciences, North Carolina State University, Raleigh, North Carolina, U.S.A., <sup>2</sup>Biological Sciences, North Carolina State University, Raleigh, North Carolina, U.S.A.

Gemination is a rare tooth pathology that has only been reported in the Mammalian clades Hominidae, Pinnipedia, Felidae, Ursidae, Cercopithecidae, Equidae, Talpidae, Canidae, Mustelidae, Cetacea, and Muridae, as well as extinct clades including *Mammuthus*, Coryphodontidae, and Condylarthra. Gemination results from a developmental aberration of the mesoderm and ectoderm in which the tooth germ divides into two crowns or one large partially separated crown. Unlike other types of dental anomalies gemination does not affect the number of teeth along the tooth row. The etiological factors of gemination are not well understood, however, vitamin deficiency, hormonal irregularities, infection, inflammation of surrounding tissues, and genetic predispositions have been suggested in human cases.

We report on the first occurrence of tooth gemination outside of Mammalia in *Carcharocles megalodon* (NCSM 33639) and *Carcharhinus leucas* (NCSM 33641 and 33640). Teeth were analyzed and compared against non-pathological teeth from their respective species. The labial gemination length (LAGL) of NCSM 33639, 33641, and 33640 are 62.62, 5.11, and 7.51 mm respectively, and extend from the apex of the crown to the neck. The lingual gemination length (LIGL) of NCSM 33639 and 33641 are 13.31 and 2.98 mm respectively, terminating prior to the mid-point of the crown. In contrast, the LIGL of NCSM 33640 is 5.40 mm, and runs from the apex of the crown, past the mid-point. The two cusp divisions on NCSM 33639 are nearly the same height and lack mesiodistal curvature. The labial face of the mesial division twists slightly over the lingual face of the distal division. The taller mesial cusp division of the *C. leucas* teeth curve distally over the shorter distal division. The two divisions on 33640 split away from each other mesiodistally, halfway between the crown mid-point and the apex,

whereas on 33641 the two cusps remain in parallel. CT scans suggest the dental abnormality in the *C. leucas* teeth are most similar to gemination, indicated by a singular bifid crown with a single, asymmetrically oriented pulp cavity. These results suggest that tooth gemination may be present across all vertebrate clades, and highlights the importance of documenting dental abnormalities in extant and extinct taxa. However, more research on the etiology of gemination is needed before we can infer any relationships with paleobiological or paleoenvironmental factors.

## **Taphonomy & Stratigraphy**

### **PREDATORS RULE THE ROOST: SMALL MAMMAL TAPHONOMY AT LANDSCAPE-SCALES**

Miller, Joshua H.<sup>1</sup>, Goff, Jennifer<sup>2</sup>

<sup>1</sup>Department of Geology, University of Cincinnati, Cincinnati, Ohio, U.S.A., <sup>2</sup>Department of Biology, University of Cincinnati, Cincinnati, Ohio, U.S.A.

The microvertebrate (<1 kg) fossil record is taphonomically complicated because small-bodied remains are easily mobilized by predators, bioturbators, and sedimentary processes. Because microvertebrates are commonly food for higher-order consumers, predator activity may be a primary control on the spatio-environmental and ecological fidelity of their death assemblages (DAs); even when predator behaviors themselves do not concentrate skeletal remains. To test the ecological fidelity of microvertebrate DAs, we evaluated small mammal DAs developing in different habitats across Yellowstone National Park, WY. To sample DAs, ten 1 km-long surveys were walked in each of four habitats: grasslands, forests, river-margins, and lake-margins. Taxonomic identifications were made in the field or using reference collections. For each recovered small mammal accumulation (e.g., owl pellet, mammal feces, partial skeleton), specimen data were summarized using the Minimum Number of Individuals (MNI). Small mammal remains were recovered from all habitats, yielding 194 individuals from 11 genera. Specimen counts (MNI) and taxonomic richness (S) were highest in forests (MNI = 90, S = 9) and grasslands (MNI = 85, S = 7). River-margins (MNI = 12, S = 5) and lake-margins (MNI = 7, S = 3) were comparatively depauperate. Grasslands were dominated by ground squirrels (*Spermophilus*), voles (*Microtus*), and pocket gophers (*Thomomys*). This rank-order abundance matches live-trapping surveys, suggesting grassland DAs are broadly representative of their rodent communities. Forest DAs include tree specialists not observed in other habitats. However, the dominant taxon (*Thomomys*) is fossorial and specializes in open habitats. Nocturnally, *Thomomys* forage above-ground where they are susceptible

to owl predation. Forest DAs also include semiaquatic muskrat (*Ondatra*), further indicating that Yellowstone forests act as taphonomic sinks. While Yellowstone grasslands provide ecologically informative samples of source communities, such habitat-level fidelity is not universal. In habitats where predators roost or reside (forests), ecological representation may skew away from the immediate habitat in favor of regional taxonomic richness. The relative rarity of small mammal remains from river- and lake-margins is consistent with biases observed in the fossil record, suggesting these biases may originate, in part, with biological factors controlling where animals live, die, and accumulate.

### **Colbert Poster Prize/Mesozoic & Early Cenozoic Mammalian Evolution**

#### **PHYLOGENETIC RECONSTRUCTION OF TWO SPECIES OF PAROMOMYID PLESIADAPIFORMS FROM A UNIQUE, HIGH ARCTIC ECOSYSTEM OF EOCENE CANADA**

Miller, Kristen, Beard, K. Christopher  
Ecology and Evolutionary Biology, University of Kansas, Lawrence, Kansas, U.S.A.

The Margaret Formation of the Eureka Sound Group in the Canadian Arctic Archipelago samples an extinct warm temperate ecosystem with a polar light regime that dates to the early Eocene Epoch, ~52 Ma. Previous paleontological expeditions have yielded a wide array of vertebrate taxa including early crocodylians and a diversity of mammals. Having no modern analogue, the ecological adaptations of the fossil vertebrates of the Margaret Formation and the overall pattern of faunal assembly of its constituent taxa remain enigmatic. Crown clade primates have never been recovered from the Eocene of Arctic Canada, but at least two new taxa of paromomyid plesiadapiforms occur there. This research aims to describe the Arctic paromomyids from Ellesmere Island and assess their phylogenetic relationships in order to reconstruct the paleobiogeographic affinities of these arboreal taxa and constrain the timing by which they colonized the Canadian Arctic. To address these questions, a phylogenetic analysis was completed using a morphological character matrix utilizing 56 dental characters coded for 16 taxa. The 50% majority rule consensus of seven trees from a maximum parsimony analysis suggests the two new paromomyid taxa are closely related to each other and nested within the *Ignacius* clade. These results suggest the Canadian Arctic paromomyids are more closely related to midlatitude North American clades than their European relatives. Their nested phylogenetic position within North American species of *Ignacius* also suggests the Arctic taxa dispersed into high northern latitudes after the initial diversification

of North American paromomyids. The lower faunal zone of the Margaret Formation (where most of the mammalian taxa occur) dates to ~53–49.5 Ma, an interval that coincides with increasing global temperatures during the Early Eocene Climatic Optimum (EECO). This suggests the northward dispersal of the Arctic paromomyids may have been in response to rising global temperatures during the EECO. Results from this analysis will inform future research directions, in which the dental topography of the Ellesmere Island paromomyid taxa will be investigated within a phylogenetic context to better understand the ecological adaptations that facilitated their survival in an ecosystem with a polar light regime.

**Funding Sources** This research was supported by grants from the Association of Earth Science Clubs of Greater Kansas City and the David B. Jones Foundation.

### Preparators

#### IF A SPECIMEN IS ON EXHIBIT DOES IT REALLY EXIST?

Millhouse, Amanda, Little, Holly  
Paleobiology, Smithsonian National Museum of Natural History, Washington, District of Columbia, U.S.A.

In June 2019, the Smithsonian National Museum of Natural History opened the “David H. Koch Hall of Fossils - Deep Time” after an extensive five-year renovation. Deep Time includes over 250 vertebrate specimens, more than one-third of all fossils in the exhibit. Historically, the Department of Paleobiology has tracked specimen exhibit data inconsistently using a combination of hand-written and digital inventories as well as various notations in current and legacy databases. As data was generated for exhibit specimens we determined that there was an increasing need for updating specimen records and creating new records in our collections information system (CIS). We also realized that we needed better guidelines for recording exhibit data for our objects.

Our main objective was to develop ways of recording data that could be used consistently within our CIS as well as providing information that could be useful to the public and external researchers. This effort involved reviewing how we document that a specimen is on exhibit and noting inconsistencies and use of multiple fields. In addition to the needs that we identified from the outset, many more complex data issues developed throughout the exhibit planning process. Some of these complexities included vertebrate composite mounts made from multiple individuals, noting that only part of a specimen was on exhibit, or that we created a replica of a specimen for exhibit. Beyond exhibit information, there were additional challenges associated with updating specimen data. During the planning and script writing stages, researchers updated

taxonomic identifications, stratigraphic data, and sometimes discovered more specific locality data. However, the way this was recorded for exhibit planning wasn't always interoperable with our CIS, so we had to develop new ways of documenting these updates.

Updating exhibit data for our specimen records is an ongoing process. We are still reviewing exhibit documentation and parsing out specimen data to incorporate into our CIS. Although challenging, this process has helped us establish much needed guidelines for a variety of data points and enables better access to and management of exhibit specimens.

### Colbert Poster Prize/Holocene & Pleistocene Mammalian Macroecology & Faunal Studies

#### PALEOENVIRONMENTAL INFERENCE USING A MODIFIED SØRENSEN'S INDEX

Mills, Samantha  
St. Cloud State University, Sartell, Minnesota, U.S.A.

Sørensen's Similarity Index is a beta diversity index used to evaluate similarity in taxonomic composition of heterogeneous samples through the use of presence/absence data. A modified version of Sørensen's Index has been used to compare 'functional similarity' between taxonomically disparate communities of extant fauna and has become increasingly prevalent in ecological studies because of its potential to identify similarities and differences in functional composition of disparate animal communities, thus capturing the signals of niche-based processes (e.g., environmental filtering).

In this study, we use the modified Sørensen's Index to evaluate similarities in small mammal locomotor frequencies between 23 modern sites, representing nine biomes from tropical and Holarctic latitudes. The relationship between clusters of functionally similar sites identified using the modified Sørensen's Index and six environmental characteristics, scored for each site, were evaluated using MANOVA. Environmental data from statistically significant clusters were subjected to Principal Components Analysis (PCA) to investigate which environmental characteristics might be driving differences between them. To evaluate the utility of this approach to interpreting paleoenvironment, locomotor frequencies for the Chadronian-age, Whitehead Creek Locality, northwest Nebraska were established through the analysis of small mammal tarsals and evaluated in conjunction with the locomotor frequency data from the modern localities using the modified Sørensen's Index.

Results of MANOVA indicate that clusters of modern faunas identified through the analysis of locomotor similarity using the modified Sørensen's Index are significantly different from each other ( $p < 0.01$ ), and PCA

indicates that differences between these localities are driven largely by temperature and rainfall seasonality, as well as number of forest levels. Comparisons of locomotor frequencies at Whitehead Creek with those of modern sites suggest that a gallery forest in the Cerrado of Brazil is a good modern analog for Whitehead Creek. This finding is consistent with previous paleoenvironmental reconstructions of the Chadronian of northwest Nebraska based on paleosols, stable isotopes, phytoliths, and vertebrate fossils.

**Funding Sources** Support for this project was provided by an IOER grant to TCA, an SCSU Faculty Improvement Grant to MAT, and an SCSU Student Research Grant to SMM.

### **Fishes & Chondrichthyans: Evolution & Distribution**

#### **A NEW LOOK AT FOSSIL HAGFISHES AND THE EVOLUTION OF DIVERGENT CYCLOSTOME CHARACTERS**

Miyashita, Tetsuto  
Palaeobiology, Canadian Museum of Nature, Ottawa,  
Ontario, Canada

Hagfishes and lampreys comprise cyclostomes, the earliest branching and sole surviving clade of the once diverse assemblage of jawless crown-group vertebrates. Lacking mineralized skeletons, the cyclostome crown group has a notoriously poor fossil record. For hagfish, *Myxini* *siroka* from the Late Carboniferous of Illinois represents the only definitive stem taxon. Previously known from a single specimen, *Myxini* has been reconstructed as a short-bodied form with pigmented eyes that is otherwise difficult to distinguish from a modern hagfish.

With a new, second specimen of *Myxini*, I re-evaluate the soft tissue anatomy of the taxon. *Myxini* has a number of general features of cyclostomes, including cartilaginous branchial baskets, separation between the esophageal and branchial passages, and a well-differentiated midline finfold. In effect, these features give a more lamprey-like appearance to this stem hagfish than previously assumed. *Myxini* still has many traits of modern hagfishes (e.g., nasohypophyseal aperture, large velar cavity, and cardinal heart) and some intermediate conditions (e.g., incipient posterior displacement of branchial region). This new information helps reinstate *Gilpichthys greenei* – an enigmatic form from the same locality – on the hagfish stem under parsimony and Bayesian methods. Serial visceral structures in a small number of specimens of *Gilpichthys* are putatively identified as gonads, consistent with reproductive biology of modern hagfishes and Paleozoic stem lampreys. Furthermore, different suites of soft tissues preserved in the Cretaceous crown-group hagfish *Tethymyxine tapirostrum*

provide important calibrations for the distinguishing features of modern hagfish morphology, including slime glands. Interestingly, all fossil hagfishes occur in depositional settings (tropical, shallow marine systems with fluctuating salinities) outside the preferred habitats of modern hagfishes.

In the new timetrees of cyclostomes, the fossil hagfishes document evolution of peculiar hagfish morphology that likely occurred between the Carboniferous and Jurassic times. Modern lampreys retain more cyclostome plesiomorphies in adult phase, but this lineage is characterized by the acquisition of a distinct filter-feeding larval phase in the similar timeframe (late Paleozoic–early Mesozoic). Collectively, the new information provides a useful guideline with which to polarize character states using modern cyclostomes as an outgroup.

**Funding Sources** Chicago Fellows Program (University of Chicago).

### **Mammalian Skeletal Morphology**

#### **THE HIP BONE TELLS US MAMMALIAN HINDLIMB POSTURE WHILE SUPPORTING BODY MASS**

Mizuno, Fumihiro  
Life and Environmental Science, University of Tsukuba,  
Tsukuba, Ibaraki, Japan

Mammalian limb joints have a wide range of motion and permit various limb movements including extension and flexion. Joints can take various angles, but the range of limb joint angles varies for each species when standing or walking. For example, giraffes take extended limb postures while standing and walking while mice take flexed limb postures. Differences in limb posture affect the length of the stride. Therefore, limb posture has an effect on terrestrial locomotor abilities. The same applies to extinct species. However, fossils do not show us their posture from when they were alive. We must piece together information from the skeleton in order to estimate the posture of extinct species.

Extant mammals maintain knee joint angles while supporting body mass when standing or walking. Stability of the joint is provided by the contraction of both extensor and flexor muscles, a condition called cocontraction. Cocontraction occurs when a joint is locked at a certain angle. For the knee joint, *musculus quadriceps femoris* acts as the extensor and *m. semimembranosus* acts as flexor. Both the origin and insertion of *m. quadriceps femoris* are covered by other muscles which run in a different direction, making it hard to observe. However, the origin and insertion of *m. semimembranosus* (ischial tuberosity and proximal anterior end of the tibia, respectively) are not covered by other muscles. The positional relationships

between the ischial tuberosity and the proximal anterior end of the tibia show us the position of the tibia while supporting body mass.

Data were collected from 13 species in 10 genera from 10 families within seven orders of extant mammals who are kept in Ueno Zoo (Tokyo). Videos of these animals were taken while they were walking using a high-speed mode (400 fps/s). Angles were analyzed from the first 75% from touchdown to lift off, because m. semimembranosus stimulates at that time. The range of angle shift during one step was less than 20 degrees among most animals. The angle between the ischial tuberosity and proximal anterior end of the tibia was  $100^{\circ} \pm 10$ . The angles were measured using skeletal position only; therefore, this method of measurement can also be used for extinct mammals.

**Funding Sources** The Sasakawa Scientific Research Grant (The Japan Science Society).

### **Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

#### **RECONSTRUCTING TRINIDAD'S LATE PLEISTOCENE VERTEBRATE COMMUNITY: NEW INSIGHTS FROM HISTORIC AND ONGOING EXCAVATIONS**

Mohammed, Ryan S.

Life Sciences, The University of the West Indies, Princes Town, Trinidad, Trinidad and Tobago

Asphaltic deposits ('tar pits') are important time capsules of past ecosystem structure, given their ability to preserve diverse tissues including bone, cellulose, and chitin in a single locality. Globally, they are mostly known from North and South America, including the famous Rancho La Brea of Los Angeles, California. Despite having the second largest asphalt deposit in the world, the asphaltic fossil record of the Caribbean island of Trinidad has been significantly underexplored. We collated data from historical excavations carried out in association with oil production to develop the first late Pleistocene faunal register for Trinidad, including representatives of Xenarthra, Rodentia, and Proboscidea, and show size-biased extinctions similar to those experienced by the South American continent. Our paleoecological reconstructions confirm a close connection with Venezuelan grasslands, consistent with a former landbridge history. By contextualizing this site within the broader data of 'tar pits' globally, we infer that this site represents a case of asphalt acting as a secondary taphonomic agent. Using this information, we informed ongoing research efforts working in collaboration with local students and researchers.

### **Mesozoic Herpetology**

#### **NEW RECORD OF TESTUDINES AND AVES FOSSILS FROM BAHARIYA FORMATION (CENOMANIAN), BAHARIYA DEPRESSION, EGYPT**

Mohesn, Amr<sup>1</sup>, Hirayama, Ren<sup>2</sup>, Abdel Gawad, Mohamed<sup>1</sup>, Sileem, Afifi<sup>3</sup>, Aly, Mohamed<sup>1</sup>

<sup>1</sup>Geology, Cairo University, Giza, Egypt, <sup>2</sup>School of International Liberal Studies, Waseda University, Tokyo, Japan, <sup>3</sup>Egyptian Geological Museum, Cairo, Egypt

Bahariya Oasis is located in the north central Western Desert, Egypt. It is characterized by a NE-oriented depression, about 380 km southwest of Cairo. The early Cenomanian Bahariya Formation outcrops along the floor of the Bahariya depression. The Bahariya Formation is divided into two members: the Gebel Ghorabi member at the base is characterized by cross-bedded, coarse-grained, non-fossiliferous sandstones, representing a fluvial environment, and the Gebel Dist member at the top is characterized by fine-grained, well-bedded, ferruginous clastics with vertebrate fossils in its lower levels. The Gebel Dist member is considered as an estuarine facies deposit. The studied materials were collected from the Gebel Dist member and are preserved at the Egyptian Geological Museum (CGM). These collected materials contain unidentified material such as testudines and birds. The testudine specimens under study, include the following: 1) a coastal bone, neural bone, peripheral bone, and elongate cervical vertebra of a small turtle with about a 20 cm long shell and a long neck, referable to Araripemydidae; 2) a coastal bone, neural bone, and pelvic remains with plastral fragments which are referred to a bothremydid with a nearly 1 m long shell; and 3) a coastal bone for a very large marine taxon (Chelonioidae), suggesting a nearly 2 m long shell. Although materials are very fragmentary, they suggest a hitherto unknown diversification of Late Cretaceous turtles. Bothremydidae had been noted previously in the Bahariya Formation as *Apertotemporalis baharijensis*. Unfortunately, the specimen was lost during the war. The avian specimen is very small caudal vertebrae from a primitive small marine bird such as *Ichthyornis*. The present study documents newly recorded material for at least two new testudine taxa and a new avian taxon. This new discovery represents the oldest known testudine lineages from Egypt, and the first and oldest records of a Cenomanian bird from Egypt.

### **Marine Reptile Diversity & Biology**

#### **A NEW, NEARLY COMPLETE SPECIMEN OF *PROGNATHODON OVERTONI* (SQUAMATA: MOSASAURIDAE) FROM THE CAMPANIAN BEARPAW FORMATION OF ALBERTA, CANADA**

Mohr, Sydney R., LeBlanc, Aaron R. H., Caldwell, Michael W.  
Biological Sciences, University of Alberta, Edmonton, Alberta, Canada

*Prognathodon* is a genus of mosasaurine mosasaurs with robust skulls, jaws, and teeth, as well as a broad geographic distribution. Within Alberta, the genus is best represented by two well-preserved skeletons of *Prognathodon overtoni* (TMP 2002.400.0001, TMP 2007.034.0001) from the Korite mines, both of which are relatively complete and articulated. *Prognathodon* is rare compared to other mosasaurs found in the Western Interior Seaway, and mostly represented by partial skull and postcranial material. Here we report a new exceptional specimen (TMP 2018.042.0005) from the same locality. This represents the largest and most complete example of *Prognathodon overtoni* to date, and potentially the most complete member of its genus. An estimated total length of the specimen exceeds 7-8 meters, compared to the other two 6-7 meter long individuals. TMP 2018.042.0005 is an articulated skeleton consisting of a complete skull and a nearly complete vertebral series including the tail, hindlimbs, and pelves. The specimen also preserves the first complete and articulated pectoral girdle and forelimb within the species. Whereas the suspensorial region of the *Prognathodon* skull is typically portrayed as streptostylic, TMP 2018.042.0005 preserves its quadrate in a near-natural, inclined position. As such, this new material provides an important data point within an ontogenetic series, and also reveals poorly understood aspects of anatomy in the genus as whole. In addition to the characteristically robust cranial elements, its referral to *Prognathodon overtoni* is supported by numerous features, including a short preidental rostrum, an overlapping prefrontal and postorbitofrontal that exclude the frontal from the orbital margin, and coarsely-textured enamel of the marginal dentition. The maxillary and dentary teeth are also heterodont, with narrower crowns concentrated anteriorly and broad crowns with inflated bases occurring posteriorly in the jaw. Differences between TMP 2018.042.0005 and other examples of *Prognathodon overtoni* include proportionately larger teeth relative to the skull, while maintaining similar maxillary and dentary tooth counts to the other specimens. As a result, TMP 2018.042.0005 reveals new important insights into the morphology of *Prognathodon*, including the opportunity to improve character scoring in phylogenetic analysis, and may potentially have broader implications regarding intraspecific variation and ontogenetic development in mosasaurines.

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## Dinosaur Systematics, Diversity & Ecology

### NEW INFORMATION ON THE CERVICAL VERTEBRAE OF MAMENCHISAURID SAUROPODS FROM THE MIDDLE-LATE JURASSIC SHISHUGOU FORMATION OF NORTHWEST CHINA

Moore, Andrew<sup>1</sup>, Clark, James<sup>2</sup>, Xu, Xing<sup>3</sup>

<sup>1</sup>Dept. of Anatomical Sciences, Stony Brook University, Stony Brook, New York, U.S.A., <sup>2</sup>Dept. of Biological Sciences, The George Washington University, Washington, District of Columbia, U.S.A., <sup>3</sup>Institute of Vertebrate Paleontology & Paleoanthropology, Beijing, China

Fossils of the earliest 'true' sauropods (Eusauropoda) are abundant in Middle-Late Jurassic Chinese deposits, but have yet to be fully leveraged in studies of early sauropod evolution. Many of these specimens appear to belong to a lineage of particularly long-necked eusauropods called mamenchisaurids. Although at least 27 species of putative mamenchisaurids have been named, their anatomy remains poorly represented in the literature. Few previously named species have clear, apomorphy-based diagnoses, and only a handful of recent studies have sought to identify characters that are unique to supraspecific Middle-Late Jurassic Chinese taxa, hindering identification of isolated but potentially diagnosable elements. Our recent comparative anatomical and phylogenetic work on various Middle-Late Jurassic East Asian sauropods produced new character information pertinent to testing the affinities of several isolated cervical vertebrae from the Shishugou Formation of northern Xinjiang. Phylogenetic analysis under equal and implied weights parsimony finds that all specimens belong to Mamenchisauridae. One specimen, comprising three articulated cervicodorsal vertebrae, bears ventrally bifurcate variants of the centropostzygapophyseal lamina, a feature that may be autapomorphic. Collectively, these vertebrae exhibit a suite of character states that are unique to mamenchisaurids or rare among coeval sauropods, including: a lateral pneumatic foramen that has a single anterodorsal septum and is restricted to the anterior two-thirds of the centrum; a prezygodiapophyseal lamina with a ventrally-directed bulge; a ventrally bifurcate postzygodiapophyseal lamina in posterior cervical vertebrae; and extensive internal pneumatization. Although some mamenchisaurids have been noted as having honeycomb-like internal structure in their cervical vertebrae, this anatomy has not been described in detail. Computed-tomography scans of two isolated middle cervical vertebrae and the fourth cervical vertebra of *Mamenchisaurus sinocanadorum* reveal a camerate to semicamellate pneumatic architecture, with air cells

extending throughout the centrum and neural arch and into the zygapophyseal rami. Preliminary estimates find some of these centra to be more than 50% air by volume, and thus comparable in extent of pneumatization to the centra of various neosauropods.

**Funding Sources** AJM support: NSF DGE 1246908 & OISE 1515288; the Jurassic Foundation. JMC and XX support: NSF EAR 0922187 and National Natural Science Foundation of China.

### Symposium: Dietary Reconstruction

#### AGGREGATION OF STABLE ISOTOPES WITHIN MUSEUM SPECIMEN DATA ELUCIDATES THE HYPERGRAZER NICHE IN PLEISTOCENE MAMMALS OF FLORIDA

Moran, Sean M., MacFadden, Bruce J.  
Florida Museum of Natural History, Gainesville, Florida, U.S.A.

Stable isotopic analyses, particularly those of carbon and oxygen, are valuable proxies in examining past climatic and dietary patterns. Over the past three decades, a large body of isotopic data has been generated, mostly on a per study basis, leading to opportunities for integration into larger data sets. Aggregation of published isotopic data potentially allows for recognition of previously unknown emergent patterns as well as more robust testing of previous hypotheses. Our analysis here uses legacy data mined from published literature that have been aggregated via Specify auxiliary data fields of Florida Museum of Natural History VP specimen records. The resultant dataset includes nearly 1,000 sampled specimens from our collection that primarily represent terrestrial herbivores from the Neogene of Florida.

In this study, we provide an example of how this database can be used to more robustly test hypotheses. Previous research has touched on the effects the dispersal of megaherbivores (e.g., *Bison* and *Mammuthus*) have on the niche occupation of endemic taxa. For example, it has been hypothesized that the introduction of *Mammuthus* and/or *Bison* in, respectively, the early and late Pleistocene, displaced *Equus* from the hypergrazer niche to one resulting in an increased reliance on C3 browse. Limited prior research has been ambiguous on what ecological effects, if any, these events had on endemic Florida taxa. Here, we use a subset of our Florida digitized stable carbon isotope data to show a significant decrease in mean  $\delta^{13}\text{C}$  values in Pleistocene equids from the Irvingtonian (-2.21‰) to the Rancholabrean (-3.52‰, i.e., after the appearance of *Bison*), though not from the Blancan to the Irvingtonian (i.e., after the appearance of *Mammuthus*). These isotopic data suggest Pleistocene *Equus* was displaced from its dietary niche as a hypergrazer by the

appearance of *Bison*, but not *Mammuthus*, resulting in increased dependence on C3 vegetation. As more stable isotope data are analyzed and subsequently digitized and aggregated into museum specimen records, these can be used to test interesting patterns. The addition of isotope data to curated museum specimens adds value to the research capacity of museum informatics by facilitating increasingly robust hypothesis testing based on more massive data sets.

**Funding Sources** Supported by NSF DBI-1115210.

### Late Cenozoic Mammalian Macroecology & Macroevolution

#### REVISIONS TO THE LATE BLANCAN MAMMALIAN FAUNA FROM ROLAND SPRINGS RANCH LOCALITY 1, SCURRY COUNTY, TEXAS

Moretti, John A., Johnson, Eileen  
Museum of Texas Tech University, Austin, Texas, U.S.A.

Over the past decade, investigations at Roland Springs Ranch Locality 1 (RSR-1) have explored the biodiversity and taphonomy of a rich vertebrate faunal assemblage contained within a small, localized alluvial deposit in western Texas. The composition of the faunal assemblage recovered from RSR-1 indicates placement within the Pliocene–Pleistocene Blancan Land Mammal Age. Initial identifications have suggested an age of early Pleistocene (~2.6–2.0 Ma) based on mammalian biochronology. Identifications of biochronologically significant mammalian taxa have been revisited in an effort to refine the age interpretation of RSR-1. Identifications have been determined through analysis of large samples of relevant extinct and extant taxa. Specimens initially identified as *Lepus* have been re-assigned to *Nekrolagus progressus*. Although a sample of large sciurid material had been identified as an early form of *Cynomys*, dental cusp morphology now precludes assignment to prairie dog. The sample instead represents an advanced ground squirrel, morphologically consistent with large Blancan species of *Otospermophilus*. The presence of *Ogmodontomys poaphagus* has been verified through comparisons with the type sample. Cheek tooth crown height and metapodial form demonstrate that small hipparionine equid material represents *Nannippus peninsulatus*. Comparisons of a felid mandible, initially identified as the late Pleistocene cheetah-like *Miracinonyx trumani*, with several extinct taxa now support assigning the felid mandible to *Felis rexroadensis* or *F. lacustris*. Overall, the revised identifications have altered the interpretation of the age of RSR-1. Mammalian specimens interpreted as indicating a Pleistocene age (i.e., *Lepus*, *Cynomys*, *M. trumani*) have been re-assigned to forms known primarily from the Pliocene. A single lower 3<sup>rd</sup> premolar remains assigned to

*Azlanolagus*. The temporal range of this small rabbit has recently been extended into the latest Pliocene (Red Corral local fauna at 3.2–2.58 Ma). *Ogmodontomys* is unknown from Pleistocene deposits. Although not common, *Nekrolagus*, *Nannippus peninsulatus*, and *Felis rexroadensis* / *F. lacustris* extend into the Pleistocene, but are absent from samples younger than 2.0 Ma. While the revised identifications do not preclude an earliest Pleistocene age, the current mammalian biochronology suggests a broader possible age range of 3.7–2.0 Ma.

### **Colbert Poster Prize/Marine Reptile Diversity & Biology**

#### **CONVERGENCE AND CONSTRAINT IN NEUROVASCULAR EVOLUTION IN THE SECONDARILY AQUATIC/MARINE SAUROPSID CLADES SAUROPTERYGIA AND MOSASAUROIDEA**

Morgan, Donald J., Witmer, Lawrence  
Biological Sciences, Ohio University, Athens, Ohio, U.S.A.

The invasion of marine and aquatic habitats has been a recurrent theme of sauropsid evolution, occurring independently in Sauropterygia, Ichthyosauria, Thalattosuchia, Thalattosauria, Phytosauria, and Mosasauroida, as well as multiple clades of turtles and birds. The transitions in the body (e.g., streamlining, flippers) are well understood, but comparative studies of cranial sensory anatomy and vasculature are rare. This study explores the role of convergence and phylogenetic constraint in the evolution of cranial vasculature around the nasal cavity and braincase in sauropterygians and mosasauroids. Osteological correlates for neurovasculature, nasal cavity, and olfactory bulbs were identified from both fossil specimens and CT-scan data. Extant sauropsids were models for the identification of endocast neurovascular structures in the extinct taxa. Extinct sampled taxa include the sauropterygians *Nothosaurus*, *Macroplata*, *Libonectes*, and *Nichollssaura* and the mosasauroids *Plotosaurus* and *Plioplatecarpus*, as well as the outgroup *Youngina*. Findings include the presence of derived paired enlarged canals within the premaxillae of both mosasaurs and plesiosaurs. These premaxillary canals are not derived from the dorsal alveolar canal (maxillary vessels and nerve), but rather from branches of the medial nasal vessels and the medial nasal branch of the ophthalmic division of the trigeminal nerve. Within mosasaurs and plesiosaurs, the premaxillary canals are exposed within the nasal cavity, traveling along the nasal septum, potentially illustrating functional convergence to a marine lifestyle within the two clades. That is, in addition to the sensory function of these canals

transmitting the ophthalmic nerve, the enhanced nasal vascular supply likely served a thermoregulatory function within the nasal cavity warming inhaled air as a countercurrent heat exchanger. Both plesiosaurs and mosasaurs also feature derived conditions for blood flow around the brain. *Plioplatecarpus* and *Macroplata* feature derived vasculature conditions near the pituitary fossa and floor of the braincase, and plesiosaurs such as *Libonectes* feature a key-hole shaped foramen magnum for an expanded occipital sinus. Future directions of this study will focus on a quantitative comparison of neurovascular size and olfactory bulb size in extinct and extant aquatic/marine sauropsids with terrestrial members of the clade.

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### **Romer Prize**

#### **FOSSIL EVIDENCE INDICATES ANCIENT ORIGIN OF THE CROCODYLIAN CRANIAL DEVELOPMENTAL PROGRAM**

Morris, Zachary S.  
Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts, U.S.A.

Anatomical convergence provides some of the most compelling proof for evolution, but the relative importance of environmental and developmental factors as mechanisms of convergence is not fully understood. The fossil record of crocodylians and their extinct relatives, Pseudosuchia, present many examples of convergence and is an ideal system in which to study these dynamics. Similar blunt-, moderate-, and slender-snouted forms have arisen several times in both living species and stem-crocodylians, potentially due to convergent dietary and ecological specialization (i.e., cranial ecomorphs). However, the developmental origins of crocodylian cranial shape and the role of developmental constraint in pseudosuchian cranial evolution remain unknown. Here, I present a 2D geometric morphometric analysis of skull shape using a novel application of PCA to quantify the multidimensional major axes of variation (MA) within pseudosuchian clades and across crocodylian development. By including the diversity of extinct pseudosuchians (n = 146) and the ontogenetic and adult ecological variation of extant crocodylians (n=305), this study tests the impact of ecology and development on the evolution of skull shape. The ontogenetic MAs of ecomorphs, with the exception of *Gavialis*, are characterized by a positive correlation of relative snout length (PC1) and snout breadth (PC2) originating from a conserved embryonic skull shape. In contrast, the MA of

extant adult crocodylians shows a negative correlation between these PCs, reflecting ecomorph specialization. These nearly orthogonal MAs, therefore, represent distinct hypotheses for the source of cranial variation: ecological pressure or developmental constraint. Triassic pseudosuchians do not fit either model well, as their MA uniquely recovers PC4 as the most important. The MA for all of Crocodylomorpha aligned with extant ecology, but the MAs of individual subclades (e.g., Metriorhynchidae, terrestrial notosuchians) were indistinguishable from ontogenetic MAs. Thus, evolution within clades likely followed ‘developmental lines of least resistance’ due to constraint by allometric correlations. Trends across clades reflect change in these correlations, potentially in response to major ecological shifts. Overall, this strongly supports the hypothesis that modern crocodylian developmental programs evolved by the Jurassic and developmental constraint was a key mechanism in the convergent evolution of snout shape within Pseudosuchia.

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### Dinosaur Systematics, Diversity & Ecology

#### CERATOPSIAN BIOGEOGRAPHY CONFIRMS THE IMPORTANCE OF THE BERING LAND BRIDGE DURING THE CRETACEOUS

Maykovich, Tyler, Morschhauser, Eric  
Biology, Indiana University of Pennsylvania, Indiana, Pennsylvania, U.S.A.

Ceratopsia is a derived clade of ornithischian dinosaurs that originates in the Late Jurassic and, among unambiguous occurrences, has an exclusively Laurasian paleobiogeographic distribution. The relative abundance of ceratopsians in both Asia and North America make it a reasonable clade to test hypotheses of the routes and timings of dispersal events between Asia, Europe, and North America. We generate a time calibrated evolutionary tree from a character matrix sampling both basal Ceratopsian and Ceratopsid diversity. We report the first quantitative analysis of ceratopsian biogeography using the likelihood-based R-package BIoGeoBEARS. The results from Ceratopsia were compared to those for other terrestrial vertebrate clades (Tyrannosauroidae, Mammalia, Hadrosauroidae) with time-calibrated evolutionary trees based on matrices taken from the literature. The results support an Asian origin of Ceratopsia, and three dispersal events from Asia to North America. We do not recover support for a European route to North America. Two of the three dispersal events are projected to occur in the Aptian and the third, an event including early diverging members of Ceratopsidae, during the early Turonian. We also find support for three dispersal events from North America to Asia, two within

Leptoceratopsidae and one within Ceratopsidae. All dispersal events to Asia are projected to occur during the Santonian or Campanian. Dating of the dispersal events in general are hampered by poor constraint on a small number of Asian localities. The ceratopsian migrations are consistent with the patterns of connectivity seen in the other clades.

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### Mesozoic & Early Cenozoic Mammalian Evolution

#### MEASURING THE RELATIVE EFFECTS OF CLIMATE CHANGE AND COMPETITION ON PRIMATE DIET DURING THE PALEOCENE–EOCENE THERMAL MAXIMUM

Morse, Paul E.<sup>1</sup>, Boyer, Doug M.<sup>1</sup>, Bloch, Jonathan I.<sup>2</sup>  
<sup>1</sup>Evolutionary Anthropology, Duke University, Durham, North Carolina, U.S.A., <sup>2</sup>Florida Museum of Natural History, University of Florida, Gainesville, Florida, U.S.A.

The fossil record of the Bighorn Basin (BHB), Wyoming, records the earliest fossils of adapid and omomyid euprimates from the same localities as ecologically similar uintrasoricine and microsypine microsypid plesiadapiforms ~56 Ma. This time period corresponds to an interval of global warming known as the Paleocene–Eocene Thermal Maximum (PETM), when temperature increased by >5° C in ~20 kyr, remained elevated for ~120 kyr, then cooled to background levels. Similarities in body size and dental morphology suggest that immigrating euprimates may have competed with endemic microsypids upon arrival during the PETM. Changes in temperature, aridity, and floral community during the cooling at the end of the PETM may have posed an ecological challenge to microsypids and euprimates and exacerbated selective pressures posed by competition between them.

Dental topography (DT) quantifies functionally relevant traits such as tooth relief, complexity, and sharpness (DNE), and is effective at discriminating among broad dietary categories in extant primates. We measured  $\mu$ CT-generated 3D digital models of m2 crowns from a high-resolution stratigraphic section spanning the PETM and post-PETM in the southern BHB to test if uintrasoricine (n = 35) or microsypine (n = 9) DT changed during the PETM coincident with the arrival of euprimates. We compared PETM to post-PETM DT in these taxa, omomyids (n = 32), and adapids (n = 22) to test the effects of climate change on primate diet. DT of a sample of extant prosimian primates (n = 109) of known diet was used to evaluate which diet best characterized the DT of fossil specimens in a linear discriminant model (LDM).

The LDM indicates that each fossil taxon occupies a unique region of multivariate 'topography space.' While uintrasoricine DT changed during the PETM ( $p = 0.04$ ), it converged on that of euprimates, indicating dental shape displacement was not the result of dietary competition between these taxa. The DT of microsypines and adapids was unchanged at the end of the PETM, while uintrasoricine crown height decreased ( $p = 0.02$ ). Omomyid DNE was lowest, consistent with omnivory, during peak PETM temperature and aridity, and increased ( $p < 0.001$ ) post-PETM, indicating a shift toward insectivory. Climate change at the end of the PETM appears to have affected primate dietary ecology more than immigration events, and may have played a role in establishing the insectivorous morphology observed in later-occurring omomyids from the BHB.

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#### **Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

#### **ECOLOGY AND BIOGEOGRAPHY OF AN UNEXPECTED SHORT-FACED BEAR (*ARCTODUS SIMUS*) FROM THE CALIFORNIA CHANNEL ISLANDS**

Mychajliw, Alexis M.<sup>1</sup>, Rick, Torben C.<sup>2</sup>, Dagtas, Nihan D.<sup>1</sup>, Erlandson, Jon M.<sup>6</sup>, Culleton, Brendan J.<sup>5</sup>, Kennett, Douglas J.<sup>4</sup>, Buckley, Mike<sup>3</sup>, Hofman, Courtney<sup>1</sup>

<sup>1</sup>Laboratories of Molecular Anthropology & Microbiome Research, University of Oklahoma, Norman, Oklahoma, U.S.A., <sup>2</sup>Anthropology, National Museum of Natural History, Washington, District of Columbia, U.S.A., <sup>3</sup>Manchester Institute of Biotechnology, University of Manchester, Manchester, U.K., <sup>4</sup>Anthropology, University of California, Santa Barbara, Santa Barbara, California, U.S.A., <sup>5</sup>Institutes of Energy and the Environment, The Pennsylvania State University, University Park, Pennsylvania, U.S.A., <sup>6</sup>Anthropology, University of Oregon, Eugene, Oregon, U.S.A.

The short-faced bear, *Arctodus simus*, was one of the largest mammalian carnivores of late Pleistocene North America. Known from more than one hundred fossil localities, the species occupied a wide geographic distribution spanning Beringia to Mexico and disappeared by the Holocene. Despite its former abundance, a firm understanding of its diet and ecology has remained elusive, with reconstructions ranging from herbivory to kleptoparasitism. Using a combination of morphological, mitogenomic, and proteomic lines of evidence, we identified the first occurrence of *A. simus* from the

California Channel Islands (CCI) at ~17,000 calibrated years before present (cal ybp). We developed a robust hypothesis-testing framework to address this biogeographic puzzle and evaluated the specimen's likely origin, transport, and deposition, distinguishing pre- and post-mortem mechanisms. *Arctodus simus* is represented by a single metapodial recovered from Daisy Cave (CA-SMI-261), a well-stratified archaeological locality documenting some of the earliest human occupation in the Americas starting ~13,000 cal ybp, with humans thus post-dating the arrival of the bear. Though the CCI experienced a history of sea level fluctuations, facilitating, for example, the dispersal of mainland Columbian mammoths, taphonomic conditions suggest that the pre-mortem individual dispersal of a single bear or existence of a standing population was unlikely. Instead, stable isotope values of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  suggest this bear was utilizing marine resources along the coast, and we posit its carcass may have been foraged by a scavenging bird, which brought the metapodial to its roost on the CCI. Deciphering this complex scenario was only possible through the use of an integrative toolkit and collaboration between paleontologists and archaeologists, and highlights the utility of such approaches in revealing cryptic translocations and vetting insular biodiversity lists worldwide.

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#### **Colbert Poster Prize/Biomechanics & Functional Morphology**

#### **MORPHOLOGICAL INDICES FOR DIGGING ABILITY AND STRATEGIES USING FORELIMBS IN EXTINCT MAMMALS**

Nakai, Daichi<sup>1</sup>, Fujiwara, Shin-ichi<sup>2</sup>

<sup>1</sup>Environmental Studies, Nagoya University, Nagoya, Aichi, Japan, <sup>2</sup>Nagoya University Museum, Nagoya, Aichi, Japan

Digging ability enabled many lineages of tetrapods to shift their ecological space from terrestrial to subterranean. Among the fossorial tetrapods, many rely on their forelimbs for digging, but the way they dig varies by taxa; for example, humeral-rotation digging (e.g., true moles), hook-and-pull digging (e.g., anteaters) and scratch-digging (e.g., armadillos). To understand the evolutionary process of the ecological shift in these lineages, it is important to reliably reconstruct digging ability and strategy using the forelimbs in extinct taxa based on the adequate quantitative morphological index for evaluating digging ability and strategies.

In this study, we focused on the differences in motion of the shoulder and elbow joints by digging strategies using

the forelimbs among mammals. The 211 extant mammalian specimens included in this analysis (205 species in 195 genera, 84 families, and 24 orders) were categorized into forelimb-dependent diggers, non-diggers, and forelimb-dependent swimmers. After which, the leverages of the shoulder retractors and medial rotators, and the leverages of the elbow extensors, flexors, and adductors were compared among the categories.

We found that forelimb-dependent diggers can be discriminated using the above indices. The forelimb-dependent diggers and the forelimb-dependent swimmers emphasized four out of the five leverages (shoulder retractor and medial rotator; elbow extensor, flexor, and adductor) relative to non-diggers, and the forelimb-dependent diggers had greater leverage of the elbow flexor relative to the forelimb-dependent swimmers. We also found that the leverage ratios reflect the digging strategies among extant forelimb-dependent diggers. Given these results, the leverage ratios of the shoulder and elbow muscles are expected to be new quantitative indices for reconstructing the digging ability and strategies using the forelimbs in extinct taxa.

We also reconstructed the digging abilities and strategies in some extinct taxa using these indices. Our results showed that *Ernanodon* (Palaeonodonta, Ernanodontidae) was a scratch digger, and *Metacheiromys* (Palaeonodonta, Metacheiromyidae) and *Diictodon* (Therapsida, Diconodontia) were humeral-rotation diggers. In contrast, our results indicate that *Moropus* (Perissodactyla, Chalicotheriidae) and *Thylacinus* (Dasyuromorphia, Thylacinidae) were non-diggers.

## **Anatomical & Developmental Explorations of the Mammalian Skull**

### **A STUDY OF SABERTOOTH CAT CRANIA: NEW CONSIDERATIONS IN THE FUNCTION OF THE SKULL AND MANDIBLE IN *SMILODON FATALIS***

Haji-Sheikh, Misty, Naples, Virginia  
Department of Biological Sciences, Northern Illinois University, DeKalb, Illinois, U.S.A.

*Smilodon fatalis* is among the most iconic of fossil sabertooths, best known for elongated canine teeth that enabled it to kill large prey. Published *Smilodon* reconstructions as well as natural history exhibits are typically modeled after living large conical tooth cat anatomy because there are no living analogues. The dental and correlated musculoskeletal differences seen between the living and extinct cats with the two different dentition types have led to misinterpretations of the appearance and

functional gape capabilities of *Smilodon*. Historically, the way in which the *S. fatalis* skull and mandible soft tissues have been reconstructed does not take into account the bite angles that are the most useful for a living cat. Specifically, the angle at which the mandible and maxilla can move in relationship to one another must also account for the muscles and tendons that also limit jaw opening and closing. The usual reconstructed display shows a mandible that could not open far enough to allow a bite wide enough to encompass even the diameter of a chicken's egg. The jaw joint engaged at maximum capacity with no clearance past the dentition would not generate much bite force. There have been computer-based studies that modeled the amount of bite force in *S. fatalis*; some showed a powerful bite whereas others predicated a weak bite. The major problem is that the canines are often mounted so far out of their alveoli that the S-shaped dentine margin is exposed; this would be very painful and would not occur in a living animal. By seating the upper canines properly, i.e., more deeply in their sockets, *S. fatalis* could use these teeth with a decreased likelihood of breakage and would generate more appropriate bite forces. For these reasons, the way the *S. fatalis* skull has been reconstructed needs to be reexamined, as we have done in this study.

## **Anatomical & Developmental Explorations of the Mammalian Skull**

### **SPECIALIZATION IS NOT CANALIZATION: DECOUPLING OF ECOLOGICAL AND MORPHOLOGICAL DISPARITY WITHIN EXTANT URSIDAE**

Napoli, James G.<sup>1</sup>, Jiangzuo, Qigao<sup>2</sup>, Liyandja, Tobit<sup>1</sup>, Harcourt-Smith, William<sup>3</sup>

<sup>1</sup>Richard Gilder Graduate School, American Museum of Natural History, New York, New York, U.S.A., <sup>2</sup>Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China, <sup>3</sup>Division of Paleontology, American Museum of Natural History, New York, New York, U.S.A.

Intraspecific variation simultaneously represents both a confounding variable and a powerful source of information in vertebrate paleontology. The myriad sources of intraspecific variation, including ontogeny, sexual dimorphism, clinal effects, and polymorphism, complicate species delimitation among extinct taxa. However, just as genomic variation within and between populations reveals important aspects of selection and evolutionary history, so too should phenotypic variation. Ecological specialization is usually hypothesized to cause phenotypic canalization, and has been proposed as a mechanism contributing to the high extinction risk suffered by specialist taxa. We chose extant Ursidae, which includes extreme dietary generalists as well as specialized carnivores, herbivores, and

insectivore/frugivores, as a model group to test this hypothesis in the context of dietary specialism. We focused on mandible shape due to its well-documented relationship with dietary ecology. We collected a 3D geometric morphometric dataset comprising 18 homologous landmarks from 469 adult specimens of all eight species of extant Ursidae, which was aligned via generalized Procrustes superimposition. Morphological disparity among and between species was computed as both pairwise Procrustes distances and the sum of variance in morphospace axes. No significant effects of ontogeny, sexual dimorphism, or clinal variation were detected intraspecifically, meaning the disparity between specimens solely represents morphological polymorphism. Our results indicate the traditional hypothesis of increased canalization among specialists is incorrect. Specialist taxa show consistently higher intraspecific variation than generalists, with the most specialized taxon (*Ailuropoda melanoleuca*) showing the greatest range of variation. These results imply that the selective pressures operating on specialists may be misunderstood, and that specialization-induced canalization is an unlikely mechanism for increased extinction risk in generalist ursids. Furthermore, they create a hypothesis-testing framework for understanding dietary niche breadth in extinct taxa. Addition of *Arctodus simus*, *Ursavus elmensis*, and *Ursus spelaeus* to our dataset reveals the likely dietary niche breadth of these extinct taxa. Future work will be invaluable for testing whether dietary specialization causes canalization in other clades and for more robustly contextualizing intraspecific variation in the fossil record.

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### **Colbert Poster Prize/Anatomical & Developmental Explorations of the Mammalian Skull**

#### **NEW VIRTUAL CRANIAL ENDOCASTS OF GIANT GROUND SLOTHS: IMPLICATIONS FOR UNDERSTANDING BRAIN EVOLUTION IN FOLIVORA (MAMMALIA, XENARTHRA, PILOSA)**

Narducci, Rachel E.<sup>1</sup>, Silcox, Mary T.<sup>2</sup>, Bloch, Jonathan I.<sup>1</sup>  
<sup>1</sup>Florida Museum of Natural History, University of Florida, Gainesville, Florida, U.S.A., <sup>2</sup>Anthropology, University of Toronto Scarborough, Scarborough, Ontario, Canada

Folivora (sloths and their extinct giant relatives) first appeared in the late Eocene (~36 Ma) of South America, expanded their range from Southern Chile into the Caribbean Islands and as far north as Canada, and diversified to 90+ genera in the fossil record. Despite this

impressive past diversity, there are only two extant genera (*Bradypus* and *Choloepus*), both with specialized suspensory arboreal lifestyles with a range of body mass limited to ca. 2.5 kg (*Bradypus pygmaeus*) to 10.6 kg (*Choloepus didactylus*). By contrast, extinct folivorans range in body mass from ca. 20.6 kg (*Neocnus* spp.) to 4,500 kg (*Megatherium* spp.) and were mostly ground dwelling. Prior to this study, understanding the anatomy of the brain in extinct folivorans has been limited.

To better understand anatomical changes to the brain throughout the evolution of Folivora we created virtual cranial endocasts derived from high-resolution X-ray computed tomography scans of 16 extinct and 14 extant folivora skulls, including all three superfamilies of Folivora: Megalocnoidea (five spp.), Megatherioidea (three spp.), and Mylodontoidea (one sp.). These are compared to cranial endocasts of extant folivorans and extinct megatheriid *Thalassocnus* spp. from the literature. Extant anteaters (four spp.), an extant armadillo (*Dasylops novemcinctus*), and extinct large bodied cingulates (three spp.) serve as outgroups. Variation in cranial endocast morphology was examined using encephalization quotients and three-dimensional geometric morphometrics.

Results highlight the variation in endocranial morphology of folivorans, even within species, with notable anatomical differences associated with body mass. Encephalization quotients show a decrease in relative brain mass with an increase in body mass, except in Megalocnoidea. There is an allometric effect on shape with large bodied (>100 kg) species plotting together. There is also evidence of a phylogenetic signal. In particular, the location of folivora taxa in morphospace is influenced by both phylogeny and size, with endocranial shape separation along the 1<sup>st</sup> Principal Component axis presenting a clear divide between Megalocnoidea and Megatherioidea, but not between large extinct and small extant Mylodontoidea taxa. These results are congruent with recent morphometric studies on mammalian virtual cranial endocasts that have found that endocranial shape is constrained by phylogeny, which complicates attempts to make functional inferences from endocast form.

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### **Evolution & Biology of Non-Avian Theropods**

#### **RECONSTRUCTING THE MIDDLE-EAR SOUND-CONDUCTION APPARATUS IN COELUROSAURIA IN THE TRANSITION TO BIRDS**

Nassif, Jann P., Ridgely, Ryan C., Witmer, Lawrence  
Ohio University, Athens, Ohio, U.S.A.

Constraining the sensory ecology of extinct taxa necessitates basic anatomical work linking soft tissues with their osteological correlates. The morphology of inner-ear organs and middle-ear pneumaticity are used commonly to infer hearing abilities in nonavian dinosaurs. Other peripheral hearing structures, such as the middle-ear sound-conduction apparatus, have received less consideration. In living archosaurs, a tympanum (eardrum) receives environmental vibrations and transmits sound energy through cartilage and the columella auris bone (stapes) to the inner ear. Birds and nonavian theropods present the opportunity to evaluate the morphology of the hearing apparatus across diverse ecologies and sizes. A diverse sample of bird, crocodylian, and lepidosaur specimens were stained using Lugol's iodine and  $\mu$ CT scanned (i.e., diceCT). Ear structures including tympana, columellae, and cartilaginous extracolumellae were digitally reconstructed in Avizo. Specimens were also dissected to validate CT-based interpretations. Osteological correlates including the dorsal attachments of the tympanum and position of the pharyngotympanic tube were identified. These correlates were then evaluated in photographed and scanned fossil coelurosaur specimens, consistent with established methods of phylogenetic bracketing. These and other well-established correlates were then used to model putative middle-ear structures in select fossil specimens. The position of the sound-conduction apparatus can be reliably identified in *Tsagaan* and other sampled coelurosaurs. The positions of the tympana of early branching clades, constrained caudally by the depressor mandibulae musculature, are similar to the inferred ancestral state among dinosaurs. The caudomedial rotation of the tympanum in maniraptoriforms suggests the expansion of an external acoustic meatus within the clade. The anatomy of morphologically extreme tyrannosauroids suggests thickening of the tympanum and bracing of the elongate columellar shaft against the wall of the tympanic cavity, which is consistent with reduced high-frequency sensitivity. Tyrannosaurs represent a potentially valuable group in which to investigate how sensory organ function interacts with extreme body and/or head size. Holistic morphological consideration of the hearing apparatus lays the groundwork for exploration of previously insoluble questions about sonic communication, predator/prey detection, and other topics in sensory ecology.

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**Colbert Poster Prize/Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

## OWL PELLETS OF THE ARCTIC NATIONAL WILDLIFE REFUGE REVEAL SPATIAL GRADIENT IN SMALL MAMMAL COMMUNITIES

Neale, Bianca<sup>1</sup>, Miller, Joshua H.<sup>1</sup>, Wald, Eric J.<sup>3</sup>, Druckenmiller, Patrick S.<sup>2</sup>

<sup>1</sup>Geology, University of Cincinnati, Cincinnati, Ohio, U.S.A., <sup>2</sup>University of Alaska Museum, Fairbanks, Alaska, U.S.A., <sup>3</sup>Arctic Network Inventory and Monitoring, National Parks Service, Fairbanks, Alaska, U.S.A.

Historical and subfossil skeletal remains provide important resources for evaluating extant small mammal diversity. Owls (Strigiformes) consume prey whole and regurgitate pellets of indigestible bones and other tissues. Accumulations of pellets faithfully record the local availability and diversity of small-bodied prey species. Because pellet accumulations are time-averaged over decades or more, they may be particularly useful for establishing long-term population metrics for microtine rodents and other species that undergo large population cycles. Here, we use pellet-derived bone accumulations to evaluate changes in rodent communities across the Coastal Plain of the Arctic National Wildlife Refuge, Alaska. The region is dominated by three microtine species: collared lemming (*Dicrostonyx groenlandicus*), North American brown lemming (*Lemmus trimucronatus*), and tundra vole (*Microtus oeconomus*). However, few data are available to indicate their expected abundance structure across space. To evaluate spatial patterns in microtine abundances, owl pellets were collected during taphonomic surveys of openly vegetated tundra habitats (Dryas Terraces). Surveys focused on seven major rivers (Canning, Katakaturuk, Hulahula, Jago, Aichillik, Kongakut, and Turner Rivers) between 2010 and 2018. Rivers extend north-south, bisecting the Coastal Plain at regular intervals across 200 km of longitude. Pellets were dissected and mammalian remains were identified using tooth morphology and comparative collections at the University of Alaska Museum. For each pellet or local bone accumulation, specimen counts were summarized using the minimum numbers of individuals. We find significant changes in microtine community composition across the Coastal Plain. The community is strongly dominated by lemmings (*Dicrostonyx* + *Lemmus*) in the east and voles (*Microtus*) in the west. The shift in arcsine-transformed proportional abundance of voles is roughly continuous across longitude and highly significant (weighted linear regression;  $p < 0.01$ ,  $R^2 = 0.79$ ). This dramatic shift in the Coastal Plain microtine community was previously unrecognized. Our results illustrate that (1) even in species-poor arctic settings, biological heterogeneity can be high, and (2) conservation paleobiological investigation of historical and subfossil records can provide novel insight for more fully understanding the biological variability and gradients of modern ecosystems.

## Quantitative Methods

### CALCULATING BODY MASS FOR NOTOUNGULATES USING HEAD-BODY LENGTH BASED ON A WIDE RANGE OF MODERN MAMMALS BEYOND UNGULATES

Nelson, Allison E., Croft, Darin A.  
Case Western Reserve University, Seattle, Washington, U.S.A.

Several major mammal clades are included within the informal moniker South American native ungulates (SANUs). SANUs lack extant representatives and have no close relatives with similar body plans, which has made reconstructing many aspects of their paleoecology challenging. This is particularly the case for notoungulates, the most diverse and speciose SANU group; notoungulate skulls, dentitions, and limb bones are quite atypical compared to modern ungulates, and this raises doubts about using modern ungulate models and equations to determine diet, body mass (BM), and other notoungulate attributes. Head-body length (HBL) is highly correlated with BM in extant mammals and has been recommended for estimating BM in extinct mammals lacking close modern analogs. Of course, a major constraint in this approach is that it requires knowledge of the complete skeleton of an extinct species. Relatively few complete skeletons are known for notoungulates, but those that are known hold promise for helping gauge the accuracy of BM estimates based on other, more limited skeletal elements.

We created a dataset of HBL and BM values for 354 extant terrestrial, non-volant mammals of 20 orders, including only mammals >500 g (the range likely spanned by most notoungulates). A representative size range of each order was included to avoid over-sampling particularly species-rich groups. From this dataset, we calculated a regression equation of BM on HBL to estimate notoungulate BM, with results as follows: *Protypotherium australe* (4.2 kg; 53 cm), *Interatherium robustum* (1.4 kg; 36 cm), *Pachyrhoxos moyani* (0.92 kg; 31 cm), *Thomashuxleya externa* (87 kg; 150 cm), *Homalodotherium cunninghami* (170 kg; 190 cm), *Adinotherium ovinum* (37 kg; 110 cm), and *Nesodon imbricatus* (140 kg; 180 cm). Percent prediction error was 51%. In general, these HBL-based BM estimates are lower than those based on cranial measurements that use modern ungulates as analogs. This suggests that: (1) broader taxonomic samples of extant mammals should be used in comparative datasets; and/or (2) craniodental morphologies of notoungulates may be so distinct from those of extant mammals that they result in misleading BM estimates. Certain limb bones, such as the astragalus, seem to be accurate indicators of BM based on comparisons with HBL-based estimates.

## Marine Mammals

### TAXONOMIC REVISION OF THE PACIFIC RECORD OF THE SQUALODONTIDAE (CETACEA, ODONTOCETI)

Nelson, Margot D., Uhen, Mark D.  
Atmospheric, Oceanic, and Earth Sciences, George Mason University, Fairfax, Virginia, U.S.A.

The Squalodontidae is a historic family of fossil odontocetes that is now recognized as a 'wastebasket taxon' for fragmentary fossils of heterodont cetaceans. As a result, the Squalodontidae are in need of taxonomic revision so that the family can be placed in an accurate phylogenetic context. Historically, squalodontids were thought to be characterized by triangular cheek teeth featuring heavily ornamented crowns and short ridges that extend towards the apex of the crown (the cristae rugosae of earlier authors). Currently, only three genera within the Squalodontidae are known from partial or nearly complete skulls: *Phoberodon*, *Eosqualodon*, and *Squalodon*. Of these genera, diagnostic material is restricted to the Atlantic Ocean. In the Pacific realm, there are two named genera reported from New Zealand: *Austrosqualodon*, a mandibular fragment with no associated teeth; and *Tangaroasaurus*, a mandibular fragment with a few associated teeth. Neither *Austrosqualodon* nor *Tangaroasaurus* have enough material preserved to be considered diagnostic and previous authors have considered *Austrosqualodon* a nomen dubium. Other Pacific records of the Squalodontidae include finds from Japan, Australia, Chile, the west coast of North America, and Costa Rica. None of these fossils are identified to species level, and most are diagnosed as *Squalodon* sp. or Squalodontidae indet. Here, we evaluate the fossil record of the Squalodontidae in the Pacific Ocean with the goal of refining the taxonomy and biogeography of the Squalodontidae. Pending further work extracting phylogenetic signals from heterodont cetacean teeth that may enable us to diagnose teeth to a family level, we conclude that 'squalodont' fossils of the Pacific should be considered Odontoceti incertae sedis. As a result, the Squalodontidae appear restricted to the north and south Atlantic.

## Mesozoic & Early Cenozoic Mammalian Evolution

### TOOTH ERUPTION AND MORPHOLOGY IN EARLY MAMMALS: A JUVENILE DRYOLESTOID SKULL FROM THE LATE CRETACEOUS OF SOUTH AMERICA.

Newton, Kayla<sup>2</sup>, Apesteguía, Sebastián<sup>3</sup>, Davis, Brian<sup>1</sup>, Rougier, Guillermo W.<sup>1</sup>

<sup>1</sup>Anatomical Sciences and Neurobiology, University of Louisville, Louisville, Kentucky, U.S.A., <sup>2</sup>School of Dentistry, University of Louisville, Louisville, Kentucky, U.S.A., <sup>3</sup>CONICET, Fundación de Historia Natural 'Félix de Azara', Buenos Aires, Argentina

Meridiolestids are a diverse and distinct clade of Cretaceous–Miocene South American dryolestoid mammals ranging in size from small shrew-sized insectivores to relatively large dog-sized omnivores. *Cronopio dentiactus* from the Cenomanian La Buitrera locality (Candeleros Fm., Argentina) is the best known of them, represented by skull material and associated jaws.

A juvenile skull referred to *Cronopio dentiactus*, based on tooth size and morphology, was collected from the type locality. The specimen, a small concretion, includes the skull and both articulated lower jaws. The fossil is poorly ossified and partially flattened; CT scanning reveals most of the dentition in place and a few floating teeth. Damage has occurred rostrally and no upper canines or incisors are present. Skull length is estimated at 16mm (adults are 27mm). The body of the jaw and snout are short and lack large diastemata, which characterize *Cronopio* adults. There is no clear evidence of replacement teeth in mandibular or cranial crypts, and there is no striking difference in thickness or gross appearance between the enamel of molars and that of teeth regarded as deciduous. None of the pristinely preserved teeth show any evidence of wear. The alveolar process is a paper-thin sheet of bone covering the bulk of the anterior dentition, while a broad Meckelian groove runs along the medial side of the dentary reaching the symphysis. The m3 appears to be close to occlusal position, while the M3s are floating in the matrix. The last premolars and the first two molars show the beginnings of root development, which are lacking in the last molars and still-erupting anterior premolars and canine. The anterior premolars and the sole preserved canine are deciduous. The dc is a broad labiolingually compressed crown and the dps are more complex than the permanent premolars in adult specimens. A lower incisor, further along in development, is preserved directly mesial to the dc, although it does not appear to be in life position. Given that the last lower molar is erupting and close to occlusal position, the specimen is technically a late juvenile; however, the small size, juvenile proportions, poor ossification, anterior premolars unerupted, and absolute lack of wear suggest the specimen is still immature and likely not fully weaned. The developmental sequence does not easily conform to known therian patterns and it is uncertain if it is viable as primitive for mammals in general.

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## Taphonomy & Stratigraphy

### HYDRODYNAMIC TRANSPORT POTENTIAL OF MODELLED TURTLE SHELL IN A CONTROLLED FLUVIAL SETTING: A CASE STUDY IN EXPERIMENTAL TAPHONOMY

Noto, Christopher R.<sup>1</sup>, Peterson, Joseph<sup>2</sup>

<sup>1</sup>Biological Sciences, University of Wisconsin-Parkside, Kenosha, Wisconsin, U.S.A., <sup>2</sup>Geology, University of Wisconsin-Oshkosh, Oshkosh, Wisconsin, U.S.A.

The Arlington Archosaur Site (AAS) is notable as the most dense and well preserved assemblage in the Woodbine Group. The taphonomic history of the AAS is complex, with multiple overlapping signatures. Among the most abundant remains at the site are whole and fragmented pieces of turtle shell. Turtle shells are composed of repeated elements of varying shape that can disarticulate and be transported separately after death. It is uncertain to what degree element shape affects hydrodynamic transport behavior and ultimate preservation potential in different depositional environments. An actualistic approach provides a framework to test the roles of water transport, substrate interactions, and/or surface exposure as factors in bone preservation. To test hypothesized processes of turtle shell deposition at the AAS, a series of taphonomic experiments were conducted to explore 1) potential entrainment velocities and transport of shell pieces, and 2) abrasion of shell pieces during transport and entrainment. To test potential entrainment velocities and settling orientations of shell pieces, representative models of common shell elements were designed using CAD software, 3D printed, molded and cast in resin. Different trials explored the effect of variable vs fixed depth and flow rate using a flume with manual velocity control. To test the potential taphonomic modification to shell pieces during fluvial transport, modern turtle elements were placed in a rock tumbler with uniform sized sediment (silt, fine sand, coarse sand, gravel) for one week to observe patterns of wear. Results show element length and degree of curvature affect transport potential. Curved elements require lower entrainment velocities while smaller, flatter elements require greater entrainment velocities but, once mobile, are transported further. Significant sediment/shell interaction at all grain sizes was observed, especially where the shell was in contact with a substrate (i.e., container), though the damage differed qualitatively. In silt and fine sand wear was concentrated around the edges, while in coarse sand and gravel the majority of the surface was abraded. The fine-grained AAS sediment suggests that shell fragments were not being abraded solely due to transport, but rather experienced post-depositional sediment-shell interactions as lag. Studying turtle shell preservation patterns may be

useful for understanding processes driving vertebrate accumulation at fossil sites such as the AAS.

### Permo-Triassic Tetrapods

#### COMMUNITY RESPONSE TO THE END TRIASSIC MASS EXTINCTION IN THE ELLIOT FORMATION OF SOUTH AFRICA AND LESOTHO

Oberg, Danielle<sup>1</sup>, Suarez, Celina<sup>1</sup>, Choiniere, Jonah N.<sup>2</sup>

<sup>1</sup>Geosciences, University of Arkansas, Fayetteville, Arkansas, U.S.A., <sup>2</sup>University of the Witwatersrand, Johannesburg, South Africa

The Elliot Formation, which spans the Upper Triassic to the Lower Jurassic in the Karoo Basin of southern Africa, is rich in both vertebrate body and trace fossils and serves as a global standard for Triassic-Jurassic boundary (TJB) studies. This fossil record includes remains of true dinosaurs, pseudosuchians, lepidosaurs, stem-group turtles, temnospondyl amphibians, and later-branching therapsids. The Elliot Formation is one of the few fossiliferous continental deposits that spans the end Triassic Mass Extinction (ETE), which makes this formation crucial for understanding changes in the terrestrial ecosystems of southern Pangaea through the TJB interval. Previous studies of vertebrate diversity in the Elliot Formation have focused on total diversity of the lower Elliot (LEF) and upper Elliot (UEF) members across all of southern Africa; however, this is too coarse to observe changes in community structure due to the ETE, therefore finer scale analysis is needed to determine how communities changed.

Vertebrate occurrence (n = 312) and abundance (n = 493) data for the Elliot Formation were collected from the Paleobiology Database. Data from the UEF and LEF members were analyzed separately. A Euclidean cluster analysis was conducted using latitude and longitude data to create multitaxic, local communities of 5 or more taxonomic occurrences within 25 km radius of each centroid, yielding n = 8 LEF and n = 9 UEF local communities. Diversity analyses (e.g., Pielou evenness, Chao richness/Shannon Diversity Index [ $\alpha$ -diversity], and Whittaker Index [ $\beta$ -diversity]) were calculated to examine change in diversity and community structure.

We found that total diversity for both the UEF and LEF is similar, and species richness for the UEF was much higher than the LEF. LEF communities had more even distribution of species abundances and greater species overlap between communities than the UEF communities. Sauropodomorph dinosaurs and archosaurs were most abundant in both the LEF and UEF, however, their contribution to each community was variable. The initial results provide new insights into the unique dynamics of the local communities of the Elliot Formation, and are an

important step in understanding how these communities were affected by the ETE.

### Holocene & Pleistocene Mammalian Macroecology & Faunal Studies

#### FIRST APPEARANCE OF GRÉVY'S ZEBRA (*EQUUS GREVYI*), KAPTHURIN FORMATION, KENYA

O'Brien, Kaedan<sup>1</sup>, Tryon, Christian A.<sup>3</sup>, Blegen, Nick<sup>2</sup>, Kimeu, Boniface<sup>4</sup>, Faith, J. Tyler<sup>1</sup>, Rowan, John<sup>5</sup>

<sup>1</sup>Anthropology; Natural History Museum of Utah, University of Utah, Salt Lake City, Utah, U.S.A.,

<sup>2</sup>Geography, University of Cambridge, Cambridge, U.K.,

<sup>3</sup>Anthropology, University of Connecticut, Storrs,

Connecticut, U.S.A., <sup>4</sup>Earth Sciences, National Museums of Kenya, Nairobi, Kenya, <sup>5</sup>Department of Anthropology,

University at Albany, State University of New York, Albany, New York, U.S.A.

The endangered Grévy's zebra (*Equus grevyi*) is an eastern African ungulate known for its large size and association with semideserts, shrublands, and grasslands. Due to dramatic human impacts in the past several decades, only about 2,000 individuals persist today in small pockets of Kenya and Ethiopia. A rich fossil history of this species has been reported from African and Asian sites spanning the past 2.3 million years. However, nearly all of these reports are represented by isolated teeth, and no reports dating to >200 ka can be confidently attributed to *E. grevyi*. All older reports better fit the description of another taxon or lack the diagnostic characteristics aligning them with *E. grevyi* to the exclusion of other large *Equus* species. This leaves the origination of Grévy's zebra unresolved. Here, we present the cranium of a large mare from the Kapthurin Formation, Kenya that represents the first definitive appearance of *E. grevyi*. Despite its middle Pleistocene age of 465–396 ka obtained by tephra correlation and <sup>40</sup>Ar/<sup>39</sup>Ar dating, this specimen falls well within the variation of the modern species and it is morphologically distinct from all other extant and fossil zebras. The presence of this specimen in the Kapthurin Formation solidifies the presence of multiple lineages of large zebras in eastern Africa during the late Quaternary and is inconsistent with proposals that large-bodied zebras represented a single conservative lineage through the past 2 million years. *Equus grevyi* was coeval with and distinct from *E. capensis/oldowayensis* and at least one other large-bodied species known from sites such as Ologesailie. This diversity sharply contrasts with the modern array of equids, as *E. grevyi* is the only relatively large-bodied species to survive on the continent today. Furthermore, the specific habitat preferences of this species provide insight into the paleoenvironment of eastern Africa in the middle Pleistocene, supporting proposals of the

expansion of the xeric ecosystems to the south and west of their modern extent in the Greater Horn of Africa.

## **Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

### **A HIGH-RESOLUTION RECORD OF MEGAFUNAL EXTINCTION FROM RANCHO LA BREA: TEMPO, MODE, AND CAUSALITY**

O'Keefe, Frank R.  
Biology, Marshall University, Huntington, West Virginia, U.S.A.

The extinction event that affected the large mammal fauna of North America in the terminal Pleistocene has been known for over a century, but the dynamics and causality of this event have proven contentious. Two factors constrain inference on causality: the sparse spatiotemporal distributions of the terminal Pleistocene paleontological and archeological records; and the synchronicity of posited extinction drivers, including climatic upheavals, human population and cultural changes, and the controversial bolide impact. Importantly, few sites preserve an unbroken record through the extinction event, and most lack sufficient data for meaningful inferences of extinction mode.

Here we present a high-resolution, continuous record of radiocarbon-dated megafaunal specimens from Rancho La Brea (RLB) in California, U.S.A., that spans from 16.3 ka to the early Holocene. We assembled a new database of 165 individuals of the five most common megafaunal species from RLB. The majority of these dates are from the SABER carbon dating project. Kernel density analyses of the date distributions reveals several key findings: (1) coyote deposition is continuous across the Younger Dryas and into the Holocene, demonstrating that there was no hiatus in deposition; (2) the extinct herbivore distribution shows steady or increasing deposition until the onset of a terminal decline circa 13.9 ka; (3) the extinct carnivore distribution shows steady deposition up to the onset of a terminal decline at 13.4 ka; and (4) the terminal declines of both herbivores and carnivores are precipitous, with herbivore numbers declining to extirpation within about 500 years, while the carnivore decline is later and more rapid, occurring over less than 150 years. This difference in extinction timing is significant as measured by a summed probability permutation test.

In summary, the disappearance of Pleistocene megafauna species from the RLB region was rapid and roughly synchronous, but the herbivore decline preceded the carnivore decline by at least 500 years; and the local megafaunal extirpation was probably concluded before 12.8 ka, predating the suggested bolide impact and the onset of the Younger Dryas. The RLB extirpation is

coincident with both gradual aridification in southern California and with human arrival. Inferences of causality must account for an extinction onset before 13 ka, and the fact that the herbivore decline predates that of the carnivores.

**Funding Sources** NSF EAR-SGP1757236.

## **Biomechanics & Functional Morphology**

### **A 3D COMPARATIVE ANALYSIS OF THE REFLECTED LAMINA OF THERAPSID PROVIDES CLUES TO ITS FUNCTION BEFORE THE EVOLUTION OF THE MAMMALIAN EAR**

Olroyd, Savannah L.<sup>1</sup>, Sidor, Christian A.<sup>2</sup>  
<sup>1</sup>Biology, University of Washington, Seattle, Washington, U.S.A., <sup>2</sup>Paleontology, Burke Museum, Seattle, Washington, U.S.A.

The hearing capabilities of non-mammalian therapsids are poorly understood. Indeed, it is uncertain what role the postdentary bones played in hearing before their incorporation into the mammalian middle ear. Probably the most mysterious of these bones is the angular, which exhibits a thin lateral extension called the reflected lamina. In Permo-Triassic therapsids, this feature is often ornamented with a wide variety of fossae, ridges, pits, and grooves, but this variation has never been comprehensively or systematically analyzed. As a consequence, there is no consensus on the function of the reflected lamina or the reason for its unique ornamentation. Some authors consider it to be related to the attachment of jaw or neck muscles. Others have proposed that the reflected lamina received sound like an eardrum and that this represented a form of synapsid hearing that existed before the evolution of the definitive mammalian middle ear.

We examined reflected laminae of 56 therapsid and sphenacodontid genera, sampling all major non-mammalian therapsid clades, in order to identify morphological patterns that may provide clues to the function of this structure. We also surface scanned each specimen and compared surface complexity between reflected laminae using Dirichelet Normal Energy, Relief Index, and Orientation Patch Count. Despite common assertions that the reflected laminae of dinocephalians and large dicynodonts are bulky, we find that the laminae of most of these taxa are at most a few millimeters in thickness, and that thick reflected laminae are restricted to a few genera (e.g., *Endothiodon*). The arrangement of the fossae and surface complexity of the reflected laminae shows surprising parallels between therocephalians and basal dicynodonts. Surface morphology is highly stereotyped within gorgonopsians and therocephalians, but dicynodonts and cynodonts show within-clade trends towards simplification, with surface features highly

variable at the base of these two clades. Given the high variation in the number of fossae present within therapsids, it is unlikely that these served as muscle attachment sites, especially given the occasional intraspecific variation in fossa count.

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### **Anatomical & Developmental Explorations of the Mammalian Skull**

#### **INTO THE MIDDLE EAR GEARS OF SEMI-AQUATIC ARTIODACTYLS: HIPPOPOTAMIDS VERSUS EARLY CETACEANS**

Orliac, Maëva J., Mourlam, Mickaël J.  
Institut des Sciences de l'Evolution, Montpellier, France

Hippos are semi-aquatic mammals capable of directional hearing both in air and water. Modifications of the morphology and acoustic properties of the ossicular chain are among the major changes that accompanied the adaptation of their closest modern relatives, the Cetacea, to the aquatic environment. Study of the morphology of the middle ear and ossicular chain of hippopotamidae indeed reveals striking similarities with that of cetaceans. We compare here the ossicular chain characteristics of the two modern representatives of Hippopotamidae, *Choeropsis liberiensis* and *Hippopotamus amphibius*, with that of the subfossil Malagasy species *Hippopotamus madagascariensis* and perform functional analyses of the different middle ear units of these three species. The results are compared to the functional profile of early cetaceans. This integrative anatomical and functional study of the middle ear highlights similarities and differences between hippopotamids and cetaceans and emphasizes the difficulty in detecting an aquatic ecological signal for semi-aquatic species with a strong terrestrial activity.

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### **Anatomical & Developmental Explorations of the Mammalian Skull**

#### **LOOKING GIFT HORSES IN THE MOUTH: AN EXAMINATION OF THE INHIBITORY CASCADE IN EQUID EVOLUTION**

Orlowski, Hayley, Birlenbach, David, Fox, David L.

Earth and Environmental Sciences, University of Minnesota-Twin Cities, Oak Creek, Minnesota, U.S.A.

The Inhibitory Cascade is a developmental model for the molar row of mammals that predicts that posterior molar size is controlled by the size of the molar directly anterior to it. According to the model, the diffusion of molecular signals from anterior molars to posterior molars provides constraints on the size of the developing molar, leading to a pattern of molars which either uniformly increase or decrease in size moving posteriorly. Many modern mammal groups adhere to this pattern; notably, however, modern horses fall outside of expected proportions in molar sizes. Given that horses have an excellent fossil record, we have examined the evolution of relative molar sizes for fossil and modern horses using tooth measurement data compiled from the literature. This allows us to trace the position of horse species through time within the Inhibitory Cascade morphospace from the first appearance of horses ca. 56 million years ago in the Eocene epoch to extant equids. The dataset, including data from 667 specimens comprising 128 living and fossil horse species from North America, Europe, Asia, and Africa, consists of linear measures of complete equid lower molar rows, composite rows, and averaged molar sizes within species. Age assignments for fossils are either for occurrences of individual specimens from the literature or for species occurrences from the Paleobiology Database. The earliest equids fall neatly within the morphospace predicted by the Inhibitory Cascade, but late Eocene to late Miocene horses are mostly outside the predicted morphospace, with m2 smallest, and a distinct trend over time towards equant size of the three molars is evident. The timing of the origin of approximately equant tooth proportions coincides with the onset of hypsodonty in horses, which is associated with the appearance of open, grass-dominated habitats. We hypothesize that developmental controls on tooth size and proportion may require that equant tooth proportions in horses precedes an increase in tooth height.

### **Colbert Poster Prize/Biomechanics & Functional Morphology**

#### **INFERRED LOCOMOTION OF SELECT FELIFORMS: IMPLICATIONS FOR BARBOUROFELIS LOVEORUM (BARBOUROFELIDAE) AND NIMRAVIDES GALIANI (FELIDAE, MACHAIRODONTINAE) FROM THE LATE MIOCENE (LATEST CLARENDONIAN) OF FLORIDA**

Ormsby, Christianne<sup>2</sup>, Wallace, Steven<sup>1</sup>, Samuels, Joshua X.<sup>1</sup>

<sup>1</sup>Don Sundquist Center of Excellence in Paleontology and Department of Geosciences, East Tennessee State

University, Johnson City, Tennessee, U.S.A.,  
<sup>2</sup>Geosciences, East Tennessee State University, Johnson  
City, Tennessee, U.S.A.

Relationships among the three feliform cat-like lineages: Felidae, Nimravidae, and Barbourfelidae remain controversial, with barbourfelids either falling within Nimravidae, or elevated to family. Ecomorphological studies of locomotion can be used to infer anatomical relationships, which may provide insight to phylogeny. Previous studies often used numerous families to infer locomotor behavior, intending their results to be applicable to any carnivoran. However, many carnivoran families are so distinct, that phyletic overprinting renders such broad applications ineffective. Within Felidae for example, most taxa are simply slight modifications on a basic body plan (one capable of arboreal/climbing locomotion), yet many species display other locomotor strategies: scansorial (occasional climbing), terrestrial (rare climbing), and cursorial (running). Here, locomotor categories within Felidae are inferred using 20 postcranial measurements on 12 extant taxa (*Acinonyx jubatus*, *Caracal serval*, *Felis silvestris*, *Leopardus wiedii*, *Lynx canadensis*, *L. rufus*, *Neofelis nebulosa*, *Otocolobus manul*, *Panthera leo*, *P. uncia*, *Pardofelis marmorata*, and *Puma concolor*), with the intent to apply the results to extinct forms. Principal component and stepwise discriminant analyses show a separation between the locomotion classifications using ratios taken from the individual measurements. Extinct cat-like classifications using the training analyses included *Nimravides galiani*, *Barbourfelis loveorum*, *Panthera atrox*, *Homotherium* spp., *Smilodon fatalis*, and the nimravids *Dinictis* sp. and *Hoplophoneus* sp. Nimravids cluster near the arboreal felids, whereas *N. galiani* is predicted to be more terrestrial. *B. loveorum* plots closest to *S. fatalis*, and both plot away from the other taxa. Nimravids and felids cluster closer to each other than either does to *B. loveorum*. Preliminary results suggest *B. loveorum* is morphologically distinct from felids and nimravids, whereas Felidae and Nimravidae are morphologically similar. Morphologically, *N. galiani* appears more similar to extant felids than to machairodonts. In North America nimravids were the only cat-like feliform present until their early Miocene extinction, while felids and barbourfelids coexisted in the mid-late Miocene. Morphological adaptations may have resulted in *B. loveorum* being distinct from both felids and nimravids, due to the lack of felid-nimavid coexistence and the presence of felid-barbourfelid competition.

#### **Paleozoic Tetrapods & Lissamphibians**

#### **A NEW RECONSTRUCTION OF *WHATCHEERIA* AND THE ECOMORPHOLOGICAL DISPARITY OF EARLY TETRAPODS**

Otoo, Benjamin<sup>1</sup>, Bolt, John<sup>1</sup>, Lombard, Eric<sup>2</sup>, Coates, Michael I.<sup>3</sup>, Angielczyk, Ken<sup>1</sup>

<sup>1</sup>Geology, Field Museum of Natural History, Chicago, Illinois, U.S.A., <sup>2</sup>Organismal Biology and Anatomy, University of Chicago, Chicago, Illinois, U.S.A., <sup>3</sup>Committee on Evolutionary Biology, University of Chicago, Chicago, Illinois, U.S.A.

The early tetrapod *Whatcheeria* is represented by hundreds of specimens from the Mississippian Delta locality (Iowa, U.S.A.). Research on the postcranial anatomy allows a full-body reconstruction to be produced for the first time. The ribcage is strongly regionalized, with long anterior trunk ribs bearing large uncinat processes, and short posterior trunk ribs. The girdles and limbs are massive; in particular, the processes of the humerus are very large, and imply bulky forelimb and shoulder musculature, especially relating to the retraction of the forelimb. The cervical region is elongated and the tail is reduced in length relative to contemporary tetrapods such as embolomeres and colosteids. The resulting proportions are more similar to terrestrial taxa such as *Seymouria* and *Eryops*. These taxa also share with *Whatcheeria* robust humeri with large processes, large olecranon processes, large scapular blades, and regionalized ribcages. Such similarities suggest convergent life habits, with an anteriorly stiffened trunk to increase the effectiveness of the powerful forelimbs and reduce lateral motion of the body.

We hypothesize that *Whatcheeria* represents an independent experiment in appendicular-dominated locomotion, with improved ability to explore terrestrial environments. The large ( $\geq 2$  m maximum) body size of *Whatcheeria* is larger than most Mississippian tetrapods, particularly those for which there is the most compelling evidence of terrestriality (e.g., *Balanerpeton*, *Westlothiana*). Aquatic locomotion may have been accomplished by bottom-walking, or rowing with the forelimbs.

Our new data include additional synapomorphies between *Whatcheeria* and *Pederpes*, and suggest that the latter is a juvenile. These data contribute to a new diagnosis for the *Whatcheeriidae* and a reassessment of material and taxa referred or compared to the family; significantly, *Ossinodus* is not a *whatcheeriid* and represents a distinct morphotype. However, these data do move *Whatcheeria* crownward in phylogenetic analyses. Rather, our findings highlight the disparity of stem tetrapods, and emphasizes *Whatcheeria*'s status as an early-diverging experiment in a morphology later revisited by crown tetrapods.

**Funding Sources** Field Museum Armour Graduate Student Fellowship.

#### **Quantitative Methods**

## **PALEOMETRY: THE DEVELOPMENT AND IMPROVEMENT OF TECHNIQUES APPLIED TO THE STUDY OF FOSSIL VERTEBRATES**

Pansani, Thais R.  
UFSCar, Sorocaba, São Paulo, Brazil

Paleometry is an interdisciplinary effort which intends to improve the robustness and the quality of data extracted from fossils. Some of its approaches include recognizing limitations, complementarity, and applications of the following methods: synchrotron-based X-ray fluorescence (XRF), energy-dispersive X-ray fluorescence (EDXRF), scanning electron microscopic (SEM), energy-dispersive X-ray spectroscopy (EDS), synchrotron-based X-ray tomography, and Raman spectroscopy, among others. In Brazil, we have a team of researchers who have been applying those techniques ranging studies of fossils from several geological times. Here, I present two cases performed by our team regarding paleometry of fossil bones. The first case is concerning Permian mesosaurids bone labile marrow tissues. It was tested the limitations of results extracted from EDS and  $\mu$ -XRF analysis and, in this case, the EDS was more efficient to detect lighter elements (such as carbon) as well as heavier ones, but not in trace quantities (as calcium), while  $\mu$ -XRF was able to detect heavier elements, but also at trace level (such as strontium). It helps us in seeking the bulk of methodologies suitable to deal with specific questions, especially about the investigation of diagenetic process. The other one is concerning a Pleistocene giant sloth tooth, with marks likely made by humans.  $\mu$ -XRF analysis showed significant differences on the content of iron and manganese (more on the marks depth and less on the surface of the tooth) in comparison to natural bone elements, as zinc and calcium (the otherwise). In the case of this tooth, we also applied Raman spectroscopy, which did not show significant results. This suggests that  $\mu$ -XRF is a better technique for this purpose than Raman (in this case, with higher sensibility to chemical elements). So far, the interesting images of iron and manganese concentrations on the marks may indicate that these marks were made before fossilization, and if it is concluded that these marks were made by humans, it can point out the evidence of humans in South America since ca. 15,000 years ago. All these results are preliminary and are on ongoing projects, but contain high-quality data that generates intriguing clues with paleontological interpretations that definitely deserves attention. Also, sharing this advanced methodology may help to answer a lot of other/new questions within paleontology worldwide.

**Funding Sources** CNPq [Conselho Nacional de Desenvolvimento Científico e Tecnológico].

## **Late Cenozoic Mammalian Macroecology & Macroevolution**

### **FLEXIBLE DIETS AMONG GRAZING-ADAPTED HERBIVORES OVER THE PAST SEVEN MILLION YEARS**

Pardi, Melissa I., DeSantis, Larisa  
Biological Sciences, Earth & Environmental Sciences,  
Vanderbilt University, Nashville, Tennessee, U.S.A.

Paleoecological interpretations based on faunal compositions rely on a precise understanding of the dietary and habitat preferences of fossil taxa. While dental and skull morphology can provide broad approximations of dietary behavior, stable isotope proxies provide detailed insights into the realized diets of ancient mammals. We present a synthesis of the isotopic ecologies of herbivores in North America since ~7 Ma, using  $\delta^{13}\text{C}$  values from fossil tooth enamel. We ask if morphological interpretations of dietary behavior agree with stable isotope data and if grazing-adapted taxa obligate graze or consume grass as part of a broader dietary niche. Our results demonstrate that morphologically inferred browsers are specialized; however, morphologically inferred mixed-feeders and grazing taxa have broad dietary niches. It has long been accepted that morphology imposes limits on what an animal can and cannot eat; this synthesis supports prior work that herbivores with 'grazing' adaptations have the ability to consume grass, but are also able to eat other foods. Collectively, this synthesis demonstrates that grazing-adapted taxa are varied in their dietary ecology across sites and through time, and we illustrate how this flexibility may help reduce competition among ancient herbivores.

**Funding Sources** National Science Foundation: EAR1725154.

## **Macroecology & Macroevolution**

### **ECOMETRIC MODELLING OF TURTLE BODY SIZE DISTRIBUTIONS: HOW TURTLES PREDICT PALEOTEMPERATURE**

Parker, Abigail K., Head, Jason  
Zoology, University of Cambridge, Cambridge, U.K.

Maximum body size in turtles has previously been used as an indicator of paleotemperature. However, the relationships between body size and climate variables have never been quantified. To estimate the predictive utility of turtle body size for inferring climate variables, we used ecometric modelling to make predictions of temperature and precipitation based on the community composition of turtle body sizes, measured as carapace length. These

models, trained using modern turtle distribution data, can be used to improve our reconstruction of paleoenvironments based on the traits of fossil species. We compared maximum likelihood models based on occurrence data drawn from the Global Biodiversity Information Facility, turtle range maps from the Turtle Taxonomy Working Group, and species distribution models projecting species ranges based on their climatic niche. Models use either two or three statistics based on the distribution of the body sizes of turtle species present at each sample point.

The models of temperature provide more accurate estimates for the modern test points than the models of precipitation values. Using the models with the lowest temperature anomalies in the modern dataset, we produced paleotemperature estimates for several sites with preserved fossil turtle communities from East Africa, including Kanapoi, Kenya (4.2 Ma) estimated at 27.8°C, and the Shungura Formation (Ethiopia, 3.6-1.1 Ma), where estimates for individual members ranged from 20.5°C to 26.6°C. Examination of these models' paleotemperature estimates alongside independent environmental proxies, including carbon isotopes and inferred vegetation types based on mammal communities, allows for more detailed description of the climatic differences between sites. This application of ecometric modelling indicates that fossil body size distributions can be informative as indicators of paleoenvironment, and the ecometric framework developed here allows for evaluation of which statistics best describe trait distributions linked to climate variables, improving quantification of trait-climate relationships for use as paleoenvironmental proxies.

**Funding Sources** AKP funded by the Herchel Smith Harvard Scholarship, Emmanuel College Gerard Evans Fund, and Cambridge University Worts Travelling Scholars Fund.

## Evolution & Biology of Non-Avian Theropods

### OSTEOHISTOLOGY OF THE EARLY CRETACEOUS THEROPOD *DEINONYCHUS ANTIRRHOPUS*

Pascucci, Thomas R.<sup>1</sup>, D'Emic, Michael<sup>2</sup>, Turner, Alan H.<sup>1</sup>  
<sup>1</sup>Stony Brook University, Stony Brook, New York, U.S.A.,  
<sup>2</sup>Adelphi University, Garden City, New York, U.S.A.

Specimens of different sizes attributed to the theropod dinosaur *Deinonychus antirrhopus* exhibit a wide range of unexplained morphological variation across their broad geographic distribution. To determine whether this morphological variation could be ontogenetic in nature, we estimated the age of six specimens via skeletochronology. We made firsthand observations of published thin sections and the corresponding skeletal elements from which they

were sampled in three individuals of *Deinonychus* (MOR 1182, MOR 1178, MCZ 8791). Additionally, we histologically sampled and/or microCT scanned the tibia and/or femur of four specimens (MCZ 4371, MOR 1178, OMNH 50268, OMNH 63061). Retrocalculated ages and body mass estimates for sampled *Deinonychus* specimens range from 1 to 14 years and under 10 kg to about 100 kg, respectively. The primary type of tissue in each specimen trends from woven and parallel-fibered bone in smaller specimens to lamellar organization in the largest individual. Osteocyte lacunar density and vascular density are highest in smaller individuals. Vascular orientation is primarily longitudinal in orientation, although smaller individuals show regions of reticular organization. None of the specimens have an external fundamental system (EFS). We created a growth model based on body mass estimates derived from annual growth markers; data from all specimens are congruent with the presence of a single ontogenetic series. *Deinonychus* growth is reconstructed as sigmoidal, with relatively slow growth for the first several years of life followed by a short period of explosive growth, and finally rapid attenuation towards asymptotic body mass. Overall, osteohistological data suggest that sampled specimens represent a growth series, and therefore observed morphological diversity is consistent with ontogenetic variation. This deeper understanding of growth in *Deinonychus antirrhopus* has implications for the functional morphology and ecology of this well-known taxon, as well as further investigations of intraspecific variation in extinct taxa.

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## Permo-Triassic Tetrapods

### CHARACTERIZATION OF DENTAL VARIATION IN A SMALL AZENDOHSOURID FROM THE CHINLE FORMATION (UPPER TRIASSIC) OF ARIZONA INDICATES THE ABUNDANCE OF AZENDOHSOURIDS IN ADAMANIAN BIOZONE ASSEMBLAGES

Patellos, Emily A.<sup>1</sup>, Kligman, Ben<sup>1</sup>, Marsh, Adam D.<sup>2</sup>, Stocker, Michelle R.<sup>1</sup>, Parker, William<sup>2</sup>, Nesbitt, Sterling J.<sup>1</sup>

<sup>1</sup>Virginia Tech, Blacksburg, Virginia, U.S.A., <sup>2</sup>Petrified Forest National Park, Petrified Forest, Arizona, U.S.A.

Isolated tooth crowns are critical to recognizing taxonomic diversity that is not represented in other skeletal material. However, those tooth crowns are challenging to identify to refined taxonomic levels because these teeth only possess a few apomorphic features, and piecing out individual,

taxonomic, and/or ontogenetic variation is difficult. To help constrain our knowledge of variation within a single species and apply these characteristics to the identification of isolated tooth crowns, we focused on quantifying and qualifying the variation in marginal dentition of a small azendohsaurid known from a monodominant bonebed from the Upper Triassic Chinle Formation of Petrified Forest National Park, Arizona. Using quantitative measurements (e.g., crown height, crown base width, crown base length) and qualitative observations, we characterized dental morphology and variation within the premaxilla, maxilla, and dentary of this taxon. The mesial teeth of the maxilla have a sharply angled recurve, and the distal maxillary teeth are spade-shaped, with little to no curve at the apex, and a restricted root. Dentary teeth are less labiolingually-compressed than those of the maxilla but have a similar shape. Denticles are found on all teeth except the anteriormost tooth of the premaxilla. These denticles are found on the mesial and distal carinae and are positioned at an angle toward the apex, rather than perpendicular to the teeth. We compared the quantitative measurements of the premaxilla, maxilla, and dentary individually and it is clear that variation in dimension (e.g., height, base width) across these elements help place isolated teeth to certain jaw elements. This novel understanding of the dental variation in this azendohsaurid indicates that taxa and morphotypes known only from isolated teeth in Triassic microvertebrate assemblages (e.g., *Protecovasaurus lucasi*) fall within its range of variation. Morphologically similar tooth morphotypes are well represented in Upper Triassic formations of western North America, as opposed to diagnostic non-dentigerous azendohsaurid material. This has enabled identification of azendohsaurids based on isolated teeth in many Chinle Formation microvertebrate sites, demonstrating their restriction to the Adamanian (early-mid Norian), where they are found in almost all sampled microvertebrate assemblages.

### Permo-Triassic Tetrapods

#### A NEW STRATIGRAPHIC FRAMEWORK FOR THE PERMO-TRIASSIC STRATA OF THE MID-LUANGWA BASIN, ZAMBIA: UPPER PERMIAN TURNOVER AND MIDDLE-UPPER TRIASSIC VERTEBRATE ASSEMBLAGES

Peacock, Brandon R.<sup>1</sup>, Angielczyk, Ken<sup>2</sup>, Kammerer, Christian F.<sup>3</sup>, Lungmus, Jacqueline K.<sup>4</sup>, McIntosh, Julia<sup>5</sup>, Sidor, Christian A.<sup>6</sup>, Smith, Roger M.<sup>7</sup>, Tolan, Stephen<sup>8</sup>, Viglietti, Pia A.<sup>2</sup>, Whitney, Megan<sup>9</sup>

<sup>1</sup>Idaho Museum of Natural History & Biological Sciences, Idaho State University, Pocatello, Idaho, U.S.A., <sup>2</sup>Field Museum of Natural History, Chicago, Illinois, U.S.A., <sup>3</sup>North Carolina Museum of Natural Sciences, Raleigh, North Carolina, U.S.A., <sup>4</sup>University of Chicago, Chicago, Illinois, U.S.A., <sup>5</sup>Southern Methodist University, Dallas,

Texas, U.S.A., <sup>6</sup>University of Washington, Seattle, Washington, U.S.A., <sup>7</sup>University of the Witwatersrand, Johannesburg, South Africa, <sup>8</sup>Chipembele Wildlife Education Trust, Mfuwe, Zambia, <sup>9</sup>Harvard University, Cambridge, Massachusetts, U.S.A.

In 2018 and 2019, our team conducted fieldwork to establish a rigorous stratigraphic framework for the Permo-Triassic beds preserved in the middle portion of the Luangwa Basin of Zambia. The mid-Luangwa Basin has large, relatively continuous areas of fossiliferous exposure, compared with extensive faulting and patchy outcrops in the historically-collected northern portion of the basin. However, understanding stratigraphy in the mid-Luangwa has been problematic due to minimal topographic relief. We were successful in both updating the faunal succession of well-sampled areas and exploring new fossil-rich areas. In the upper Permian Madumabisa Mudstone Formation, we found evidence of faunal turnover, most obvious in a high-level taxonomic shift of the dicynodont fauna. The lower assemblage is dominated by cryptodonts like *Oudenodon* and various geikiids, and also contains Zambian records of *Endothiodon*, whereas the upper assemblage preserves the dicynodontoids *Daptocephalus*, *Dicynodon*, and lystrosaurids. The theriodont fauna also shifts, with the therocephalian *Theriognathus* and gorgonopsian *Rubidgea* only known in the upper assemblage. These faunal changes mirror those seen in the main Karoo Basin of South Africa between the *Cistecephalus* Assemblage Zone (AZ) and the overlying lower *Daptocephalus* AZ, offering a geographically distinct study system for ecosystem changes leading up to the end-Permian mass extinction.

In the Triassic, we revisited sites in the Ntawere Formation and Red Marl last studied in the 1970s, and also explored the stratigraphically highest reaches of the succession for the first time. We propose a lower assemblage in the mid-Luangwa Basin that resembles the familiar 'upper Ntawere' of the northern Luangwa Basin: dominated by dinosauriform and paracrocodylomorph archosaurs, gomphodont cynodonts, stahleckeriid dicynodonts, temnospondyls, and lungfish. Our proposed upper assemblage in the mid-Luangwa Basin contains the first rhynchosaur records from Zambia, as well as evidence of dinosauriforms, pseudosuchians, dicynodonts, and cynodonts.

Middle-Late Triassic assemblages across south-central Pangea are linked biostratigraphically, but lack absolute age constraints to tie them to the increasingly well-calibrated picture of Triassic terrestrial ecosystem evolution in South America. Improving the resolution of faunal turnover in the Luangwa Basin allows for more precise correlations as work to achieve absolute age control continues.

**Funding Sources** National Geographic Society NGS-158R-18; NSF EAR-1337569.

## **Colbert Poster Prize/Late Cenozoic Mammalian Macroecology & Macroevolution**

### **COMPARISONS OF MORPHOLOGICAL DISPARITY IN MODERN AND MIOCENE NORTH AMERICAN RODENTS**

Peng, Amanda W., Hopkins, Samantha S., Davis, Edward B.

Earth Science, University of Oregon, Eugene, Oregon, U.S.A.

Biological diversity gradients have been described across a variety of geographic variables, including latitude, elevation, and landscape complexity. In North America, the landscape complexity gradient is of particular interest given that varying tectonic regimes have led to pronounced west–east differences in topographic complexity. It is thought that tectonism and subsequent landscape complexity drives speciation among mammals, and as a result, species richness (i.e., taxonomic diversity) has been closely examined across these tectonically active and passive regions of North America. However, morphological disparity, which might distinguish the roles of geographic barriers and habitat diversity, has not been similarly addressed. Morphological disparity is the diversity in morphological form and is an important aspect of overall biodiversity. Measures of disparity capture the breadth of morphospace occupation and offer a taxon-free estimation of morphological diversity. As such, morphological disparity plays a critical role in understanding overall biodiversity. In this study, we investigate the link between morphological disparity and landscape evolution in Miocene rodents of North America and make comparisons to the modern day. We obtained data from the MioMap and Paleobiology databases and estimate the disparity in body mass, which is reconstructed from the occlusal area of the lower m1. We utilize a suite of metrics which capture morphological disparity for this purpose, including the mean distance from the centroid, the sum of ranges, and the sum of variances. We find that body mass disparity in the tectonically active and passive regions of North America are not constant through time. Whereas body size disparity in the tectonically active West was highest in the Arikareean North American Land Mammal Age (NALMA; 30.8–10.4 Ma), the Hemingfordian NALMA (20.4–15.9 Ma) shows greater disparity in the Great Plains. This trend is largely carried into the present day, with the exception of a brief period during the Hemphillian NALMA (10.3–4.9 Ma). These changes occur against a backdrop of significant climatic and landscape change, which we investigate in tandem. These results indicate that morphological disparity is dynamic in responding to both biotic and abiotic drivers and does not

vary predictably with taxonomic diversity in this setting. An understanding of these patterns through time can inform morphological evolution on a geologic time scale.

### **Marine Mammals**

#### **PALATAL FORAMINA IN STEM WHALES AND TERRESTRIAL ARTIODACTYLS OBFUSCATE THEIR POTENTIAL FOR INFERRING BALEEN IN STEM MYSTICETES**

Peredo, Carlos M.<sup>1</sup>, Pyenson, Nicholas<sup>2</sup>

<sup>1</sup>Earth and Environmental Science, University of Michigan, Ann Arbor, Michigan, U.S.A., <sup>2</sup>Paleobiology, Smithsonian Institution, Washington D.C., District of Columbia, U.S.A.

Baleen whales (mysticetes) filter-feed using specialized keratinous plates, called baleen, to sieve large quantities of prey laden water. Baleen represents a wholly novel integumentary structure, with no apparent homologous structure in any living animal. The origins of baleen, and filter-feeding in whales, have been the topic of much debate. In particular, the lack of osteological correlates for baleen makes it unclear which (if any) stem mysticetes first had keratinous structures for filter feeding. One potential osteological correlate are palatal foramina and sulci: structures in the roof of the mouth that may vascularize the baleen plates. Palatal foramina are present and well developed in extant and fossil crown mysticetes and are preserved in some stem mysticetes as well. Here, we report the presence of numerous and well-developed palatal foramina in non-filter-feeding cetaceans, including crown and stem odontocetes and in stem cetaceans (so-called archaeocetes). Additionally, we observe the presence of palatal foramina in 61 observed species of terrestrial artiodactyls. CT scanning demonstrates consistent internal morphology across all observed palatal foramina, suggesting that the palatal foramina observed in extant mysticetes are homologous to those of terrestrial artiodactyls. The presence of palatal foramina in non-filter-feeding whales (odontocetes and archaeocetes) and in terrestrial artiodactyls suggest that the structures are more probably associated with an elaborate gingiva or other oral tissue and are alone not reliable osteological correlates for the presence of baleen in fossils.

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### **Mesozoic & Early Cenozoic Mammalian Evolution**

#### **FOOD HABIT INFERENCES FROM A WHITE RIVER BRONTOTHERE (PERISSODACTYLA, BRONTHOTHERIIDAE, *BRONTOPS* SP.)**

Pérez-Crespo, Víctor A.<sup>1</sup>, Arroyo-Cabrales, Joaquín<sup>2</sup>, Osorio Segura, Alfonso<sup>3</sup>, Cienfuegos-Alvarado, Edith<sup>4</sup>, J. Otero, Francisco<sup>4</sup>

<sup>1</sup>Paleontology, Instituto de Geología, México City, Federal District of Mexico, Mexico, <sup>2</sup>Laboratorio de Arqueozoología 'M. en C. Ticul Álvarez Solórzano', Subdirección de Laboratorios y Apoyo Académico, INAH, Ciudad de México, Ciudad de México, Mexico, <sup>3</sup>Museo Nacional de las Culturas del Mundo, Instituto Nacional de Antropología e Historia, Ciudad de México, Ciudad de México, Mexico, <sup>4</sup>Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad de México, Ciudad de México, Mexico

Brontotheres or titanotheres (Perissodactyla, Brontotheriidae) were a mammalian herbivore order that appeared during the late Eocene (early Chadronian) and disappeared by the early Oligocene (Orellan). Based on the presence of brachiodont-selenodont molars, these animals are considered grazers; however, studies using dental microwear and stable isotope analyses indicate that they ate tree leaves, fruits, and shrubs or C<sub>3</sub> plants, and inhabited forest or open forested areas. In the National Museum of World Cultures (INAH, Mexico City), there is a mounted specimen on deposit of a brontothere mandible, which was acquired at the beginning of the 20th century from the Ward & Howell Company for exhibits.

Specimen locality data shows that it is from White River, Badlands National Park, South Dakota. In order to learn about the food habits of these animals, dietary inferences were made based on the carbon isotopic relationship found in the dental enamel, compared with the previous known values for specimens from White River. For grading the dental enamel diagenetic state, a FTIR analysis was assayed to determine the cristallinity index, which was 3.953, indicating that dental enamel was not affected by diagenetic processes. This supports the reliability of the C<sub>3</sub> isotopic value of -9.8‰. Such a value means that the animal was mostly feeding upon plants, similar to what has been found for other *Brontops* from White River. All of the previous data indicate they lived in forests present in the region during the Eocene.

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## Quantitative Methods

## MACROEVOLUTIONARY TRENDS IN NOTOUNGULATA, AN ENDEMIC RADIATION OF EXTINCT SOUTH AMERICAN HERBIVOROUS MAMMALS

Perini, Fernando A.<sup>1</sup>, Casali, Daniel d.<sup>1</sup>, Flynn, John J.<sup>2</sup>  
<sup>1</sup>Zoology, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil, <sup>2</sup>Vertebrate Paleontology, American Museum of Natural History, New York, New York, U.S.A.

During most of the Cenozoic, South America (SA) was an isolated continent, leading to evolution of a unique and endemic fauna. Among these were the Notoungulata, an extinct group of ungulate-like mammals that included a wide array of species assigned to 14 families and more than 150 genera, occupying many distinct herbivorous niches and showing convergent morphologies with distantly related mammalian herbivore groups. Despite this diversity, few studies have addressed the evolution of morphological disparity among notoungulates. In this study, we applied modern comparative methods to investigate macroevolutionary patterns within the clade. We used a comprehensive morphological matrix to perform a Bayesian phylogenetic analysis, obtaining a fully resolved phylogeny and divergence time estimates for the major groups of notoungulates. This phylogeny supports the division of Notoungulata into Toxodontia and Typotheria, including many traditionally recognized families, as well as indicates paraphyly of some groups such as 'Notohippidae', 'Notopithecidae', and 'Isotemnidae'. For exploratory visualization of morphological disparity, we generated a pairwise distance matrix of the discrete characters and subjected it to a principal coordinate analysis (PCO), plotting the resultant values in morphospace. We also plotted the PCO results into three time-bins, to compare the disparity of Toxodontia and Typotheria over time. The diversity of Notoungulata rose steadily from the beginning of the Paleocene, reaching its apex by the end of the Oligocene, with marked decreases in the beginning, middle, and end of the Miocene, until final extinction in the Pleistocene. Toxodontia and Typotheria show no overlap, but occupy increasingly more distinct areas of the morphospace over time. Typotheria in particular, despite their fall in diversity, expanded occupancy of the morphospace until the end of the Cenozoic. A decomposition of diversity analysis (decddiv) revealed that most of the morphological disparity in notoungulates is concentrated in relatively few clades, particularly at the nodes representing the splits between Toxodontia and Typotheria, between Intertheriidae and Typotherioidea, and close to the root of Typotherioidea. Our results document that Typotheria evolved to occupy a wide range of dimensions within the morphospace, concentrating most of the disparity observed within Notoungulata, while Toxodontia was more morphologically conservative throughout its history.

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## Cenozoic Herpetology

### INTRASPECIFIC VARIABILITY IN AN EXTANT SQUAMATE AND ITS IMPLICATIONS FOR USE OF SKELETOCHRONOLOGY IN EXTINCT VERTEBRATES

Petermann, Holger<sup>1</sup>, Gauthier, Jacques A.<sup>2</sup>

<sup>1</sup>Department of Earth Sciences, Denver Museum of Nature and Science, Denver, Colorado, U.S.A., <sup>2</sup>Geology and Geophysics, Yale University, New Haven, Connecticut, U.S.A.

Intraspecific variability is an important phenomenon in biology. It poses significant challenges in vertebrate paleontology, mostly because terrestrial species are often represented by so few specimens. Here we report potential consequences of our inability to assess intraspecific variability in growth rates. An investigation of life-history parameters in the extant iguanian lizard *Sauromalus ater* (the Common Chuckwalla), a sexually dimorphic species from the SW U.S.A., revealed remarkable intraspecific variability. We found expected differences in growth strategies between males and females, but also within each sex, relating to body size and the timing of sexual maturity. Males and females can grow rapidly to size-at-sexual-maturity, producing above-average adult body sizes. Or, they can grow slowly to size-at-sexual-maturity, yielding adults at or below average body sizes. Neither growth strategy influences longevity. As a result, we found that body size of similar-aged individuals varied by 53% for males and 38% for females, and maximum differences in 'adults' of 64% for males and 38% for females.

Our results add to previous reports of intraspecific variability in extant and extinct vertebrates. High levels of intraspecific size-variability have multiple implications for vertebrate paleontology. 1) Morphologically similar specimens from the same locality could belong to the same species even if the size difference among adult individuals exceeds 50%, which is a higher level than previously thought. 2) Specimens that have been analyzed skeletochronologically and have been found to be similar or identical in chronological age, may not exhibit similar sizes. 3) Variability in growth strategies may lead to mistaking males and females (especially among sexual dimorphs), or individuals using different growth strategies, as belonging to separate species.

We previously presented evidence that a sequence of sub-terminal skeletal suture fusions relates to maximum body size in squamates, and not to chronological age. This indicates that late-ontogenetic, suture-fusion events could be used to evaluate whether two or more specimens of similar morphology and chronological age are differently-sized conspecifics. Likewise, skeletal suture fusions may aid discerning different growth strategies within a single species, as opposed to the presence of two morphologically

similar, but nonetheless separate, species in a single taphonomic assemblage.

**Funding Sources** Yale Institute for Biospheric Studies  
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## Biomechanics & Functional Morphology

### BITE FORCE ESTIMATES IN JUVENILE *TYRANNOSAURUS REX* BASED ON SIMULATED PUNCTURE MARKS

Peterson, Joseph<sup>1</sup>, Tseng, Z. Jack<sup>2</sup>, Brink, Shannon<sup>1</sup>

<sup>1</sup>Department of Geology, University of Wisconsin Oshkosh, Oshkosh, Wisconsin, U.S.A., <sup>2</sup>Department of Integrative Biology, University of California Berkeley, Berkeley, California, U.S.A.

Bite marks attributed to adult *Tyrannosaurus rex* are common in the fossil record and have been subject to numerous studies. However, few of the bite marks attributed to *T. rex* have been traced to juveniles, limiting direct insight into ontogenetic changes in bite mechanics and bite force. This lack of information leaves considerable gaps of understanding the ontogeny and paleoecological role of juvenile tyrannosaurs in the late Cretaceous. Here we present bite force estimates for a juvenile *Tyrannosaurus rex* based on mechanical tests designed to replicate bite marks previously attributed to a *T. rex* of approximately 13 years old; the centrum of a caudal vertebra of *Edmontosaurus* (BMR P2007.4.1) and the left maxilla and nasal of a juvenile *Tyrannosaurus* (BMR P2002.4.1). A maxillary tooth of the juvenile *Tyrannosaurus* specimen BMR P2002.4.1 was digitized, replicated in cobalt, and mounted to an electromechanical testing system. The tooth was then pressed into bovine long bones in various locations with differing cortical bone thicknesses. Post-indentation, the long bones were imaged in a computed tomography scanner, cortical thicknesses were measured at each puncture site, and comparisons made to known fossil bite marks attributed to juvenile *Tyrannosaurus rex*. Results indicate that the bite marks found on the caudal vertebra centrum of BMR P2007.4.1 would have required ~3,500 N of force to bite through the 0.4–0.5 mm thick cortical bone of the centrum. However, the bite marks located on the left maxilla and nasal of BMR P2002.4.1 would have required a force of 5,000–6,000 N to break through the 20 mm maxilla, which possesses 7.5 mm of cortical bone. These findings are considerably higher than previously estimated bite forces for a juvenile *Tyrannosaurus rex* of approximately the same size as BMR P2002.4.1, but fall within the expected range when compared to estimates of adult *T. rex*. The estimates of juvenile *Tyrannosaurus* bite forces add further insight into ontogenetic changes and potential dietary trends between late-stage juvenile and adult *Tyrannosaurus rex*.

**Funding Sources** This research was funded by the UW Oshkosh Faculty Student Collaborative Grant program.

### **Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

#### **DIETARY BEHAVIOR OF ALASKAN POLAR BEARS (*URSUS MARITIMUS*) IN RESPONSE TO ARCTIC WARMING, AS INFERRED FROM PAST (~1 KA) AND PRESENT SPECIMENS VIA DENTAL MICROWEAR TEXTURES**

Petherick, Ansley<sup>1</sup>, Reuther, Joshua<sup>2</sup>, Anderson, Shelby<sup>3</sup>, Shirar, Scott<sup>2</sup>, DeSantis, Larisa<sup>1</sup>

<sup>1</sup>Vanderbilt University, Nashville, Tennessee, U.S.A.,

<sup>2</sup>University of Alaska Museum of the North, Fairbanks, Alaska, U.S.A., <sup>3</sup>Portland State University, Portland, Oregon, U.S.A.

Arctic climate change poses serious threats to polar bears (*Ursus maritimus*), as spatiotemporal recession of sea ice and lengthened melt seasons in the Arctic have resulted in range contraction and body condition declines for regional populations. Their elongated skulls and reduced molar dentition compared to their sister species, the grizzly bear (*Ursus arctos*), are adaptations associated with hunting seals on sea ice and a soft lipid-rich diet of blubber and meat. However, as seal prey becomes inaccessible with reduced sea ice and marine ecosystems undergo bottom-up reorganization, it is unclear if and how polar bears are altering their diets. Here, we test the hypothesis that hard-food consumption, inferred from dental microwear texture analysis, increased with Arctic warming and climatic variability. Polar bears demonstrate an absence of hard-object feeding in Alaska through time (including approximately 1,000 years ago, during the Medieval Warm Period) until the 21<sup>st</sup> century. Our results suggest that the 21<sup>st</sup> century may represent an adaptive ‘tipping point’, after which point polar bears began consuming harder foods (e.g., increased carcass utilization, terrestrial foods including garbage), despite having a skull poorly suited for such a diet. Prior to this shift, only polar bears with larger mandibles demonstrated relatively increased hard-object feeding. Morphologically specialized polar bears have biomechanical constraints that may limit their ability to consume mechanically-challenging dietary alternatives, with dietary shifts occurring only under the most extreme scenarios. Extending the study of polar bears into archeological and paleontological records provides greater insight into the ecology of these animals through time and provides context to current biotic responses to Arctic warming and climatic variability.

**Funding Sources** This work was performed on equipment funded by the National Science Foundation (1053839).

### **Mammalian Skeletal Morphology**

#### **EVOLUTIONARY DIVERSIFICATION OF MARSUPIAL LIMBS IS MORE STRONGLY INFLUENCED BY FUNCTIONAL LOCOMOTOR MODES THAN BY DEVELOPMENTAL CONSTRAINTS**

Pevsner, Spencer K.<sup>1</sup>, Grossnickle, David<sup>2</sup>, Luo, Zhe-Xi<sup>3</sup>  
<sup>1</sup>School of Earth Science, University of Bristol, Bristol, U.K., <sup>2</sup>Department of Biology, University of Washington, Seattle, Washington, U.S.A., <sup>3</sup>Department of Organismal Biology and Anatomy, University of Chicago, Chicago, Illinois, U.S.A.

Marsupials possess fewer locomotor modes than placental mammals, and therefore do not occupy the same breadth of ecological niches as placental mammals. A well-established explanation for this discrepancy is that the forelimb morphology of marsupials is constrained by the necessity for neonates to crawl from the birth canal to the pouch. According to this developmental constraint hypothesis, the requirement for neonatal forelimbs to be capable of climbing has been the primary constraint preventing marsupials from developing more disparate forelimbs or evolving more locomotor modes than placental mammals. This hypothesis was recently challenged by a study that found greater morphological disparity in marsupial forelimbs than in hindlimbs, contrary to predictions of the constraint hypothesis on a macroevolutionary scale. To independently test the predictions of the developmental constraint hypothesis, we pursue a comparative morphometric study on marsupial limbs, with a novel emphasis on functionally informative traits. We first established a large, independent dataset of limb skeletal metrics for a taxonomically diverse sample of marsupials. We pruned the dataset to only include skeletal metrics that strongly differentiate among locomotor modes, and then apply these functionally relevant traits to subsequent analyses of morphological disparity. An expected consequence of the developmental constraint hypothesis is that marsupial forelimbs should be less functionally diverse than hindlimbs, and thus hindlimb characters should be significantly better predictors of ecological traits than forelimbs. We test the predictive power of forelimbs versus hindlimbs for identifying locomotor modes by implementing multivariate analyses such as linear discriminant analyses and phylogenetic MANOVAs. Contrary to the predictions of the constraint hypothesis, our findings demonstrate that forelimb morphology is often a better predictor of locomotor mode than hindlimb morphology; or, taken conservatively, forelimbs and hindlimbs show similar levels of ecomorphological differentiation. These findings generally hold true after accounting for possible biases, including subjective locomotor mode assignments, phylogeny, and

trait choices. Thus, our results suggest that developmental constraints placed on marsupial forelimbs, if present, are overcome on a macroevolutionary scale by additional factors, such as selection associated with ecological traits.

**Funding Sources** Funding source for data collection: 2018 University of Chicago BSCD Ecology & Evolution Fellowship.

## **Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

### **HUMANS HAVE SHAPED THE CLIMATIC DISTRIBUTIONS OF MODERN NORTH AMERICAN MAMMALS**

Pineda-Munoz, Silvia<sup>2</sup>, Wang, Yue<sup>1</sup>, Tóth, Anikó B.<sup>3</sup>, Lyons, S. K.<sup>4</sup>, McGuire, Jenny L.<sup>1</sup>

<sup>1</sup>Georgia Institute of Technology, Atlanta, Georgia, U.S.A., <sup>2</sup>Georgia Institute of Technology, Atlanta, Georgia, U.S.A., <sup>3</sup>University of New South Wales, Sydney, New South Wales, Australia, <sup>4</sup>University of Nebraska Lincoln, Lincoln, Nebraska, U.S.A.

Human population has increased substantially since the last glaciation, especially across temperate areas with easy access to water sources. Human mediated landscape transformation can exclude mammal species from their former habitats. Thus, we anticipate a change in the realized niches of mammal species as increased human population forces them to shift within their fundamental niches. In our study, we collected modern and fossil species occurrences from 11,700 ybp to the present for 46 North American mammal species covering six taxonomic Orders (Artiodactyla, Carnivora, Chiroptera, Insectivora, Lagomorpha, and Rodentia). We inferred temperature and precipitation for each location using paleoclimate simulations (CCSM3). We calculated niche overlap between multiple past time intervals and the present to identify whether the realized niches of these mammals did indeed shift through time. Time intervals included Post-Glacial (11,700 to 4,200 ybp), Early Agricultural (4,200 to 450 ybp), European (450 to 100 ybp), Industrial (100 to 0 ybp), and Present (0 ybp to the Present). We also estimated the environmental niches of modern habitat types and calculated their niche overlap with mammal species' niches at each time interval. Habitat types included: urban areas, croplands, alpine areas, grasslands, and forests.

Our results suggest that human impacts have caused North American mammals to alter the ranges of climatic conditions they inhabit. Sixty-seven percent of the studied mammals have significantly different niches today than they did before the onset of the Industrial Revolution. Mammalian climatic niches change the most in the portion that overlaps with human-impacted landscapes. Large-bodied dietary specialists are being extirpated from

climates in human-impacted areas; whereas smaller, generalist mammals are being facilitated, colonizing climates now occupied by urban and agricultural landscapes. Importantly, the climates where we find mammals today do not necessarily represent their natural habitats. This disagreement between modern and historical niches has critical implications for niche-based conservation models. Integrating fossil and modern data has the potential to make better predictions about species distributions to conserve biodiversity going forward. Without mitigation, as we move further into the Anthropocene, we can anticipate a low standing biodiversity dominated by small, generalist mammals.

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## **Biomechanics & Functional Morphology**

### **LIMB BONE ADAPTATIONS TO POSTURAL CHANGES IN EARLY ARCHOSAURS: QUANTIFICATION OF FEMORAL SHAPE VARIATION BETWEEN QUADRUPEDS AND BIPEDS**

Pintore, Romain<sup>1</sup>, Houssaye, Alexandra<sup>2</sup>, Nesbitt, Sterling J.<sup>3</sup>, Hutchinson, John R.<sup>1</sup>

<sup>1</sup>Comparative Biomedical Sciences, Royal Veterinary College, Hatfield, Hertfordshire, U.K., <sup>2</sup>UMR 7196, CNRS/Muséum National d'Histoire Naturelle, Paris, France, <sup>3</sup>Department of Geosciences, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, U.S.A.

The evolutionary history of archosaurs and their closest relatives is characterized by a wide diversity of locomotor modes. The locomotor superiority hypothesis suggests that this diversity was the main driver of early dinosaur success over pseudosuchians across the Triassic-Jurassic extinctions. The impacts of postural changes (e.g., more sprawling/erect; crouched/upright; quadrupedal/bipedal) on the appendicular skeleton across these taxa have never been studied using 3D geometric morphometrics (3D GMM) which allows quantification of the percentage of shape variation that would most likely be linked to the postural transition from quadrupedal to bipedal (or the converse) in early archosaurs. Using 3D image acquisition tools and 3D GMM, we isolated the morphofunctional changes associated with postural transformations across Triassic-Jurassic archosauriforms using a wide sample of both extinct and extant taxa (47 femora from 26 species). Our results show that at least 15% of the global shape variation is linked to the difference between quadrupedal and bipedal archosaurs. Most quadrupedal femora have straight shafts with a twist between the proximal and distal epiphyses, whereas biped shafts are bent antero-posteriorly without rotation between epiphyses. In addition, the fourth

trochanter is more expanded among bipeds than quadrupeds. There is a clear distinction between shapes of quadrupedal pseudosuchians and bipedal dinosaurs whereas bipedal pseudosuchians and both bipedal and quadrupedal dinosauriforms do not display such strong differences in shape. Thus, this separation between bipeds and quadrupeds seems to bear a phylogenetic signal in addition to the morphofunctional one. We also compare the shape variation between bipeds and quadrupeds in the light of changes linked with mass and posture between cursorial and graviportal morphotypes. It shows that the femoral morphospace is wider among pseudosuchians, for example with small crocodylomorphs having relatively more slender femora than early dinosaurs. It also shows that some early dinosaurs in the Triassic had similar graviportal specializations as pseudosuchians. Our novel quantitative dataset illuminates qualitative aspects of how quadrupedality/bipedality, body size, and graviportal/cursoriality is associated with femoral shape variation across early archosauriform, revealing convergences, but also considerable disparity in morphofunctional adaptations of pseudosuchians and avemetatarsalians.

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### **Bird Biology & Evolution**

#### **NON-SEQUENTIAL FLIGHT-PERFORMANCE-RELATED WING MOLTING AROSE EARLY IN AVIALAN EVOLUTION**

Pittman, Michael<sup>1</sup>, Kaye, Thomas G.<sup>2</sup>, Wahl, William R.<sup>3</sup>  
<sup>1</sup>Vertebrate Palaeontology Laboratory, Division of Earth and Planetary Science, The University of Hong Kong, Pokfulam, Hong Kong, <sup>2</sup>Foundation for Scientific Advancement, Sierra Vista, Arizona, U.S.A., <sup>3</sup>Wyoming Dinosaur Center, Thermopolis, Wyoming, U.S.A.

The first feathered dinosaurs were not flight-adapted, and molting would not have been flight-specific. The transition to flight resulted in flight-related molting strategies, but when and how this happened is unknown. Here we report the oldest record of molting in a feathered dinosaur from the earliest unequivocal fossil bird, *Archaeopteryx* of the Late Jurassic Solnhofen Limestones. Laser-Stimulated Fluorescence of the Thermopolis specimen of *Archaeopteryx* revealed feather sheaths otherwise not visible under regular light. These detected molting remains are separated by one feather and are not in sequential order. In falcons, non-sequential molting preserves maximum flight performance, so this pattern in *Archaeopteryx* suggests that it also had this function to maintain hunting prowess. This demonstrates that a sophisticated flight-

performance-related molting strategy evolved close to the origin of avialans. This molting strategy evolved shortly after the appearance of asymmetrical feathers, but before the evolution of the first avialan sternum. This unexpected prioritisation over iconic avialan features like a keeled sternum and triosseal canal, underscores the usual and complex nature of flight-related changes along the lineage to modern birds.

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### **Anatomical & Developmental Explorations of the Mammalian Skull**

#### **STABILIZING SELECTION ON THE VARIABILITY OF SPACING OF *LOBODON CARCINOPHAGA* (CRABEATER SEAL) POSTCANINE TEETH FOR SUCCESSFUL FILTER-FEEDING FORAGING STRATEGIES**

Pollak, Megan, Tate-Jones, Kellum  
Earth Sciences, University of Oregon, Eugene, Oregon, U.S.A.

Pinnipeds, the group that includes true seals, eared seals, and walruses, generally display highly variable tooth spacing. Previous studies have credited this variability to the typical pinniped feeding mechanism, a combination of suction feeding and pierce feeding known as the 'grab-and-gulp' method, which does not require precise dental occlusion. However, the crabeater seal (*Lobodon carcinophaga*) is unique among pinnipeds as an obligate filter-feeder with a diet consisting of mainly krill. The distinct sieve-like postcanine teeth feature high-cuspation and intricate trellis-like morphology, which allows *L. carcinophaga* to effectively strain small krill from the water. We hypothesize that there is a strong selective pressure from this feeding ecology for postcanine occlusion in the crabeater seal. To test the variability in crabeater seal tooth spacing compared to that of generalist bearded seals (*Erignathus barbatus*), we measured the tooth gaps between the postcanine teeth of 21 adult specimens of *L. carcinophaga* and 11 adult specimens of *E. barbatus*. We then performed an F test of equal variance on these two datasets in R. We found that crabeater seal tooth gaps are significantly less variable in spacing than those of bearded seals. This result supports our hypothesis that there is a strong stabilizing selection for lower variability in tooth spacing of *L. carcinophaga*. Our work demonstrates that differential feeding ecologies can significantly impact morphological variation in pinniped dentition.

### **Taphonomy & Stratigraphy**

## PATTERNS OF CHEWING DAMAGE TO MODERN BONES FROM A STRIPED HYENA DEN IN SOUTHERN KENYA

Pontieri, Kyle, Pobiner, Briana, Potts, Richard  
Anthropology, Smithsonian Institution, Washington,  
District of Columbia, U.S.A.

Documenting chewing damage in fossil assemblages can aid in identifying carnivores responsible for the accumulation and modification of those assemblages. A first step in such documentation is studying chewing damage inflicted by extant carnivores, with an aim towards identifying taxon-specific chewing damage patterns to different sized prey. Much of this research has focused on chewing damage by spotted hyenas, which have specific adaptations for bone crushing to access marrow within the bones of their prey. Fewer studies of chewing damage by striped or brown hyenas have been undertaken, although they are prolific bone accumulators and modifiers.

This study describes damage to over 1,000 modern prey bones recovered from a striped hyena den near the prehistoric site of Olorgesailie in Kenya during 1987, 1988, 1992, and 1994. A range of wild and domestic species comprise the assemblage, from small to medium ungulates, primates, and carnivores, to a few giraffe bones. The majority of the taxonomically identifiable skeletal elements are from goats or sheep, followed by gazelles, then cows. We quantified the intensity of chewing damage observed on all skeletal elements using a recently published method that uses a 5-stage scale to assign a chewing damage intensity score for skeletal elements and portions (0 = no damage, 1 = tooth marks only, 2 = minimal chewing damage, 3 = moderate chewing damage, and 4 = severe chewing damage, fragmentation, or destruction).

Based on previous studies, we predicted that both predator taxon and prey size would condition the intensity of chewing damage inflicted by striped hyenas. As we expected, in this sample, striped hyenas inflicted less intense chewing damage to smaller (size 1 and 2) prey bones than published observations of chewing damage by spotted hyenas, which often fragment or completely destroy bones of smaller prey. The striped hyena chewing damage pattern and intensity were broadly similar to findings in previous studies of lion chewing damage on smaller prey bones. The most damaged skeletal element of smaller prey is the sacrum, with an average chewing damage intensity of 3.38, followed by the cranium (3.14), humerus (2.91), and ribs (2.61). This is the first application of this method to a hyena-chewed bone assemblage; future studies of additional samples of bones chewed by known carnivores will increase our ability to identify taxon-specific carnivore bone damage chewing patterns.

## Holocene & Pleistocene Mammalian Macroecology & Faunal Studies

### A NEW WOOLLY MAMMOTH (*MAMMUTHUS PRIMIGENIUS* BLUMENBACH, 1799) FROM KOTELNY ISLAND, NOVOSIBIRSK ARCHIPELAGO, RUSSIA

Potapova, Olga<sup>1</sup>, Pavlov, Innokentiy S.<sup>2</sup>, Plotnikov, Valerii V.<sup>2</sup>, Maschenko, Evgeny<sup>7</sup>, Dehasque, Marianne<sup>3</sup>, Shapiro, Beth<sup>4</sup>, Dalen, Love<sup>3</sup>, Suzuki, Naoki<sup>5</sup>, Hoffecker, John F.<sup>6</sup>, Protopopov, Albert<sup>2</sup>

<sup>1</sup>Research & Collections, The Mammoth Site of Hot Springs, SD, Inc., Hot Springs, South Dakota, U.S.A.,

<sup>2</sup>Dept. of Mammoth Fauna Studies, Academy of Sciences of Sakha (Yakutia), Yakutsk, Republic of Sakha (Yakutia), Russian Federation, <sup>3</sup>Dept. of Bioinformatics and Genetics, Stockholm University, Centre for Palaeogenetics, Stockholm, Sweden, <sup>4</sup>Paleogenomics Lab, University of California Santa Cruz, Santa Cruz, California, U.S.A.,

<sup>5</sup>Jikei University School of Medicine, Tokyo, Japan, <sup>6</sup>Institute of Arctic and Alpine Research, Boulder, Colorado, U.S.A., <sup>7</sup>Mammals, Borissiak Paleontological Institute, Moscow, Russian Federation

Despite numerous finds of isolated bones and tusks on the Arctic islands of the Laptev and North-Siberian Seas, discoveries of complete woolly mammoth skeletons or mummies are extremely rare (e.g., Bolshoy Lyakhov and Maly Lyakhov). In 2019, the Academy of Sciences of Sakha (Yakutia, Russia) organized several expeditions to this region. Three partial skeletons of woolly mammoth were discovered on Kotelny Island, including a relatively complete skeleton labeled the 'Pavlov Mammoth' (PM). Metric and morphological attributes of the tusks and bones indicated a young adult (possibly male) lacking bone pathology. AMS radiocarbon dating placed it within the Last Glacial Maximum or LGM (~20–24 ka BP; GS3–GS2.1b) and molecular analysis yielded its haplogroup designation, confirming the taxonomic identification.

Cartographic analysis of the PM site revealed that the individual was represented chiefly by the axial skeleton, along with two forelimb bones with pectoral and pelvic girdles, collected on and below the surface, within an area of 15 x 20 meters. All the remains exhibit breakage and modification, including the heavily damaged tusk, cranium, 5<sup>th</sup> to 8<sup>th</sup> thoracic vertebrae, humerus, pelvis, and two forelimb bones with gnawed-off epiphyses. The scapula appeared to contain an embedded foreign object fully penetrated through the supramammary process. The CT values indicated the bony origin of this object, while the scans revealed damage to the internal structure of the scapula and regrown cortical (surface) tissue surrounding this object.

The discovery of the external object ((?) arrowhead remnants) in the scapula and an ivory spatula-shaped

artifact associated with the remains along with the presence of apparent tool cutmarks on several bones, suggest that the PM was butchered and possibly hunted by humans, as well as being scavenged by carnivores. The PM is the first evidence of a human presence on the Arctic islands during the LGM. It indicates that during the LGM the exposed East Siberian Arctic Shelf supported a stable ecological system containing the largest late Pleistocene mammals and their predators. This region apparently sustained a local human population during the LGM as far as 75° North and constitutes a possible refugium for the ancestral Native American population or founder group, which now appears likely to have diverged genetically from its Northeast Asian parent population before or during the early phase of the LGM.

### Mesozoic & Early Cenozoic Mammalian Evolution

#### AN EARLY NIMRAVID (CARNIVORAMORPHA) FROM THE EOCENE OF CALIFORNIA REVEALS A RAPID DISPERSAL OF THE HYPERCARNIVOROUS GUILD

Poust, Ashley W.<sup>1</sup>, Tomiya, Susumu<sup>2</sup>

<sup>1</sup>Department of Paleontology, San Diego Natural History Museum, San Diego, California, U.S.A., <sup>2</sup>Kyoto University Primate Research Institute, Inuyama, Japan

The Nimravidae were hypercarnivorous mammals first found in the middle Eocene. Filling cat-like morphological and ecological roles across the northern continents until the Miocene, nimravids were not cats at all, but have been interpreted as stem-feliforms or even as stem-carnivorans. The early phase of the clade's evolutionary history in North America has remained unclear, with only a few fragmentary and generically-indeterminate specimens known from before the middle Chadronian North American Land Mammal Age (late Eocene). Here we reinterpret and describe a specimen that demonstrates the wide occurrence and early dispersal of this distinctive group.

The new nimavid fossil comprises a partial maxilla with P3–P4. Discovered during a mitigation project in the Pomerado Conglomerate of coastal San Diego County, CA (late Duchesnean to early Chadronian), it had been previously identified as an hyaenodontid. We re-identify it as carnivoran on the basis that: (1) the carnassial paracone and metacone are not coupled and (2) the P3 lacks a protocone. We further attribute the fossil to Nimravidae using a suite of dental characters including the absence of a deep P4 incisure. Additional features of the specimen show conditions in some ways intermediate to those present in later North American nimravids, such as *Dinictis* and *Hoplophoneus*, but it is assignable to neither.

The recognition that this nearly puma-sized predator is a nimavid and not a hyaenodontid alters our conception of the pattern of reassembly of mammalian carnivore guilds during an early phase of the Eocene–Oligocene transition in southwestern North America. In addition to its local importance, it revises our understanding of the dispersal of the group. Even with some temporal uncertainty in the dating of the Pomerado Conglomerate, this specimen may represent the earliest definitive record of the group in North America, preceding the common nimravids with which it shares affinities, and is one of the earliest records worldwide. This San Diego specimen, combined with other possible records of early nimravids in North America, including fragmentary canines from the latest Uintan or early Duchesnean Clarno Formation of Oregon and the early Chadronian Little Egypt local fauna of Texas, suggests that Nimravidae became widespread in western North America quickly after they arrived on the continent and demonstrates an early, multi-continental flowering of this group of hypercarnivores.

### Permo-Triassic Tetrapods

#### NEW SPECIMENS OF THE ARCHOSAURIFORM *VANCLEVEA CAMPI* FROM THE UPPER TRIASSIC (RHETIAN) REDONDA FORMATION OF EASTERN NEW MEXICO INDICATES *VANCLEVEA CAMPI* WAS AN APEX PREDATOR

Price, Ryan C.

Mesalands Community College, Tucumcari, New Mexico, U.S.A.

The basal archosauriform *Vancleavea campi* has long been thought to represent a relatively small, semi-aquatic, predator from the Late Triassic ecosystems found in the entire Upper Triassic strata of western North America. Here, I describe four partial dentaries recovered from the Duke Ranch Member of the Redonda Formation of eastern New Mexico. All specimens are referred to *Vancleavea campi* on the basis of a number of characters of the dentary shared with a complete individual of the taxon, here postulated to represent autapomorphies of *Vancleavea campi*. These dentaries show that *Vancleavea* was a much larger animal than previously thought, and an estimate of the total minimum length is presented using isometric scaling. The total length of the largest individual is estimated close to four meters. This size may have allowed *Vancleavea* to hunt larger prey within its environment and therefore shifts its role in the ecosystem to that of a semi-aquatic apex predator. I interpret the size increase as a growth series within the taxon, but acknowledge that further evidence is needed in support of this hypothesis.

### Permo-Triassic Tetrapods

## OSTEOLOGY AND PHYLOGENETIC AFFINITIES OF THE EARLY GLIDING REPTILE *WEIGELTISAURUS JAEKELI*

Pritchard, Adam C.<sup>1</sup>, Sues, Hans-Dieter<sup>2</sup>, Reisz, Robert<sup>3</sup>, Scott, Diane<sup>3</sup>

<sup>1</sup>Department of Paleontology, Virginia Museum of Natural History, Martinsville, Virginia, U.S.A., <sup>2</sup>Department of Paleontology, National Museum of Natural History, Washington, District of Columbia, U.S.A., <sup>3</sup>Department of Biology, University of Toronto at Mississauga, Toronto, Ontario, Canada

Weigeltisauridae is a clade of small-bodied Permian diapsids that represent the oldest known vertebrates with skeletal features for gliding. It is characterized by a cranium with a posterior bony casque, prominent horns on the temporal arches, and a series of elongate bony spurs projecting from the ventrolateral surface on both sides of the trunk. Definitive specimens are known from upper Permian of Germany, Russia, and Madagascar, but the quality of their preservation previously limited understanding of the skeletal structure and phylogenetic affinities of these reptiles.

Here, we present a revised account based on a nearly complete skeleton of *Weigeltisaurus jaekeli* from the Kupferschiefer of central Germany and a revised phylogenetic analysis of early Diapsida and early Sauria. The specimen preserves all elements of the skeleton, save for the braincase, palate, some dorsal vertebrae, the carpus, and the tarsus. The well-preserved teeth in the maxilla are not conical but leaf-shaped, resembling those in the middle portion of the maxillae of the Russian weigeltisaurid *Rautiania*. The parietals bear rows of dorsolaterally oriented horns similar to those on the squamosals. The quadrate is a dorsoventrally short element with a tapering dorsal margin that lacks a cephalic condyle. The squamosal appears to cover the quadrate both laterally and posterodorsally. The manual and pedal phalanges are elongate and slender, similar to those of extant arboreal squamates. The unguals have very prominent flexor tubercles. A patagium was supported by elongate, slender bony rods. They are situated superficial to the preserved dorsal ribs and gastralia, corroborating the hypothesis that these structures represent dermal ossifications independent of and greater in number than the bones of the dorsal axial skeleton.

Our phylogenetic analysis focuses on non-saurian Diapsida and early Sauria (339 characters, 61 operational taxonomic units), including three weigeltisaurid taxa. We recover a monophyletic Weigeltisauridae stemwards of a clade comprising *Youngina capensis*, the Malagasy diapsids *Acerosodontosaurus*, *Hovasaurus*, and *Thadeosaurus*, and Sauria. Weigeltisauridae form a monophyletic Aviccephala with Drepanosauromorpha. These results highlight the importance of Weigeltisauridae as part of a previously

poorly known, anatomically disparate and ecologically diverse radiation of diapsid reptiles outside of crown-group Sauria during the Permian Period.

**Funding Sources** This work is supported by a Peter Buck postdoctoral Fellowship (to A. Pritchard), the Smithsonian Institution (to H.-D. Sues), and an NSERC Discovery Grant (to R. Reisz).

## Late Cenozoic Mammalian Macroecology & Macroevolution

### REVIEW OF THE MIOCENE PECCARY *PROSTHENNOPS* (MAMMALIA, TAYASSUIDAE): THE ULTIMATE WASTEBASKET TAXON, AND ITS IMPLICATIONS FOR PALEOBIOLOGICAL DATABASES

Prothero, Donald R.

Vertebrate Paleontology, Natural History Museum of LA County, La Crescenta, California, U.S.A.

The genus *Prosthennops* was first proposed by J. W. Gidley in 1904, based on a lower jaw from the Hemphillian of Sappa Creek in northwest Kansas, originally named '*Dicotyles serus*' by E. D. Cope in 1879. Since then, *Prosthennops* has become the wastebasket name for nearly all middle and late Miocene peccary teeth that are bunodont and do not show specializations in the skull or zygomatic arches. A recent monographic review of all the North American Tayassuidae has established that most tooth fossils referred to *Prosthennops* do not in fact belong to that genus. The only valid species of the genus is *P. serus*, which is restricted to the latest Clarendonian–Hemphillian (late Miocene). Complete skulls from the early Hemphillian Cambridge l.f. of Nebraska (formerly '*Prosthennops graffhami*' from the Kimballian) show that *Prosthennops serus* was a very derived peccary, with enormous flaring arched zygomatic flanges. Late Barstovian–early Clarendonian specimens formerly referred to '*Prosthennops niobrarense*' do not in fact belong to that genus, but are a much less derived genus without any flaring zygomatic flanges or wings that will be formally named soon. Early–middle Barstovian specimens once called '*Prosthennops xiphidonticus*' represent an even more primitive taxon, also lacking any unusual zygomatic structures, that will be formally named yet another genus. The famous 'Nebraska man' tooth, *Hesperopithecus haroldcookii*, mistaken for an anthropoid primate in 1922, cannot be assigned to *Prosthennops* either, since it is not complete enough or well enough preserved to attribute it to any of more than five peccary genera known from the late Clarendonian. Likewise, nearly all fragmentary and isolated teeth and jaws from the middle and late Miocene in collections cannot be assigned to *Prosthennops* or possibly any peccary genus unless they

are associated with diagnostic skull material. Thus, collections records and paleontological databases that record *Prosthennops* from anywhere other than the latest Clarendonian–Hemphillian are in error, and they cannot be used to construct elaborate conclusions about diversity dynamics of Miocene mammals.

### Symposium: Dietary Reconstruction

#### NICHE PARTITIONING AND SUBTLE DIETARY SHIFTS – TESTING THE SENSITIVITY OF MULTIVARIATE MICROWEAR TEXTURE ANALYSIS

Purnell, Mark A.<sup>1</sup>, Adams, Neil<sup>1</sup>, Bestwick, Jordan<sup>2</sup>  
<sup>1</sup>University of Leicester, Leicester, U.K., <sup>2</sup>University of Birmingham, Birmingham, U.K.

The fossil record should provide crucial evidence to test and constrain models linking trophic ecology and macroevolution through deep time, but this potential is generally unrealized. In large part this is because of the difficulty, for fossil taxa, of obtaining evidence of diet – and the use and partitioning of resources – that is independent of the morphological data from which macroevolutionary patterns are themselves derived. Non-morphological proxies for diet, including microwear texture analysis, can break this circle, and quantitative approaches to analysis based on parameterization of surface texture are increasing the robustness and repeatability of this widely used technique.

It is also notable that microwear tracks diet over timescales that are much shorter than those of the adaptive, evolutionary changes in morphology that most analyses of fossil taxa rely on. Analysis of microwear texture thus has the potential to detect dietary differences between sympatric species and between the same species at different time periods, the former providing evidence of niche partitioning, and the latter indicating evolutionary changes in the dietary niche. Such analyses allow us to detect ecological responses to environmental and climatic changes, and changes in the potential selective pressures that drive adaptive shift in morphology.

All this relies on microwear texture analysis being sensitive enough to detect subtle dietary differences between populations of species, and while the browser-grazer spectrum in herbivores are well studied, other dietary shifts are less well understood. We have used microwear texture analysis to investigate differences between sympatric shrew species (largely insectivorous), between frugivorous and insectivorous treeshrews, through ontogeny in pterosaurs, and in an archaic ungulate across a rapid thermal event. In all cases the ability of quantitative multivariate microwear texture analysis to detect subtle dietary differences is confirmed. We can be confident that

the technique offers powerful insights into dietary change in a range of taxa and within dietary guilds over short spatial and temporal scales.

### Late Cenozoic Mammalian Macroecology & Macroevolution

#### THE FIRST MACRACHENIID (MAMMALIA, LITOPTERNA) FROM THE NEOGENE BAHÍA INGLESA FORMATION: ANATOMICAL DESCRIPTION AND COMMENTS ON BODY SIZE IN MACRACHENIIDS

Puschel, Hans P.<sup>1</sup>, Shelley, Sarah L.<sup>2</sup>, Soto-Acuña, Sergio<sup>3</sup>, Alarcón-Muñoz, Jhonatan<sup>3</sup>, Ugalde, Raúl<sup>4</sup>, Brusatte, Stephen<sup>1</sup>

<sup>1</sup>University of Edinburgh, Edinburgh, U.K., <sup>2</sup>Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A., <sup>3</sup>Universidad de Chile, Santiago, Chile, <sup>4</sup>Universidad Mayor, Santiago, Chile

During most of the Cenozoic, South America was mostly isolated from all other continents, which allowed the independent evolution of a particular mammalian fauna of South American ungulates (SANUs). Among SANUs, litopterns were the most diverse order after notoungulates with species ranging from the base of the middle Paleocene to the late Pleistocene. Although most Paleogene litopterns have uncertain affinities, Neogene taxa are classified into three well established families: Macrauchiinae, Protheroheriidae, and Adiantidae. Macrauchiinae are medium to large-sized litopterns with long necks, three-toed feet and a reduced nasal region. This family is known from the late Eocene, represented by the genus *Polymorphis*, to the late Pleistocene, with the emblematic genus *Macrauchenia*, reaching their highest diversity during the late Miocene. Macrauchiinae is usually grouped into two subfamilies: Cramauchiinae (Eocene to middle Miocene) and Macrauchiinae (late Miocene to late Pleistocene), although only the latter has been shown to be monophyletic. Here we describe a new specimen (SGO.PV.2170) that represents the first macrauchiinid (and SANU) from the Mina Fosforita Member of the Bahía Inglesa Formation, a siliciclastic unit, commonly interpreted as a continental slope to shallow marine system, in which more than 60 species of vertebrates have been found so far, including marine mammals and rare continental mammals. This member has been constrained from ~8 to 6 Ma (Tortonian to Messinian), according to Sr/Sr stable isotopes on pectinids and K/Ar geochronology. SGO.PV.2170 consists of 32 elements, including a fragment of right dentary, atlas and axis fragments, postaxial cervical vertebrae, the distal end of left radius-ulna, carpals, metacarpals, and proximal and medial phalanges. Although the postcranial skeleton is highly

conserved in macraucheniids, the presence of a totally fused radius-ulna allowed us to assign SGO.PV.2170 to Macraucheniinae. We took linear measurements of the specimen and by using regression equations in ungulates we estimated its body mass at 121.2 kg. Considering that body mass estimations in macraucheniines range between ~160 and 1200 kg, SGO.PV.2170 would be the smallest macraucheniine and among the smallest members of Macraucheniidae. These findings expand the early diversity of macraucheniines in the late Miocene and provide a unique window into a previously unknown ungulate fauna living on land, close to the seashore.

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### Evolution & Biology of Non-Avian Theropods

#### COMPARATIVE OSTEOHISTOLOGY OF ALVAREZSAURS INFORMS HYPOTHESES FOR THEIR BODY SIZE EVOLUTION

Qin, Zichuan<sup>1</sup>, Zhao, Qi<sup>2</sup>, Choiniere, Jonah N.<sup>3</sup>, Benton, Michael J.<sup>1</sup>, Xu, Xing<sup>2</sup>

<sup>1</sup>School of Earth Sciences, Bristol, U.K., <sup>2</sup>Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China, <sup>3</sup>University of the Witwatersrand, Johannesburg, South Africa

Alvarezsauridea is a group of bizarre theropods with highly specialized anatomy. Some of the late-branching members of this clade evolved extremely small body size, as small as early birds. Alvarezsauroids until now have generally been overlooked in studies of theropod body mass evolution because they lacked sufficient lineage sampling and because the evidence for skeletal maturity of tiny specimens was lacking. Moreover, unlike the evolution of flight in paravians, the phylogenetically independent reduction in alvarezsaurid body mass lacks an obvious functional correlate. The recent discoveries of early-branching alvarezsaurid fossils from China make a more thorough investigation of body mass evolution in this clade possible. We conducted detailed osteohistological analysis and bone co-ossification comparisons for Chinese alvarezsauroids, including the Late Jurassic *Haplocheirus sollers*, *Aorun zhaoi*, and *Shishugounykus inexpectus*, the Early Cretaceous relatively large-sized alvarezsauroids *Xiyunykus pengi* and *Bannykus wulatensis*, and the Late Cretaceous alvarezsaurid *Xixianykus zhangii*. Together with previously published histological data and observations of anatomical characters such as bone ossification, we present a general age and ontogeny estimation for alvarezsaurid specimens. We use our results to estimate adult body mass of all alvarezsauroids

and to critically assess the hypothesis of lineage-specific size decrease in Alvarezsauridea. Our results reveal that size evolution within alvarezsauroids had an initially divergent start followed by a single body size miniaturization event. This miniaturization process started at around 90 million years ago, had a significantly high rate, and culminated in parvicursorines that attained the smallest non-paravian dinosaur body masses in its final stage. Alvarezsaurid lineage richness increased after the miniaturization began, and potentially involved a secondary radiation of small-sized taxa at the end of the Cretaceous. Our results also support the idea that these late-branching small-sized alvarezsauroids occupied an obligate myrmecophagous (termite-eating) ecological niche. This hypothesis is also supported by their unusual low growth rates strategies revealed by our osteohistological studies, and their highly specialized anatomical features indicated by previous research.

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### Romer Prize

#### FOOD WEB ANALYSIS OF EARLY MESOZOIC ECOSYSTEMS SHED NEW LIGHT ON EARLY DINOSAUR EVOLUTION

Qvarnström, Martin

Department of Organismal Biology, Uppsala University, Uppsala, Sweden

Dinosaurs evolved prior to 230 Ma ago. Dinosaur-dominated terrestrial ecosystems, which would characterize the remainder of the Mesozoic, however, did not appear until around the Triassic-Jurassic transition. To understand early dinosaur evolution, and the rise of these ecosystems, it is therefore crucial to study the dynamics of Late Triassic tetrapod communities which contained some early dinosaurs along with various other tetrapods (e.g., therapsids, temnospondyls, and archosaurs). Here I present trophic structures in three fossil assemblages from the Polish Basin that span from the mid-late Carnian to the early Hettangian and represent snapshots of three stages of early dinosaur evolution. They can be described as assemblages in which dinosauriforms/dinosaurs played a minor ecological role (inferred from the mid- to late Carnian sites Krasiejów and Wozniki), a moderate role (inferred from the late Norian/early Rhaetian site Lisowice) and completely dominated the terrestrial fauna (inferred from the early Hettangian site Soltyków). A large dataset of fossils with direct evidence on feeding is analyzed, including numerous bones with bite marks and over 500 bromalites (fossil droppings and regurgitates). Synchrotron scanning of over 80 coprolites revealed a wide range of food remains including various tetrapod bones,

articulated fish remains, plants, possible parasites, and exceptionally preserved three-dimensional beetles. Many bromalites are attributable to producers known from the body fossil record of the sites enabling reconstructions of large parts of the ecosystems. It appears that Late Triassic carnivores typically fed on fish and insects, except for single top predators which were also feeding on various tetrapods. Moreover, the abundance and diversity of herbivores increased drastically across the Triassic–Jurassic transition. Based on this model from northern Pangea, it is proposed that the dinosaurs' rise to ecological dominance can be described in three steps: 1) the appearance of small opportunistic insectivorous/omnivorous dinosauriforms, 2) the appearance of relatively small carnivorous theropods as well as herbivorous ornithischian-like dinosaurs and sauropodomorphs, and finally, 3) a dinosaurian diversification and expansion of ecospace occupation in the earliest Jurassic as a result of new dietary key adaptations that enabled exploitation of new food resources in new humid climates in an unprecedented way.

#### Quantitative Methods

#### TOTAL-EVIDENCE APPROACH TOWARDS GLIRES PHYLOGENY: TOPOLOGICAL AND BIOGEOGRAPHIC DIFFERENCES WHEN INCLUDING ULTRACONSERVED ELEMENTS (UCES)

Rankin, Aime H., Asher, Robert J.  
Department of Zoology, University of Cambridge,  
Cambridge, U.K.

Thanks to technological advances, we can now combine the morphology of fossils with various types of molecular evidence when reconstructing phylogenies. As the total-evidence approach becomes increasingly more common, we are seeing that some new types of data produce different topologies. The traditional root of rodents, for example, has recently been reconsidered in studies which incorporate ultraconserved elements (small pieces of largely non-coding DNA). To investigate the implications of topological incongruence in Glires caused by UCEs, we selected 61 extant and 63 extinct taxa and then used Maximum Likelihood (ML) methods to analyse a matrix combining several types of data: 14 protein coding genes, 219 morphological characters and 900,000 bp of UCEs. We compared these results to ML and Bayesian tip-dated analyses of the same matrix excluding the UCEs. The resulting trees for these two matrices have major topological differences, offering different hypotheses for the rodent root. Our UCE tree suggests a Mouse-related (Sciuromorpha+Ctenohystrica) clade, whereas the loci+morphology matrix recovers a more traditional Sciuromorpha (Ctenohystrica+Mouse-related) clade.

Furthermore, our UCE tree places *Tataromys*, an anatomically hystricomorphous rodent, at the base of Rodentia. This goes against the commonly held view that the first rodents would have had a simple protrogomorphous arrangement of the masseter muscles. In addition, the tree that includes UCEs places eurymylids and *Heomys*, traditionally stem-group rodents, on the Lagomorph stem. The topological differences incurred by the inclusion of UCEs also lead to different hypotheses of biogeography. We estimated the biogeographic origins of each clade using parsimony ancestral state reconstruction on each tree. Our UCE tree proposes an Afro-Asian origin of crown-group Rodentia, whereas the dataset excluding UCEs suggests a North American origin. However, both datasets agree on an Asian origin for Glires as a whole.

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#### Romer Prize

#### UNTANGLING THE MODE AND TEMPO OF ARMORED DINOSAUR MACROEVOLUTION

Raven, Thomas  
Department of Earth Sciences, Natural History Museum  
London, London, U.K.

Thyreophoran (armored) dinosaurs were significant components of terrestrial ecosystems during the Jurassic and Cretaceous. However, a patchy fossil record and highly modified anatomy hinders our understanding of their evolutionary history. For example, the relationships of many early diverging taxa are labile and the degree of convergence between the two major groups, Ankylosauria and Stegosauria, has been difficult to assess. Thus, investigation of macroevolutionary questions, such as the mode and tempo of morphological evolution and biogeographic history, has been unfeasible.

I address these issues with a new whole-group, species-level phylogenetic dataset of 340 characters and 91 thyreophoran taxa. Equal and implied weights parsimony and Bayesian inference demonstrate a novel hypothesis for thyreophoran relationships. The traditional ankylosaurian dichotomy is not supported: instead, four distinct ankylosaur clades evolved independently, with Nodosauridae rendered paraphyletic. Ankylosauridae, Nodosaurinae, Polacanthinae, and Struthiosaurinae have distinct morphotypes, typified by *Euoplocephalus*, *Edmontonia*, *Gastonia* and *Struthiosaurus*, respectively. *Isaberrysaura* is an early stegosaur and *Scelidosaurus* is a non-eurypodan.

This phylogenetic framework allows the first rigorous assessment of macroevolutionary trends within Thyreophora. Biogeographic analysis using BioGeoBEARS shows stegosaurs originated in China

before dispersals into Europe and North America. The earliest ankylosaurs were from the Middle Jurassic of China, with subsequent dispersals of nodosaurines into North America during the Late Jurassic, polacanthines into Europe and North America during the Early Cretaceous, and struthiosaurines into Asia in the Early Cretaceous and back to Europe in the Late Cretaceous. Ankylosaurids dispersed from Europe into Asia and later into North America. Character-based disparity analysis shows morphospace occupation of stegosaurs and ankylosaurs was anticorrelated; stegosaurs decreased in disparity while ankylosaurs diversified, and evolutionary rates follow the same trend. These results could indicate that stegosaurs were outcompeted by ankylosaurs, with their extinction in the Early Cretaceous coincident with the appearance of polacanthines, nodosaurines and ankylosaurids. This might have been facilitated in part by more complex chewing mechanisms and increased defensive osteoderm coverage found in ankylosaurs.

**Funding Sources** University of Brighton Science Scholarship.

#### Preparators

#### REMOVING PAINT FROM A MASTODON THAT WAS ON EXHIBIT FOR 90 YEARS

Redman, Cory<sup>1</sup>, Landstra, Ryleigh<sup>2</sup>

<sup>1</sup>Grand Rapids Public Museum, Grand Rapids, Michigan, U.S.A., <sup>2</sup>Grand Rapids Community College, Grand Rapids, Michigan, U.S.A.

In 1904 a partial mastodon (*Mammuth americanum*) skeleton was discovered in Moorland, Michigan and purchased by the Grand Rapids Public Museum (GRPM) for \$300. The bones were almost immediately put on exhibit in an articulated, standing position and stayed on exhibit almost continuously until 1994, when the skeleton was partially dismantled and moved into storage. In 2019, work began on completely disassembling and repairing the skeleton for better long-term preservation and returning it to a state more similar to when it was found. Here we report on the methodology used to remove multiple layers of water- and oil-based paints from non-permineralized bone without the use of an air abrasion unit.

A bone was placed on a pedestal in a sealed container with 0.5-1 inch of acetone and left in the vapors for 24 hours. The bone was then scrubbed for 15-30 minutes with a moderately stiff nylon brush dipped in 70% isopropyl alcohol to remove any peeled paint. The bone was then rinsed with water and placed back into a sealed container with acetone for another 24 hours. This process was repeated two to four times, depending on paint thickness and the bone's surface roughness. Wax sculpting tools were used to remove paint from problematic cracks and

crevasses, after the second acetone vapor bath. The paint was easier to remove using multiple, shorter vapor treatments opposed to trying to remove all the paint after one longer treatment ( $\geq 48$  hrs). A thin, black layer composed of an unknown, man-made coating makes up the fourth layer on the bone, but a methodology for its complete removal has not yet been identified. This black layer will sometimes flake off the smoother bone surfaces after the second or third vapor bath, but is largely unchanged even after being completely exposed and sitting in acetone vapors for a week.

Acetone, water, 2% hydrogen peroxide, 70% isopropyl alcohol, and paint thinner were all tested for removing the paint, by directly brushing the liquid onto the bone and placing the bone in a vapor bath for various lengths of time (1-144 hrs). Acetone vapors and brushing with isopropyl alcohol has proven to be the most efficient method for removing the paint without degrading or damaging the non-permineralized bone.

#### Dinosaur Systematics, Diversity & Ecology

#### HISTOLOGIC GROWTH DYNAMIC STUDY AND POPULATION BIOLOGY OF THE CERATOPSID DINOSAUR *EINIOSAURUS PROCURVICORNIS* FROM A DEATH ASSEMBLAGE OF THE UPPER CRETACEOUS TWO MEDICINE FORMATION OF NORTHWESTERN MONTANA

Reizner, Julie A.<sup>1</sup>, Woodward, Holly<sup>2</sup>, Freedman Fowler, Elizabeth<sup>3</sup>

<sup>1</sup>Physics, Geology, and Engineering Technology, Northern Kentucky University, Highland Heights, Kentucky, U.S.A., <sup>2</sup>Anatomy and Cell Biology, Oklahoma State University Center for Health Sciences, Tulsa, Oklahoma, U.S.A., <sup>3</sup>Natural Sciences, Dickinson State University, Dickinson, North Dakota, U.S.A.

The centrosaurine ceratopsid dinosaur *Einiosaurus procurvicornis* is known exclusively from two monodominant bonebeds from the upper Campanian (Upper Cretaceous) Two Medicine Formation of northwestern Montana. The larger of these, Canyon Bonebed, is a drought-induced assemblage representing a population of individuals, ranging from juveniles to alleged adults, that lived and died together. Therefore, paleohistological studies can be used to test hypotheses on growth dynamics and population biology, including reproductive and social behavior, of this extinct species.

While detailed growth rates and life histories of members of several dinosaur clades have been reported, those of ceratopsids remain understudied by comparison. Previously, details on bone growth of *Einiosaurus* were assessed and growth lines were used to determine the ages of the individuals at their time of death. Those

interpretations have now been revised in consideration of current imaging technology and statistical methods used in paleohistology.

Sixteen tibiae representing the full available range of sizes (mid-diaphyseal circumferences range from less than 10 cm to more than 40 cm) were sampled at the mid-diaphysis and examined for Lines of Arrested Growth (LAGs), and an External Fundamental System (EFS) that would indicate skeletal maturity. Primary tissue and an absence of LAGs were observed in the smallest tibiae, suggesting that these individuals were less than one year old. The other 13 tibiae preserve 1–5 LAGs, and most likely are missing additional LAGs due to medullary expansion and remodeling. The growth curve based on these 13 specimens is compared to that reported in *Pachyrhinosaurus*, another centrosaurine ceratopsid.

As expected from any death assemblage past or present, most individuals were babies, juveniles, and subadults when they succumbed to drought. The largest individuals in the sample were likely over 10 years old at death, yet lack an EFS, indicating that they were not yet skeletally mature adults. Thus, the distinctive cranial ornamentation of *Einosaurus* is based on subadult individuals and the full adult morphology is not currently known, which has implications for future taxonomic resolution and morphometric studies of ceratopsians. This study helps elucidate the life history of a relatively little-known species of dinosaur and further adds to the understanding of how the horned dinosaurs lived.

## Late Cenozoic Mammalian Macroecology & Macroevolution

### BEYOND MISSING BROWSERS: OLIGO-MIOCENE COMMUNITY STRUCTURE AND FUNCTIONAL DIVERSITY IN THE NORTHWEST

Reuter, Dana M., Hopkins, Samantha S., Davis, Edward B. Earth Sciences, University of Oregon, Eugene, Oregon, U.S.A.

Region-specific studies have highlighted the variability of North American grassland expansion and community composition change over the last 20 million years. Most of this work has focused on the Great Plains, the onset of C<sub>4</sub> grasses, or large herbivore ecology. During this time interval, Oregon was topographically complex and in a climatic zone that favors C<sub>3</sub> plants over C<sub>4</sub> plants, making it ecologically distinct from the Great Plains region. Studies of taxonomically limited groups of Northwest ungulates have hinted at differences between the story derived from the plains and that of the west. Our study aims to determine how past climate and vegetation changes influenced Oregon mammalian functional diversity and community structure dynamics. By focusing on Oregon's

well-sampled Oligo-Miocene record and including all mammals, this study aims to add to our biogeographical knowledge of Cenozoic ecosystem change and help develop an understanding of ecological processes driving these dynamics. We evaluated functional diversity and community structure within the last 25 million years by evaluating body mass and diet. Species were classified into the diet categories browser, mixed feeder, grazer, carnivore, omnivore, and insectivore based on primary literature reviews. Estimated food webs were reconstructed for each assemblage using processes derived from modern documented predator-prey ecological relationships. These food webs were then used to calculate community structure metrics such as number of unique trophic nodes, link density, and overall connectance. The functional diversity datasets were compared with previously published data for the Great Plains to investigate biogeographical patterns of ecological change. Community structure and functional diversity results show that between 16 and 7 Ma there was an overall decrease in taxonomic diversity and a shift in functional diversity. This change is characterized by a decline in herbivorous species and omnivores being replaced by more specialized hypercarnivores. Similar trends have been observed in the Great Plains and other studies that have looked at modern environmental gradients. The functional diversity changes lead to a less connected food web that had more unique trophic nodes in the late Miocene. Our work shows that Oregon's changing climate affected not only the taxonomic diversity of mammalian communities but the functional structure of those communities as well.

## Permo-Triassic Tetrapods

### CRANIAL ANALYSIS OF AETOSAURIA BASED ON THE CRANIAL ANATOMY AND DENTITION OF *TYPOTHORAX COCCINARUM* (ARCHOSAURIA: PSEUDOSUCHIA) FROM THE UPPER TRIASSIC CHINLE FORMATION OF NORTHERN ARIZONA

Reyes, William A., Parker, William, Marsh, Adam D. Petrified Forest National Park, Arizona, U.S.A.

Aetosaur bones are some of the most common vertebrate remains found in Upper Triassic strata in North America. Most of our understanding of these early pseudosuchian archosaurs is based on postcranial material, primarily their osteoderms, vertebrae, and pelvic bones. Within the last decade, new cranial material has been described for a variety of aetosaur taxa, including *Aetosauroides scagliai*, *Coahomasuchus chathamensis*, *Paratypothorax andressorum*, *Stagonolepis olenkae*, *Stenomylus huangae*, and *Scutarx deltatylus*. Here we present the first complete articulated skull of *Typothorax coccinarum*, from the Late

Triassic Chinle Formation in Petrified Forest National Park. We used the cranial characters of *Tyothorax coccinarum* to assess the relationships of Aetosauria. The overall skull morphologies vary between the two major clades (i.e., the Stagonolepidoidea and the Aetosaurinae) of Aetosauria. Stagonolepidoids share a more robust skull with transversely expanded premaxillae and large external nares. On the other hand, aetosaurines share a more gracile skull with tapered premaxillary tips and proportionately larger orbits. Additionally, the heterodont dentition of *Tyothorax coccinarum* also lends further support to the challenge to the historical interpretation of aetosaurs being strictly herbivorous. *Neoaetosauroides engaeus*, *Aetosauroides scagliai*, and now *Tyothorax coccinarum* support the more recent hypothesis that aetosaur diets ranged between omnivory, insectivory, and herbivory.

### **Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

#### **DIRE WOLF IDENTIFIED FROM THE LATE PLEISTOCENE OF ALBERTA USING GEOMETRIC MORPHOMETRICS**

Reynolds, Ashley R.<sup>1</sup>, Lowi-Merri, Talia<sup>1</sup>, Brannick, Alexandria L.<sup>3</sup>, Evans, David<sup>2</sup>

<sup>1</sup>Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario, Canada, <sup>2</sup>Palaeobiology, Royal Ontario Museum, Toronto, Ontario, Canada, <sup>3</sup>Biology, University of Washington, Seattle, Washington, U.S.A.

Late Pleistocene deposits near Medicine Hat, Alberta have yielded over 1,200 vertebrate fossils now held at the Royal Ontario Museum. Recent work on these deposits has confirmed the presence of iconic large Rancholabrean fauna, such as *Smilodon fatalis* and *Panthera atrox*, suggesting that the Rancholabrean carnivore guild extended further north than previously known. In 1970, C. S. Churcher collected a dentary that, based on its large size and morphology, he ascribed to the dire wolf *Canis dirus*. This would be the most northerly record of the dire wolf, but the specimen has not been described and illustrated in the literature. The size and robusticity of the specimen are consistent with an identification of *C. dirus*, but this may be due to allometric shape change associated with large body size. Heavy tooth wear and tooth loss have obliterated dental characters that could confirm its taxonomic assignment. Thus, the taxonomic identity of this specimen cannot be ascertained based on qualitative morphological characters alone.

To test the taxonomic identity of the Medicine Hat dentary we applied a 2D geometric morphometric analysis using a previously published dataset for *C. dirus*, fossil *C. lupus*, and modern *C. lupus*, which was modified to remove landmarks missing in the Medicine Hat specimen. We

performed a Principal Component Analysis (PCA) to visualize the morphological variation between known *C. dirus*, *C. lupus*, and the unknown specimen. We then calculated the typicality probability of the Medicine Hat specimen belonging to each group based on its distance from the group means, using the first five PC axes of variation.

The PCA identified 20 PC axes of morphological variation. PC1 is driven by dorsoventral depth below the m1 and explains ~33% of variation. There is some overlap between groups along PC1, with the Medicine Hat specimen falling within this range of overlap. However, the Medicine Hat dentary clusters with the dire wolves along PC2. This axis explains ~15% of morphological variation and is correlated with dorsoventral depth of the mandible below the pre-massial teeth. There was a typicality probability of 0.738 that the Medicine Hat specimen belongs within *C. dirus*, and much lower probabilities that it would belong in either of the other groups. These results suggest that, in addition to other large Rancholabrean carnivores, dire wolves were present in Alberta, thus expanding their known range into the Pleistocene of Canada.

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### **Biomechanics & Functional Morphology THE KINETIC FORAGING SYSTEM OF SNAKES IS HIGHLY INTEGRATED**

Rhoda, Daniel<sup>1</sup>, Segall, Marion<sup>2</sup>

<sup>1</sup>Committee on Evolutionary Biology, University of Chicago, Chicago, Illinois, U.S.A., <sup>2</sup>Department of Herpetology, American Museum of Natural History, New York, New York, U.S.A.

Snakes must detect, capture, manipulate, and swallow large prey using exclusively their heads. These different functions require the coordinated movements of different combinations of bones, forming functional modules. To do so, snakes have evolved a highly kinetic skull composed of several bones that work in concert to perform these different tasks; the hyperkinetic skull is a unique feature in snakes. Bones within a functional module are expected to covary over evolutionary time (i.e., morphological integration and modularity), as they share selective pressures associated with the function. Alternatively, kinesis of the snake trophic system (i.e., the bones physically involved in foraging) allows for the independent movement of its individual bones, potentially encouraging modularity. Therefore, in the trophic system of snakes there exists a tension between the functional relationships between bones promoting integration and cranial kinesis promoting modularity. We used 3D surface morphometrics methods and developed a new superimposition strategy for

mobile systems to quantify evolutionary integration and modularity of the trophic system in 33 species of snakes from 70 mCT-scanned specimens. The most supported hypothesis of modularity only contains two modules out of the possible seven, with the mandible and cranial elements as individual modules. Complete modularity (each bone as a separate module) was only the 12<sup>th</sup> most supported hypothesis of modularity. Our findings suggest that the kinetic skulls of snakes are not as modular as expected, with functional relationships between bones driving strong integration.

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### **Cenozoic Herpetology**

#### **QUATERNARY CAVE DEPOSITS OF JAMAICA: REGIONAL SQUAMATE EXTIRPATION AND FIRST RECORD OF ANURAN EXTINCTION IN THE GREATER ANTILLES**

Riegler, Mitchell S., Vinola, Lazaro W., Vallejo-Pareja, Maria C., Campins, Anthony R., Bloch, Jonathan I. Florida Museum of Natural History, University of Florida, Gainesville, Florida, U.S.A.

The Caribbean Islands are considered a biodiversity hotspot and the Greater Antilles likely played an important role in building that diversity. While the fossil record has improved with increased collecting efforts, taxonomic research biases often result in lack of focus on squamates and amphibians despite their abundant presence. To help address this, we studied the herpetofauna from an extensive collection of Quaternary fossils from three cave deposits from Jamaica: Ty Dixon, Wallingford Roadside, and Portland Ridge. Radiocarbon-dates from an adjacent cave yielded dates from 36,000 to 270 years B.P. (20 to 30 cm deep).

Fossils from the three caves range from 0-10 cm to >100 cm deep, and likely represent prey-catch by owls dwelling within the caves. Fossils were excavated and documented layer-by-layer. Four genera of squamates (*Celestus*, *Pholidoscelis*, *Anolis*, and *Leiocephalus*), identified largely from fossil dentitions, were recovered, and their abundance at each horizon was recorded. Fossils of *Celestus* were the most abundant relative to those of other squamates, with those of *Anolis* and *Pholidoscelis* consistently less abundant. Fossils of *Leiocephalus* were as abundant as those of *Celestus* in the deeper horizons (>50 cm) of Ty Dixon and Portland cave, became less abundant moving up section, and were absent closer to the surface. Fossils most similar in morphology to that of the gecko *Aristelliger titan* were also recovered, but with much lower relative abundance.

Anuran fossils were also recovered and classified here in two distinct genera: *Eleutherodactylus* and *Osteopilus*.

Fossil humeri with distinctive morphology shared with those of the hylid frog *Boana* were also recovered, representing the first record for this taxon (extant or fossil) from Jamaica. Presently, this genus is only located in Trinidad & Tobago and Hispaniola. Because it is not present in the extant ecosystem, this record provides the first evidence for the extinction of a frog in the Greater Antilles. While both the disappearance of *Boana* and the gradual regional loss of *Leiocephalus* is not yet understood, a majority of recent species loss in the Antilles has been explained by the arrival of humans and associated taxa (rats, domestic animals). Current estimates place human arrival to Jamaica at ~1,500 years B.P., which could coincide with these extinctions and extirpations. Planned radiocarbon-dating of these deposits should provide an important test of this possible explanation.

### **Evolution & Biology of Non-Avian Theropods**

#### **NEW DINOSAUR LOCALITIES FROM THE OLMOS FORMATION (CAMPANIAN-MAASTRICHTAN) IN NORTHERN COAHUILA**

Rivera-Sylva, Hector E.<sup>1</sup>, Guzmán-Gutierrez, Rubén<sup>1</sup>, Zapata-Jaime, Régulo<sup>2</sup>, García-de la Garza, Juan Pablo<sup>2</sup>, Guajardo-Guajardo, Raúl<sup>2</sup>, Porras-Múzquiz, Héctor<sup>3</sup>, Galicia-Chávez, Martín<sup>4</sup>

<sup>1</sup>Museo del Desierto, Saltillo, Coahuila, Mexico, <sup>2</sup>PASAC, Sabinas, Coahuila, Mexico, <sup>3</sup>Museo de Paleontología de Múzquiz, Múzquiz, Coahuila, Mexico, <sup>4</sup>Xpora Región Carbonífera, Palaú, Coahuila, Mexico

Recent fieldwork and research in the Upper Cretaceous Olmos Formation of northern Coahuila has greatly increased our knowledge and understanding of dinosaurs from the Campanian–Maastrichtian of southern Laramidia. This research has documented evidence of ceratopsian and nodosaurids from this unit.

The newly recovered dinosaur materials from the Olmos Formation are an important part of a rebirth that has occurred over the past decade. The chasmosaurine record reveals unusual patterns of endemism and faunal exchange in southern North America during the Campanian. Additional work, particularly the description and interpretation of new or poorly known taxa, will undoubtedly clarify both the details and broader aspects of the dinosaur radiation.

### **Macroecology & Macroevolution**

#### **PATTERNS IN RATES OF DISCRETE-CHARACTER AND BODY-SHAPE EVOLUTION: ARE 'LIVING FOSSILS' ALIKE?**

Rivero Vega, Rafael A., Friedman, Matt

Department of Earth and Environmental Sciences,  
University of Michigan Museum of Paleontology, Ann  
Arbor, Michigan, U.S.A.

Coelacanths, lungfishes, and holosteans represent three emblematic ‘living fossil’ clades, with two of them cited by Darwin when introducing the concept in ‘The Origin’. Since then, numerous qualitative and quantitative attempts to document their rates of morphological evolution have yielded contrasting results both among and within the groups. However, it is unclear whether this reflects genuine evolutionary differences or stems from contrasting analytical approaches. Here, these groups were examined in a common framework to investigate variation in rates of change of: (1) discrete characters derived from cladistic matrices and (2) shape based on geometric morphometric analysis of fossil specimens. For each clade, we inferred phylogenetic relationships and jointly estimated branch divergence times and evolutionary rates using published character matrices in a Bayesian framework under the fossilized-birth death model. Branch-specific evolutionary rates generated during this analysis were used to estimate rates of discrete character evolution over time for each clade. Additionally, we fit a series of explicit models of phenotypic evolution using a subset of taxa in each group for which shape data are available. Among these were so-called ‘epoch’ models that posit two separate modes of evolution before and after a specific point in a clades’ history. We designated these shift points a priori based on hypotheses in the literature. The results indicate these ‘living fossil’ groups do not show comparable patterns of morphological evolution over time. In the case of discrete traits, lungfishes show the highest rates in the Devonian and a monotonic decline in over time; coelacanths show peaks in the Devonian, Permian, and Triassic, with declining rates to recent; and holosteans show peaks in the Late Permian, Jurassic, and Early Cretaceous. Patterns of body shape evolution also show differences between groups, but there are some similarities between patterns of discrete character and shape evolution within groups. These results show that even among the type examples of ‘living fossils’ there is no consistent pattern of phenotypic evolution, mirroring the heterogeneous range of patterns reported for groups referred to as ‘adaptive radiations.’ Results of these and other analyses stress the significance of explicitly characterizing the patterns of morphological evolution within lineages rather than applying imprecise, and potentially misleading, historical classifications.

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**Anatomical & Developmental Explorations of the Mammalian Skull**

## THE PETROSAL MORPHOLOGY OF THE BASAL OROMERYCID *PROTYLOPUS*

Robson, Selina V.<sup>1</sup>, Ludtke, Joshua A.<sup>2</sup>, Theodor, Jessica<sup>1</sup>  
<sup>1</sup>Biological Sciences, University of Calgary, Calgary, Alberta, Canada, <sup>2</sup>Biological Sciences, MiraCosta College, Oceanside, California, U.S.A.

Oromerycids are a family of Eocene artiodactyls thought to be closely related to camelids. Oromerycid cranial material is rare and, to our knowledge, there are no published descriptions of oromerycid petrosals. Petrosal morphology may be important for resolving the evolutionary relationships of oromerycids, camelids, and other early artiodactyls. We used micro-computed tomography (micro-CT) scanning to image the cranium of the basal oromerycid *Protylopus* and reconstruct the petrosal morphology. The dorsal margin of the petrosal is very thin. The rostral margin is excavated, creating a large, crescent-shaped indentation, and there is a pronounced ridge on the ventrostral border. The mastoid region is large and wedge-shaped. The endocranial face of the petrosal contains a wide and deep subarcuate fossa with a smooth border. The subarcuate fossa and the internal auditory meatus are roughly equal in size. Unlike in ruminants, there is no ridge separating the cerebral and cerebellar faces. The basicapsular groove is fully on the petrosal and is located ventrally. The surface of the tympanic face is incomplete because of X-ray diffraction caused by metallic inclusions, but many features can still be observed. The wall of the petrosal rostral to the promontorium curves laterally. Both the fenestra vestibuli and fenestra cochleae can be located, although parts of the cochlea are also visible through the incomplete surface. The fenestra vestibuli is dorsal and rostral to the fenestra cochleae, and the fossa for the musculus tensor tympani is dorsal and rostral to the fenestra vestibuli, almost at the rostral border of the petrosal. The epitympanic recess is directly dorsal to the fenestra cochleae. On the dorsolateral face, the tegmen tympani is moderately inflated and the rostral face ends in a rounded projection. The cochlear aqueduct is located ventrally. Overall, the petrosal morphology of *Protylopus* is similar to that of camelids, suggesting a close evolutionary relationship between the two families.

**Funding Sources** NSERC Discovery Grant.

## Mesozoic Herpetology

## FURTHER EVIDENCE OF NICHE PARTITION BETWEEN BAURUSUCHID CROCODYLIFORMS AND ABELISAURID DINOSAURS IN THE UPPER CRETACEOUS BAURU GROUP (BRAZIL)

Melotti, Mateus<sup>1</sup>, Dantas, Mário<sup>2</sup>, Riff, Douglas<sup>3</sup>, Marinho, Thiago<sup>4</sup>, Pereira, Egberto<sup>5</sup>, Rodrigues, Taissa<sup>1</sup>

<sup>1</sup>Universidade Federal do Espírito Santo, Vitória, Brazil, <sup>2</sup>Universidade Federal da Bahia, Vitória da Conquista, Brazil, <sup>3</sup>Universidade Federal de Uberlândia, Uberlândia, Brazil, <sup>4</sup>Universidade Federal do Triângulo Mineiro, Uberaba, Brazil, <sup>5</sup>Universidade do Estado do Rio de Janeiro, Rio de Janeiro, Brazil

Baurusuchidae was a group of medium to large-sized notosuchians abundant in the fossil record of the Adamantina Formation (Upper Cretaceous, Bauru Group). They present several morphological adaptations typical of apex predators and convergent with some carnivore dinosaurs, mainly on the skull, teeth, ilium, femur, and ischium. No baurusuchids occur in the overlying Marília Formation, where theropods are more common, including abelisaurids and maniraptorans. This faunal turnover is not so noticeable in groups such as peirosaurids, titanosaurs, ostracods, and bivalves. Their morphological adaptations and the faunal composition of the Bauru paleoecosystem led previous authors to hypothesize that baurusuchids and theropods could be mutually exclusive, ecologically dominant predators.

Aiming to bring more data to the discussion, we analyzed the carbon ( $\delta^{13}\text{C}$ ) and oxygen ( $\delta^{18}\text{O}$ ) isotopic signatures of the dentin apatite carbonate of seven abelisaurid teeth from the Marília Formation and 13 baurusuchid teeth from the Adamantina Formation. Because theropod fossils are not common in the latter, they could not be obtained for a destructive analysis but the data can nevertheless be useful for comparisons.

A Shapiro-Wilk test showed that both  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  measurements were found outside the normal distribution. A Mann-Whitney test indicated that the  $\delta^{18}\text{O}$  values had no significant variation between the clades (Baurusuchidae:  $\mu\delta^{18}\text{O} = 27.98 \pm 0.57$ ; Abelisauridae:  $\mu\delta^{18}\text{O} = 28.44 \pm 0.65$ ;  $p = 0.113$ ). Previous studies using charophyte  $\delta^{18}\text{O}$  suggest similar temperature and salinity of water sources in the paleoenvironments of both formations, and our results are consistent with this interpretation. Other researchers proposed that baurusuchids lived (or died) close to abundant flood plains while abelisaurids did not, but our results suggest that they occupied similar environments.

The  $\delta^{13}\text{C}$  measurements presented significant statistical differences between the two taxa (Baurusuchidae:  $\mu\delta^{13}\text{C} = -5.92 \pm 0.69$ ; Abelisauridae:  $\mu\delta^{13}\text{C} = -8.02 \pm 0.4$ ;  $p = 0.0003626$ ) and suggest different ecological scenarios for them. Published biomechanical analyses demonstrated that baurusuchids had a weaker bite force than theropods thus pointing to different prey selection. Our results add yet another evidence that some degree of niche partition could have existed between baurusuchids and theropods. Future analyses should include samples from the same geological unit and taxa that could have been their prey.

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## Dinosaur Systematics, Diversity & Ecology

### A POSSIBLE LAMBEOSAURINE (HADROSAURIDAE: DINOSAURIA) HUMERUS FROM THE LATE MAASTRICHTIAN HELL CREEK FORMATION OF SOUTH DAKOTA

Rolleri, L., Gates, Terry A., Zanno, Lindsay E.  
North Carolina Museum of Natural Sciences, Raleigh, North Carolina, U.S.A.

Both hadrosaurine and lambeosaurine hadrosaurs were common components of Campanian faunas in North America. However, to date, only hadrosaurines (e.g., *Edmontosaurus annectens*) are definitely known to have survived into the late Maastrichtian on the continent. This is in contrast to the European and Asian record, where lambeosaurine species have been described from Maastrichtian formations (e.g., *Amurosaurus*, *Charonosaurus*, *Blasisaurus*), some of which are hypothesized to be closely related to North American species from the Campanian. Intriguing evidence of a lambeosaurine from the widely prospected Hell Creek Formation (late Maastrichtian) was presented nearly two decades ago, but these data have not yet been published. Here we describe a large, isolated humerus (NCSM 21814, North Carolina Museum of Natural Sciences) discovered in 1998 in Harding County, South Dakota, that may provide additional evidence on this topic.

NCMNS 21814 is robust, bearing a pronounced, triangular deltopectoral crest (DPC). The general proportions of this specimen do not compare well with *Edmontosaurus*, the only currently accepted hadrosaurid from the formation, and some aspects, particularly a robust well-developed DPC, resemble the morphology of lambeosaurines. In order to more accurately compare NCSM 21814 to other hadrosaurids, we utilized several sources of previously published humeral measurements. In the ratio of DPC length to humeral length, NCSM 21814 is most similar to saurolophine taxa such as *Edmontosaurus*. However, using morphometrics that include the breadth of the DPC as a variable, NCSM 21814 aligns with lambeosaurines. In addition, the shape of the DPC of NCSM is unusual, in being more triangular than quadrilateral. This morphology may represent an extreme for *Edmontosaurus*, or may be a feature of a new taxon. Regardless, the discovery of a morphologically atypical hadrosaurid humerus in the otherwise widely sampled Hell Creek Formation, demonstrates higher morphological disparity than

currently appreciated amongst hadrosaurids within one of the best studied Late Cretaceous ecosystems.

## Mesozoic Herpetology

### EVIDENCE FOR DETERMINATE GROWTH IN SYNAPSIDS, MARINE REPTILES, AND DINOSAURS: NON-DESTRUCTIVE DETERMINATION OF SKELETAL MATURITY

Rothschild, Bruce M.  
Vertebrate Paleontology, Carnegie Museum, Muncie, Indiana, U.S.A.

The character of ontology in extinct reptiles has been subject of controversy related to the nature of their growth: determinate or indeterminate? Contrasted with growth in mammals, longitudinal growth of bones in reptiles occurs by calcification of articular (as opposed to epiphyseal) cartilage and its subsequent transformation into bone. The blood supply for this process in both orders is derived from subjacent bone. Longitudinal growth ceases when that circulation is lost and the residual (articular) cartilage obtains its nutrition solely from the joint cavity and can no longer transform. Histologic studies document growth slowing, but not the point when it ceases (skeletal maturity). Articular surfaces of dinosaur, marine reptile, and synapsid taxa were subjected to epi-illumination microscopy to assess persistence of vascular channels. Findings were correlated with bone length measurements. Articular channels were universally observed, up to specific taxon-dependent sizes at which they were no longer observed. This included *Apatosaurus* whose femurs had reached 130 cm in length; *Camarasaurus*, 157; *Haplocanthosaurus* femur, 175; *Daspletosaurus*, 91; *Allosaurus*, 91; and *Dimetrodon*, 20; *Maisaurus* with 75 cm tibia and *Dolichorhynchops* with 40 cm humeri. Reduction in number of channels was noted in 117 cm *Triceratops* tibiae. At 72 cm length, closure was noted in some *Allosaurus* tibia, absent in others. Closure was not achieved by reaching 159 cm femoral length in *Diplodocus*; 83 cm, in *Centrosaurus*; 113 cm, in *Tyrannosaurus*; nor by tibial length of 63 cm in *Brachyceratops*. Articular surface microscopy documents determinate growth in extinct reptiles, at least in the studied taxa. Given the challenges of lag line interpretation (e.g., loss with growth), loss of articular channels may be the best measure of skeletal maturity. While size, itself, has been validly challenged as a measure of skeletal maturity, surface microscopy identifies the size range at which longitudinal growth ceases. As anticipated, evidence of skeletal maturity documented *Brachyceratops* as an adult. This technique may be valuable in distinguishing diminutive new species from juveniles of known species. Not anticipated was documentation that the largest *Tyrannosaurus* specimens

had not reached skeletal maturity and were still growing. The study also evidences that most extinct reptiles discovered to date appear to be skeletally immature and that their full growth potential was not realized.

## Taphonomy & Stratigraphy

### SEDIMENT-ENCASED THERMAL MATURATION EXPERIMENTS CHEMICALLY SIMULATE NATURAL FOSSILIZATION

Roy, Arindam<sup>1</sup>, Pittman, Michael<sup>1</sup>, Colleary, Caitlin<sup>2</sup>, Kaye, Thomas G.<sup>3</sup>, Saitta, Evan T.<sup>4</sup>

<sup>1</sup>Division of Earth and Planetary Sciences, The University of Hong Kong, Hong Kong, Hong Kong, <sup>2</sup>Department of Vertebrate Paleontology, Cleveland Museum of Natural History, Cleveland, Ohio, U.S.A., <sup>3</sup>Foundation for Scientific Advancement, Sierra Vista, Arizona, U.S.A., <sup>4</sup>Integrative Research Center, Section of Earth Sciences,, Field Museum of Natural History, Chicago, Illinois, U.S.A.

Reconstructions of in vivo color patterns and hues in fossils provide unique insights into what long extinct animals looked like. Preserved melanin pigments in fossilized integumentary structures have allowed specific ecological and behavioral hypotheses relating to countershading, crypsis, and predator-prey interactions to be formulated. Experimental maturation is especially important for paleocolor reconstruction because it can disentangle the complex physico-chemical variables influencing exceptional preservation of fossil pigments. Prior open and closed system experiments on the thermal maturation of melanin used aluminium fossil wrappings and sealed metal capsules respectively. Both methods have operational limitations and do not consider the role of sediment porosity in selectively filtering labile chemical fractions from recalcitrant ones during natural fossilization. Sediment-encased thermal maturation offers a way to resolve this issue and has previously demonstrated selective loss versus retention of organics at the ultrastructural level, in a manner comparable to carbonaceous compression fossils.

Here we simulate late diagenesis of phaeomelanin and eumelanin in modern bird feathers using an updated sediment-encased maturation setup and compare these to fresh and existing capsule-matured melanin extracts. Principal component analysis of TOF-SIMS data on modern, matured (sediment encased and capsule) and fossil feathers show chemical trends consistent with diagenesis from small to large nitrogen (N) and sulphur (S) bearing molecular fragments. As PC1 increases, ~190–250°C/250 bar/24 hr sediment-encased samples undergo loss of labile/volatile compounds and organic polymerization/cross-linking and start resembling fossils. Fossils separate from modern/experimental samples along

PC2, which correlates with organic compounds lacking N and S, due to loss of integumentary lipids due to early microbial decay and/or prolonged oxidative weathering. Thus, as in natural fossilization, sediment-encased maturation simulates the diagenetic decomposition/volatilization and loss of labile organic components like keratin protein, while inducing polymerization/cross-linking and retention of recalcitrant melanin in the matrix.

Future experiments with pre-maturation microbial decay and subsequent oxidative weathering as additional steps will bring us closer to more faithfully recreating natural diagenetic processes in artificial fossils.

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## Quantitative Methods

### IMPROVING PALEOCOLOR RECONSTRUCTION WITH MACHINE LEARNING

Roy, Satyaki<sup>1</sup>, Roy, Arindam<sup>2</sup>, Pittman, Michael<sup>2</sup>

<sup>1</sup>Department of Genetics, University of North Carolina, Carrboro, North Carolina, U.S.A., <sup>2</sup>Division of Earth and Planetary Science, The University of Hong Kong, Pokfulam, Hong Kong

Melanin-bearing microbodies called melanosomes have been detected in fossilized skin, feathers, and visceral organs. Their geometry, arrangement, and chemistry have served as the primary determinants of paleocolor in multiple studies. Based on the shape and specific color associations, the melanosomes from modern and fossil feathers have been grouped into five categories: (1) black (elongate), (2) brown (spheroidal), (3) iridescent (hyper-elongate), (4) grey (variable), and (5) penguin-specific (large spheroidal). Paleocolor prediction relies on statistical analyses to quantify modern melanosome diversity and extrapolate their shape-color relationships to fossil taxa. This has so far been achieved using methods such as quadratic discriminant analysis, principal components analysis, and multinomial logistic regression, which are precursors to machine learning.

Machine learning is a field of data science that works primarily on algorithms and models that take up specific tasks and gradually improve their accuracy over time. Machine learning has generated significant scientific interest and has been successful in a range of fields such as agriculture, medicine, cancer biology and genetics. We curated three comprehensive datasets on (1) feather melanosomes, (2) vertebrate integument melanosomes, and (3) vertebrate organ-specific melanosomes, from prior publications on melanosome geometry and paleocolor reconstruction. We analysed these datasets using three tiers of machine learning, namely, unsupervised, supervised, and deep learning. Unsupervised data clustering methods

show that aspect ratio (long axis / short axis) deemed highly significant by prior work, leads to information loss. Tests using supervised learning techniques (i.e., support vector machine, stochastic gradient descent, decision tree classifier, and gaussian naïve bayes) show that the decision tree classifier technique is the most accurate one (~73%) across all datasets in predicting melanosome geometry-color associations. Finally, our use of deep neural network models shows limited efficiency (~40–60%) due to small sampling sizes, a limitation that prior non-machine-learning studies also suffered from. Based on our results, we propose the creation of a big data repository based on large-scale data collection to address prevailing data scarcity and the use of machine learning to analyse it. We believe these changes will lead to substantial improvements in the accuracy of paleocolor prediction.

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## Mammalian Skeletal Morphology

### CAN TOOL USAGE IMPACT MORPHOLOGY? AN INTERSPECIFIC ANALYSIS OF OTTERS

Russell, Rachel<sup>1</sup>, Jacquemetton, Christiane<sup>1</sup>, Hupka, Brandon<sup>1</sup>, Drexler, Abigail<sup>1</sup>, Ralls, Katherine<sup>2</sup>, van Valkenburgh, Blaire<sup>1</sup>

<sup>1</sup>Ecology and Evolutionary Biology, University of California, Los Angeles, Los Angeles, California, U.S.A., <sup>2</sup>Smithsonian Institution, Washington, District of Columbia, U.S.A.

Sea and river otters are similar in their aquatic and semi-aquatic lifestyles as well as in their fusiform body plans. However, different species have been known to use their forelimbs for alternate purposes such as digging and walking, as in the North American river otter *Lontra canadensis* or using tools to access food, as in the California sea otter, *Enhydra lutris*. Given that tool use relies on the forelimbs, we predicted that forelimb shape will be significantly different between tool using and non-tool using groups (both within sea otters and between otter species). We also included several ancient sea otter specimens recovered from human middens on San Miguel Island to explore possible differences in limb morphology in pre-fur trade sea otters. We collected landmark data for the humerus, ulna and radius of 74 individuals from 16 species of otters to compare forelimb shape across the subfamily Lutrinae. For each, we placed 15–17 landmark points using ImageJ and analyzed those landmarks using the Geomorph and Stereomorph packages in R. Within the sea otters, those from the eastern Pacific (*E. l. nereis*) clustered at one extreme of PC 1 with the other two subspecies placed at the opposite end of PC1, indicating that tool use may have an impact on forelimb shape

between sea otter subspecies. When other non-tool using species of otter were included, the river otters exhibited significantly greater variability than the tool-using sea otters. Ultimately, locomotor differences such as tool use or digging may contribute to differences in forelimb morphology within Lutrinae.

## Mesozoic & Early Cenozoic Mammalian Evolution

### NEW SPECIMENS OF *EKGMOWECHASHALA* FROM THE GERING FORMATION (EARLY ARIKAREEAN) OF NEBRASKA

Rust, Kathleen, Beard, K. Christopher  
Biodiversity Institute, Ecology and Evolutionary Biology,  
University of Kansas, Lawrence, Kansas, U.S.A.

*Ekgmowechshala* is an enigmatic and highly autapomorphous primate known from the late Oligocene of western North America, making it the latest surviving North American primate prior to the arrival of anatomically modern humans at the end of the Pleistocene. Its unique dental anatomy has led to conflicting phylogenetic reconstructions for *Ekgmowechshala*, including possible omomyiform, dermopteran, or adapiform affinities. The fossil record of *Ekgmowechshala* is generally poor, being restricted to a maxilla fragment, several partial dentaries, and isolated teeth from the upper Sharps Formation, South Dakota and the upper part of the Turtle Cove Member of the John Day Formation, Oregon (both early Arikareean in age). Additionally, several isolated teeth of *Ekgmowechshala* are known from Durnal Ranch Quarry (DRQ) in the early Arikareean Gering Formation of western Nebraska, but these specimens have never been formally described in the literature. Here, we focus on the sample of *Ekgmowechshala* from DRQ, which includes the first well-preserved upper molar known for this taxon. The Gering Formation specimens are characterized by low crowns with bulbous cusps and crenulated enamel, conforming to the classic *Ekgmowechshala* morphology exhibited in previously described specimens. p4 is molariform with a distinct ectostylid. m1 lacks a paraconid and exhibits shape proportions similar to the holotype for *E. philotau*. The DRQ upper molar is remarkably preserved and demonstrates interesting differences from the upper molars in the John Day Formation partial maxilla that was recently reassigned to the new species *E. zancanellai*. Specifically, the paracone and metacone in the DRQ upper molar are more broadly spaced, yielding a longer centrocrista and a more expansive trigon than occurs in the John Day maxillary fragment. M1 in the latter specimen bears a large, inflated parastyle that is lacking in the DRQ specimen. *Ekgmowechshala* specimens from DRQ are consistent with distinct species being represented by known samples from Oregon and the Great Plains and also

support phylogenetic analyses placing *Ekgmowechshala* within an Asian adapiform clade.

**Funding Sources** This research was supported by grants from the Association of Earth Science Clubs of Greater Kansas City and the David B. Jones Foundation.

## Mesozoic Herpetology

### THE OLDEST GAVIALOID CROCODYLIFORM ('THORACOSAUR') FROM THE CAMPANIAN QUSEIR FORMATION OF BARIS OASIS, WESTERN DESERT, EGYPT

Saber, Sara<sup>5</sup>, Sertich, Jopseph<sup>3</sup>, Abu El-Kheir, Gebely<sup>4</sup>, Ouda, Khaled<sup>5</sup>, El-Sayed, Sanaa<sup>1</sup>, O'Connor, Patrick M.<sup>6</sup>, Seiffert, Erik<sup>7</sup>, Sallam, Hesham<sup>2</sup>

<sup>1</sup>Department of Geology, Mansoura University, Mansoura, Egypt, <sup>2</sup>School of Sciences and Engineering, American University in Cairo, New Cairo, Egypt, <sup>3</sup>Department of Earth Sciences, Denver Museum of Nature & Science, Denver, Colorado, U.S.A., <sup>4</sup>Geology Department, New Valley University, Kharga, Egypt, <sup>5</sup>Department of Geology, Assiut University, Assiut, Egypt, <sup>6</sup>Department of Biomedical Sciences, Ohio University, Athens, Ohio, U.S.A., <sup>7</sup>Department of Integrative Anatomical Sciences, University of Southern California, Los Angeles, California, U.S.A.

Upper Cretaceous (Campanian) deposits of the Quseir Formation exposed in the New Valley, Western Desert of Egypt have yielded abundant remains of bony and cartilaginous fishes, turtles, and non-marine archosaurs, of which crocodyliforms are among the best represented. Here we report a new crocodyliform from the El Hindaw Member of the Quseir Fm. from the Baris Oasis, southern Kharga Oasis. The specimen consists of a nearly complete skull that is missing only portions of the mid-rostrum and both premaxillae. The new form shares a broad interfenestral bar with *Eothoracosaurus* but differs from other 'thoracosaur' gavialoids in the following: (1) posterior process of squamosal short and medially deflected; (2) weakly sculpted postorbital on otherwise deeply sculpted cranial table; (3) supraoccipital with a pronounced medial ridge separating two deep fossae; (4) narrow posterior fenestral bar on the cranial table; and (5) dorsally arched cranial table in posterior view. The El Hindaw Member of the Quseir Fm. near Baris was deposited in a largely marginal marine, lagoonal setting and contains both non-marine (e.g., sauropod dinosaurs) and nearshore semiaquatic (e.g., pleurodire turtles, lungfish, the large neosuchian *Wahasuchus*) taxa. This new discovery extends the temporal range of Gavialoidea into the upper Campanian, though like other 'thoracosaur,' represents a relatively derived form indicating much deeper origins for gavialoid crocodyliforms. Together with

other late Mesozoic forms, this new taxon suggests a Tethyan or North African origin of the clade.

**Funding Sources** Mansoura University research grant, National Geographic Society (NGS) Waitt Foundation (W88-10).

### Preparators

### RESTORING OUTREACH, DISPLAY, AND RESEARCH VALUE TO A SPECIMEN OF *TRICERATOPS* FROM THE UPPERMOST CRETACEOUS HELL CREEK FORMATION OF NORTH DAKOTA THROUGH INSTRUCTION IN PREPARATION AND CONSERVATION

Sailar, Ciara, Heckert, Andrew B.  
Department of Geological and Environmental Sciences,  
Appalachian State University, Boone, North Carolina,  
U.S.A.

In 1975 an Appalachian State University (ASU) crew recovered an incomplete *Triceratops* skeleton from badlands near Marmath, North Dakota. After initial retrieval and preparation, several *Triceratops* bones have been on display, but most remained undisturbed in storage. Recently, ASU paleontology classes have used these fossils to teach paleontological preparation, conservation, and research methods, while enhancing the specimen's scientific value by inventorying and preparing it for accession into a recognized repository. The *Triceratops* includes at least one incomplete postorbital horn core, much of the left and right squamosals, dozens of frill and other skull fragments, an incomplete right lower jaw, one complete and several fragmentary vertebrae, several complete ribs, hundreds of rib fragments, an incomplete scapula, many femur fragments, and several small unopened jackets. A small tyrannosaurid(?) tooth and incomplete turtle carapace were also collected from the site. Preparation work included cleaning and removal of sediment and non-archival adhesives using pin vises and acetone as well as reconstructing fractured bones, initially with PaleoBond® products, but increasingly with more archival paraloid (B-72) and/or polyvinyl acetate (Butvar B-76). Conservation work also included removing old jackets, building support cradles, and archiving related collections data, while replication was carried out by molding and casting with platinum silicone rubber molds and urethane resins. We are now using photogrammetry to generate 3-D models of various bones (right lower jaw, both squamosals, the postorbital horn core and dorsal vertebra) with Agisoft PhotoScan.

A histologic study was also performed on a rib fragment to evaluate the microstructure preservation in this specimen. The rib was embedded in resin and mounted to slides using a curing epoxy. The microstructure, including numerous

secondary osteons, was very well preserved, suggesting that the femur or other rarer elements could provide more histologic data.

As a result of this project, students learned a variety of paleontological preparation, conservation, and research methods while removing the specimen from storage and placing it on exhibit in support cradles on archival materials. Replication methods allow for a greater use of this specimen for outreach events, continuing its use as a teaching specimen while preparing for its accession to a recognized repository.

### Dinosaur Systematics, Diversity & Ecology

### NON-AVIAN DINOSAUR EGG SHELL CALCITE CONTAINS ANCIENT, ENDOGENOUS AMINO ACIDS

Saitta, Evan T.<sup>1</sup>, Vinther, Jakob<sup>2</sup>, Crisp, Molly<sup>3</sup>, Abbott, Geoffrey<sup>4</sup>, Kaye, Thomas G.<sup>9</sup>, Pittman, Michael<sup>10</sup>, Bull, Ian<sup>2</sup>, Fletcher, Ian<sup>5</sup>, Chen, Xinqi<sup>6</sup>, Collins, Matthew<sup>7</sup>, Sakalauskaite, Jorune<sup>8</sup>, Mackie, Meaghan<sup>7</sup>, Dal Bello, Federica<sup>8</sup>, Dickinson, Marc<sup>3</sup>, Stevenson, Mark<sup>4</sup>, Donohoe, Paul<sup>4</sup>, Heck, Philipp<sup>1</sup>, Demarchi, Beatrice<sup>8</sup>, Penkman, Kirsty<sup>3</sup>

<sup>1</sup>Field Museum of Natural History, Chicago, Illinois, U.S.A., <sup>2</sup>University of Bristol, Bristol, U.K., <sup>3</sup>University of York, York, U.K., <sup>4</sup>Newcastle University, Newcastle, U.K., <sup>5</sup>University of Surrey, Guildford, U.K., <sup>6</sup>Northwestern University, Evanston, Illinois, U.S.A., <sup>7</sup>University of Copenhagen, Copenhagen, Denmark, <sup>8</sup>University of Turin, Turin, Italy, <sup>9</sup>Foundation for Scientific Advancement, Sierra Vista, Arizona, U.S.A., <sup>10</sup>The University of Hong Kong, Pokfulam, Hong Kong

Rates of peptide bond hydrolysis and other diagenetic reactions are not favourable for Mesozoic protein survival. Proteins hydrolyse into peptide fragments and free amino acids that, in open systems such as bone, can leach from the specimen and be further degraded. However, closed systems are more likely to retain degradation products derived from endogenous proteins.

Amino acid racemisation data in experimental and subfossil material suggests that mollusc shell and avian eggshell calcite crystals can demonstrate closed system behavior, retaining endogenous amino acids. Here, high-performance liquid chromatography reveals that the intracrystalline fraction of Late Cretaceous (estimated ~80 Ma) titanosaur sauropod eggshell is enriched in some of the most stable amino acids (Glx, Gly, Ala, and possibly Val) and those that racemise are fully racemic, despite being some of the slowest racemising amino acids. These results

are consistent with degradation trends deduced from modern, thermally matured, sub-fossil, and ~3.8 Ma avian eggshell, as well as ~30 Ma calcitic mollusc opercula. Selective preservation of certain fully racemic amino acids, which do not racemise in-chain, along with similar concentrations of free versus total hydrolysable amino acids, likely suggests complete hydrolysis of original peptides.

Liquid chromatography-tandem mass spectrometry supports this hypothesis by failing to detect any non-contamination peptide sequences from the Mesozoic eggshell. Pyrolysis-gas chromatography-mass spectrometry reveals pyrolysates consistent with amino acids as well as aliphatic hydrocarbon homologues that are not present in modern eggshell, suggestive of kerogen formation deriving from eggshell lipids. Raman spectroscopy yields bands consistent with various organic molecules, possibly including N-bearing molecules or geopolymers.

These closed-system amino acids are possibly the most thoroughly supported non-avian dinosaur endogenous protein-derived constituents, at least those that have not undergone oxidative condensation with other classes of biomolecules. Biocrystal matrices can help preserve mobile organic molecules by trapping them (perhaps with the assistance of resistant organic polymers), but trapped organics are nevertheless prone to diagenetic degradation even if such reactions might be slowed in exceptional circumstances.

**Funding Sources** University of Bristol Bob Savage Memorial Fund.

### **Anatomical & Developmental Explorations of the Mammalian Skull**

### **INFLUENCE OF BIOMECHANICS ON THE MANDIBLE SHAPE AMONGST CARNIVOROUS THERIAN MAMMALS**

Salcido, Charles J., Polly, P. David  
Earth and Atmospheric Sciences, Indiana University,  
Bloomington, Indiana, U.S.A.

Members of the clade Mammalia have radiated many times into carnivorous ecological niches including hypercarnivores and bone-crackers. It has been previously postulated that the shape of the mandibles of these carnivores is reflective of their ecology, diet, and functionality. This study uses geometric morphometrics on a wide variety of mandibles from carnivorous therian mammals, both extant and extinct, including clades Metatheria, Mesonychia, 'Creodonta,' and Carnivora, to see the relationship between mandibular shape, relative bite force, and the morphology needed for structural support during biting to see how this reflects ecology and diet across disparate clades. Strength in biting around the

canine and the carnassial (or its geometric equivalent) and stress on the jaw from biting around the canine and carnassial are measured by relative bite force via mechanical advantage, and stress and strain via finite element analysis, respectively.

Our analysis of geometric morphometric shape shows that most shape variance is attributed to the offset between the horizontal ramus and the posterior end of the mandible, followed by the curvature of the mandibular notch and the condyle-angular notch of the posterior side of the mandible. Some variables of bite performance (bite force and stress) are well-linked to certain forms of mandibular shape. Most notably, increased mechanical advantage of the jaw adductor muscles and the carnassial links to the dorsal movement of the carnassial to the ascending ramus and the steepening angle of the ascending ramus. These specific shape changes affect the overall shape of the mandible. Shape regression for stress variables shows greater change in shape around the canine across principal components with the best fit shape variable being the curvature of the ventral side of the mandible. These results show that each of these biomechanical factors is linked to a unique aspect of mandibular shape variation. The shape of the posterior end of the mandible and its position relative to the horizontal ramus is more influenced by bite force while the shape of the anterior end is more influenced by stress. This effect on the shape of the mandible can infer the possible feeding ecology of disparate therian taxa.

### **Dinosaur Systematics, Diversity & Ecology**

### **A NEW TITANOSAURIAN SAUROPOD DINOSAUR PARTIAL SKELETON FROM THE LATE CRETACEOUS (CAMPANIAN) OF THE KHARGA OASIS, WESTERN DESERT OF EGYPT**

Salem, Belal S.<sup>1</sup>, Abu El-Kheir, Gebely<sup>2</sup>, Lamanna, Matthew C.<sup>3</sup>, Gorscak, Eric<sup>4</sup>, El-Sayed, Sanaa<sup>5</sup>, Sallam, Hesham<sup>6</sup>

<sup>1</sup>Department of Geology, Benha University, Benha, Egypt, <sup>2</sup>Department of Geology, Faculty of Science, Al Wadi Al Gadid University, Kharga, Egypt, <sup>3</sup>Section of Vertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A., <sup>4</sup>Anatomy Department, Midwestern University, Downers Grove, Illinois, U.S.A., <sup>5</sup>Department of Geology, Mansoura University, Mansoura, Egypt, <sup>6</sup>School of Sciences and Engineering, American University in Cairo, New Cairo, Egypt

Sauropod dinosaurs from the post-Cenomanian Cretaceous (PCC; ~94–66 Ma) of continental Africa (excluding Madagascar) and the then-conjoined Arabian Peninsula are almost exclusively represented by isolated, poorly-informative fossils. One of the handful of exceptions in this regard is the lithostrotian titanosaur *Mansourasaurus shahinae*, recently identified from an associated partial

cranial and postcranial skeleton excavated from the Upper Cretaceous (Campanian) Quseir Formation of the Dakhla Oasis, Western Desert of Egypt. Here we describe a new and well preserved associated titanosaurian partial skeleton recovered from penecontemporaneous beds of the Quseir Formation in the Kharga Oasis, Egypt. The skeleton pertains to an osteologically mature individual that is comparable in estimated body size to the *Mansourasaurus* type specimen. The new skeleton includes one strongly opisthocoelous posterior cervical vertebra, five incomplete and moderately opisthocoelous anterior to posterior dorsal vertebrae, a procoelous anterior caudal vertebra, and the articulated right tibia and astragalus. The bones exhibit features found in other titanosaurs, such as camellate internal tissue and coalesced posterior centrodiapophyseal and centropostzygapophyseal laminae in all preserved dorsal vertebrae. The posterior dorsals possess a distinctive lamina complex that is 'M-shaped' in lateral view and that results from the extensive ventral bifurcation of the centroparapophyseal and centrodiapophyseal laminae into wide anterior and posterior centroparapophyseal and centrodiapophyseal laminae, respectively. These vertebrae also have deep, dorsoventrally elongate parapophyseal centrodiapophyseal and postzygapophyseal centrodiapophyseal fossae. The centrodiapophyseal fossa is divided by a weakly developed lamina, as in dorsal vertebrae of *Mansourasaurus*. The posterior dorsal vertebrae lack the postzygodiapophyseal lamina, a trait seen in some European and Asian titanosaurians. The tibia appears more robust than those of another undescribed titanosaurian partial skeleton from the Quseir Formation of the Kharga Oasis collected by a German expedition in 1977. The new specimen augments the meager record of PCC titanosaurian sauropods from the Afro-Arabian mainland and offers additional anatomical information regarding the axial skeleton of these herbivorous dinosaurs. Ongoing study of the specimen promises to clarify its phylogenetic affinities and paleobiogeographic significance.

**Funding Sources** Al Wadi Al Gadid University and Mansoura University research grant.

## **Late Cenozoic Mammalian Macroecology & Macroevolution**

### **MAMMAL COMMUNITY STRUCTURE EVOLUTION IN RESPONSE TO CLIMATE AND HABITAT CHANGES THROUGH THE CENOZOIC OF OREGON**

Samuels, Joshua X.

Geosciences, East Tennessee State University, Johnson City, Tennessee, U.S.A.

Central and eastern Oregon is well-known for having an incredibly detailed and dated sequence of rocks and fossils

that document floral and faunal evolution through most of the Cenozoic. The John Day and Crooked River Basins record approximately 50 million years of time, and have over 30 dated tuffs and lava flows. Regional climate and habitat changes over that interval have been reconstructed based on paleosol data and paleobotanical records. Those records indicate cooling, increased aridity, and greater seasonality starting in the early Oligocene, which was accompanied by the opening of habitats. Multiple lines of evidence indicate the region became warmer and more humid at the time of the Middle Miocene Climatic Optimum.

While varying in completeness, the faunas of the John Day and Crooked River Basins represent every North American Land Mammal age from the Uintan to the Hemphillian, with the exception of the Clarendonian. To examine the evolution of the mammalian community in this region over time, taxa from each fauna were coded into a series of categories, including crown height and locomotion. This analysis was restricted to examination of Carnivora, Creodonta, Perissodactyla, Artiodactyla, Proboscidea, Rodentia, Lagomorpha, and Primates, which form the vast majority of species across all faunas. Abundances of categorical attributes were compared across faunas, and changes in community structure over time were compared to changes in climate and habitats.

Overall, mammal communities show distinct changes at the time of climate and habitat changes in the region. In the Whitneyan, smaller herbivores (rodents and lagomorphs) shifted to be dominated by taxa with higher-crowned teeth, and the earliest cursorial rabbits and burrowing rodents appeared at the same time. Through the Arikarean, the first high-crowned and cursorial ungulates appeared, as did the first running-adapted carnivorans and likely saltatory rodent. Over that interval open habitat specialists (cursorial and burrowing taxa) became more common, while forest dependent groups declined. At the time of the Middle Miocene Climatic Optimum, forest-adapted taxa (low-crowned browsing herbivores and arboreal mammals) were still fairly common, but by the later Barstovian many of those taxa vanished, yielding later Miocene communities with both large and small mammals dominated by high-crowned taxa and open habitat specialists.

## **Taphonomy & Stratigraphy**

### **TAPHONOMY OF VERTEBRATE MICROSITES IN THE UPPER CRETACEOUS (LATE CAMPANIAN–EARLY MAASTRICHTIAN) WILLIAMS FORK FORMATION OF NORTHWESTERN COLORADO**

Sanchez, Israel<sup>1</sup>, Heckert, Andrew B.<sup>1</sup>, Brand, Nickolas A.<sup>2</sup>, Foster, John R.<sup>4</sup>, Hunt-Foster, ReBecca K.<sup>3</sup>, Eberle, Jaelyn J.<sup>5</sup>

<sup>1</sup>Geological and Environmental Sciences, Appalachian State University, Roseboro, North Carolina, U.S.A., <sup>2</sup>East

Tennessee State University, Johnson City, Tennessee, U.S.A., <sup>3</sup>Dinosaur National Monument, Jensen, Utah, U.S.A., <sup>4</sup>Utah Field House of Natural History State Park Museum, Vernal, Utah, U.S.A., <sup>5</sup>University of Colorado Museum of Natural History, Boulder, Colorado, U.S.A.

The Williams Fork Formation (WFF) is a paleontologically understudied Upper Cretaceous unit of Kirtlandian to Edmontonian (latest Campanian–Maastrichtian) age that crops out extensively in northwestern Colorado and eastern Utah. The tetrapod assemblage of the WFF is poorly known and, other than a few fragmentary dinosaurs, crocodylians, and turtles, is largely preserved as microvertebrates. Collections dating to the 1980s appear to fall into two broad categories – mudstone-dominated (MD) or sandstone-dominated (SSD) microvertebrate sites, with some sampling of each carried out both in situ and on anthills, with a minor component recovered incidentally during the collection and preparation of larger vertebrates. Relocating all of these sites is challenging, and reconstructing their collection history to the extent that meaningful taphonomic comparisons are possible is even more so. Fortunately, newly discovered sites, the J&M site (SSD) and ReBecca’s Hollow (MD), afford the opportunity to assess WFF microvertebrate taphonomy. The J&M site consists of channel deposits of conglomerate and sandstone that were first exploited for larger tetrapod fossils but which had additional smaller scales, bones, and teeth visible as clasts. Breakdown of this sediment required the use of heated dimethyl sulfoxide (DMSO), but yielded numerous taxa not previously described from the WFF, including multiple rays and non-batoid sharks, the osteichthyan *Paralbula*, and other taxa from a relatively small (<100 kg) sample of matrix. In spite of the more aquatic nature of the J&M assemblage, it did also preserve some dinosaurian and mammalian microvertebrates, indicating that it is sampling diverse environments. Thus, although it required DMSO disaggregation not used in the WFF, it may serve as an analog for SSD sites composed of scour-fill, trough crossbedded sandstone and conglomerate. ReBecca’s Hollow, discovered last year, facilitates comparisons of richness and diversity to the J&M site. Like many MD sites, abundant lepisosteid (gar) scales litter the surface and are the first indication of the presence of the locality. Surface collections from ReBecca’s Hollow yielded not only lepisosteid scales, other osteichthyans, and fragmentary turtle (*Adocus?* and trionychid) shell, but also a crocodylian osteoderm and teeth of osteichthyans, crocodylians, hadrosaurs, and ceratopsians, and ongoing screening of a similar sample will afford direct comparisons with the J&M site.

### **Holocene & Pleistocene Mammalian Macroecology & Faunal Studies**

### **NEW PLEISTOCENE LOCALITY FROM CHIHUAHUA, MEXICO**

Sanchez-Urbe, Iván Erick<sup>2</sup>, Guzmán-Gutierrez, Rubén<sup>1</sup>, Rivera-Sylva, Hector E.<sup>1</sup>, Lopez-Diaz de Leon, Vanessa G.<sup>2</sup>, Lopez-Palma, Cesar A.<sup>2</sup>

<sup>1</sup>Paleontología, Museo del Desierto, Saltillo, Coahuila, Mexico, <sup>2</sup>Museo del Desierto Chihuahuense, Delicias, Chihuahua, Mexico

Fieldwork carried out during 2013–2015 by a team from the Museo del Desierto Chihuahuense in the late Pleistocene continental deposits of the central portion of Chihuahua, northern Mexico, resulted in the collection of vertebrate fossils, which were located in fluvial sediments outcropping in an area 20 km north from the town of Julimes, in the San Jose del Carrizo locality. The material consists of cranial and postcranial material of mammals identified preliminarily as *Equus* sp., *Mammuthus* sp., and *Bison* sp., as well as an indetermined rodent. The presence of *Bison* sp. indicates a Rancholabrean North American Land Mammal age for the faunal assemblage. This is the first record of the genus *Bison* as a fossil for the state of Chihuahua during the late Pleistocene.

### **Marine Reptile Diversity & Biology**

### **TERRESTRIAL VS. MARINE ORIGIN OF VIVIPARITY IN MARINE REPTILES: EVIDENCE FROM A NEW *CYMBOSPONDYLUS* SKELETON**

Sander, P. Martin<sup>1</sup>, Schmitz, Lars<sup>2</sup>, Wintrich, Tanja<sup>1</sup>, Klein, Nicole<sup>1</sup>

<sup>1</sup>University of Bonn, Bonn, Germany, <sup>2</sup>Keck Science Department, Claremont Colleges, Claremont, California, U.S.A.

Cymbospondylid ichthyosaurs are an early-branching clade of primarily large-bodied and pelagic ichthyosaurs best known from Middle Triassic open-water sediments of Nevada, U.S.A. The holotype skeleton (LACM DI 158109) of a new species of *Cymbospondylus*, *C. duelferi* from the late Anisian of the Augusta Mountains, Nevada, is a pregnant female. Body length is estimated at 4.3 m, making it the smallest of the *Cymbospondylus* species. The specimen represents the geologically second-oldest record of viviparity in ichthyosaurs. Here, we explore the implications of this find for competing hypotheses about the origins (terrestrial vs. marine) of viviparity in marine reptiles from the Permian to the Cenozoic.

Viviparity offers great selective advantages to marine reptiles because it obviates the need of oviposition on land and the associated difficulties and dangers as well as the need to retain minimal terrestrial capabilities. Among marine reptiles, only sea turtles are unequivocally not

viviparous because recent work suggests viviparity even in thalattosuchian crocodiles. Viviparity is thus widely spread across the sauropsid tree and always associated with a marine lifestyle. The oldest example of viviparity in ichthyosaurs is *Chaohusaurus* from the Early Triassic of China. The early-branching position of this taxon and its apparent head-first birth position has been used to argue that viviparity in the clade, and in marine reptiles in general, had already evolved in their terrestrial ancestors. In this view, viviparity is a preadaptation to a marine lifestyle. This ‘terrestrial origin’ hypothesis requires numerous independent origins of viviparity in distantly related clades without offering a unifying selective advantage. The ‘marine origin’ hypothesis, on the other hand, explains the correlated multiple origins of viviparity and marine adaptation by a uniform selective advantage.

Ventral to the dorsal column of the *C. duelferi* holotype there are three straight strings of small articulated vertebrae that have anterior opposite to the dorsal vertebrae. The small vertebra are on average 32% of the size of the large ones. Due to the small size of these strings and their position within the trunk region, they most likely represent fetuses. The specimen thus indicates that head-first birth was possible even in large pelagic ichthyosaurs that certainly gave birth under water. This questions the argument that this position indicates a terrestrial origin of viviparity.

## **Late Cenozoic Mammalian Macroecology & Macroevolution**

### **TAXONOMY AND PALEOECOLOGY OF A REMARKABLY DIVERSE NEW PROBOSCIDEAN ASSEMBLAGE FROM THE TERMINAL EARLY MIOCENE SITE OF BULUK, KENYA**

Sanders, William J.<sup>1</sup>, Miller, Ellen R.<sup>2</sup>, Nengo, Isaiah<sup>3</sup>, Semprebon, Gina<sup>4</sup>, Arney, Irisa<sup>5</sup>

<sup>1</sup>Museum of Paleontology, University of Michigan, Ann Arbor, Michigan, U.S.A., <sup>2</sup>Anthropology, Wake Forest University, Winston-Salem, North Carolina, U.S.A., <sup>3</sup>Turkana Basin Institute, Stony Brook University, Stony Brook, New York, U.S.A., <sup>4</sup>Biology, Bay Path University, Longmeadow, Massachusetts, U.S.A., <sup>5</sup>Anthropology, University of Michigan, Ann Arbor, Michigan, U.S.A.

The fossil site of Buluk, Kenya, east of Lake Turkana provides a valuable record of African faunal evolution at the end of the early Miocene. Recent collecting substantially increased the vertebrate sample from the site, which now comprises an abundant fauna with approximately 30 mammalian species, including several catarrhine primate taxa. Among the fauna is a proboscidean cohort of deinotheres and at least five elephantimorph species (mammutids, gomphotheriines, amebelodontines,

and choerolophodontines). The diversity of the proboscidean cohort is extraordinary compared with the narrower presence of elephants in modern African ecosystems. This cohort is critical for documenting the breadth of paleohabitats at the site and morphological diversification of competing sympatric lineages of mastodons, gomphotheres, and deinotheres. Morphometric criteria of dental dimensions, loph(id) number and configuration, expression of accessory conules, and cross-sectional attributes of tusks were employed to identify the taxa in the Buluk proboscidean assemblage. The deinotheres belong in *Prodeinotherium hobleyi* and constitute one of the most extensive dental samples known of the species, a common denizen of early-to-middle Miocene African sites. A few isolated mammutid teeth are recognized as belonging to a diminutive new species of *Zygalophodon*. Choerolophodont teeth are fragmentary and cannot be assigned to species. Gomphotheriine isolated teeth belong in *Gomphotherium* but are too rare to be allocated to species. Skulls, postcrania, and a rich sample of isolated teeth represent a species of the early shovel-tusked amebelodontine *Archaeobelodon* that is now recognized as a different species than the more primitive amebelodont from the older site of Kajong, Kenya. Unexpectedly, new finds document the oldest record of *Protanancus macinnesi*, a putative descendant of *Archaeobelodon*, at the site. With the identification of the Buluk fossils, the chronostratigraphy, taxonomy, and phylogeny of amebelodontines is now the best resolved of the early-to-middle Miocene gomphotherine lineages. Preliminary isotopic and microwear analyses indicate that all Buluk proboscideans were browsing, but suggests that they foraged in different habitats contrasted by the extent of tree cover.

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## **Quantitative Methods**

### **ULTRACONSERVED ELEMENTS OVERWHELM MORPHOLOGICAL SIGNAL IN COMBINED-EVIDENCE ANALYSES**

Scarpetta, Simon  
Department of Geological Sciences, University of Texas at Austin, Austin, Texas, U.S.A.

Genomic datasets are increasingly popular in phylogenetics, but morphological data are still necessary to systematically place fossils, calibrate phylogenetic trees, and corroborate molecular hypotheses. Additionally, we have yet to exhaust the capacity of the phenotype and the fossil record to inform topological hypotheses in both morphology-only and combined-evidence analyses.

Although previous authors suggested that large molecular alignments would override morphological signal in combined-evidence analyses, no efforts have been made to explore the feasibility of simultaneous analysis of genomic datasets generated by next-generation sequencing and morphological data. Here, I provide the first such analyses, using iguanian lizards as an empirical example. I performed combined-evidence analyses of ultraconserved elements (UCEs) and two morphological datasets using both maximum likelihood and Bayesian methods. One of the morphological datasets was previously used to infer squamate phylogeny, and the other dataset was previously used to estimate iguanian phylogeny; both included several extinct taxa known only from fossils. In all combined-evidence analyses, the molecular topologies were imposed upon the morphological data, and some support values were reduced relative to UCE-only analyses. In maximum likelihood analyses, the phylogenetic positions of fossils did not change, but in Bayesian analyses the positions of a few fossils changed substantially. Perhaps most importantly, the morphological data did not help clarify relationships that were poorly supported in UCE-only trees. These results substantiate concerns that morphological data will not be able to affect tree topology in combined-evidence analyses with genomic data, and reiterate the need to investigate the future of morphological data in a phylogenomic context.

## **Anatomical & Developmental Explorations of the Mammalian Skull**

### **THE MORPHOLOGY OF THE AUDITORY BULLA ENABLES LOCOMOTORY INFERENCES IN EXTINCT RODENTIA**

Scarpitti, Erica A.<sup>1</sup>, Calede, Jonathan<sup>2</sup>

<sup>1</sup>Earth Sciences, The Ohio State University, Columbus, Ohio, U.S.A., <sup>2</sup>Evolution, Ecology, & Organismal Biology, The Ohio State University, Columbus, Ohio, U.S.A.

Rodentia is a taxonomically and ecologically diverse order of mammals. Rodents live in almost all environments from tropical forests to deserts. Such ubiquitousness is enabled by many evolutionary adaptations, including some in the sensory systems. Hearing is essential to survival; it enables predator evasion, prey detection, and conspecific recognition. It is also constrained by the physical environment. As such, we hypothesize the hearing system of rodents to be ecology-specific. Although the auditory apparatus of select species has been studied, the link between tympanic bulla morphology and ecology has never been investigated across a broad swath of species. Yet, this avenue of research offers the potential to explore the ecological affinities of many fossil species only known from skulls. We here present a comparative study of bullar

morphology in rodents. We used geometric morphometrics to quantify the shape of the auditory bulla of 203 specimens of modern rodents representing 94 species from 17 families and four different locomotory modes (arboreal, semi-fossorial, fossorial, and terrestrial). We placed landmarks and semi-landmarks on photos of the ventral and lateral views of each specimen to capture characteristics of bullar inflation and external auditory meatus (EAM) extension. The results of our principal component analyses and canonical variate analyses demonstrate an association between bullar morphology and locomotion in rodents. Fossorial rodents are characterized by kidney-shaped bullae associated with an extended EAM; arboreal rodents (including gliders) have inflated bullae and a very short EAM. The classification phase of the analysis correctly classified 76.8% of species. We also explored the role of evolutionary history in shaping the auditory bulla of rodents using a pFDA of our extant training set. The results showed a weak phylogenetic signal concentrated in muroids. We applied our landmarking to select fossil rodents within the clade Castorimorpha whose locomotion is known from other proxies. Our results are consistent with published data and further strengthen this method as a valid approach to reconstruct the locomotion of extinct rodent species that lack skeletons. We make the first locomotory inferences for the Florentiamyidae *Florentiamys kingi*, *F. kennethi*, *Sanctimus faulkenbachi*, and *S. stouti*; they were all semi-fossorial. This work will enable more complete analyses of the evolution of burrowing in geomorph rodents.

**Funding Sources** The Ohio State University Second-Year Transformational Experience Program.

## **Late Cenozoic Mammalian Macroecology & Macroevolution**

### **ECOMETRIC ESTIMATION OF PRESENT AND PAST CLIMATE OF NORTH AMERICA USING CROWN HEIGHTS OF RODENTS AND LAGOMORPHS**

Schap, Julia<sup>1</sup>, Samuels, Joshua X.<sup>2</sup>

<sup>1</sup>Biological Sciences, Georgia Institute of Technology, Atlanta, Georgia, U.S.A., <sup>2</sup>Geosciences, East Tennessee State University, Johnson City, Tennessee, U.S.A.

Studies of ungulate crown heights in relation to climate and habitat changes have revealed an association between increasing tooth crown height (hypsodonty) and a shift to more arid environments over the Cenozoic. Ecometric studies have also been used to examine the relationship between current climate conditions and crown height of ungulate communities, and very successfully used to estimate past precipitation. Small herbivorous mammals (rodents and lagomorphs) have been shown to similarly

adapt to changing habitats over the Cenozoic, but did so millions of years earlier than larger mammals. Here, we have utilized ecometric methods to examine the relationships between rodent and lagomorph crown height and diversity with current climate conditions, finding strong correlations of community structure parameters with climate, particularly mean annual temperature, maximum temperature of the warmest month, and minimum temperature of the coldest month. We applied the resultant regression equations to well-sampled fossil localities from North America, spanning over 37 million years, allowing estimation of climate conditions in deep time. As expected, estimates show a general pattern of decrease in both precipitation and temperature across North America from 37 Ma to the present. Overall, these findings provide a new broadly-applicable proxy for estimation of Cenozoic climate conditions.

**Funding Sources** East Tennessee State University, Don Sundquist Center of Excellence in Paleontology.

### Permo-Triassic Tetrapods

#### STANDARD OSTEOLOGICAL AND VIRTUAL 3D ANATOMICAL RE-INVESTIGATION OF *MACROCNEMUS* (TANYSTROPHEIDAE, ARCHOSAUFROMORPHA), A RARE MIDDLE TRIASSIC TERRESTRIAL REPTILE WITH A TETHYS-WIDE DISTRIBUTION

Scheyer, Torsten M.<sup>1</sup>, Miedema, Feiko<sup>2</sup>, Wang, Wei<sup>4</sup>, Li, Chun<sup>4</sup>, Spiekman, Stephan<sup>1</sup>, Fernandez, Vincent<sup>3</sup>, Reumer, Jelle J.<sup>5</sup>

<sup>1</sup>Palaeontological Institute and Museum, University of Zurich, Zurich, Switzerland, <sup>2</sup>Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany, <sup>3</sup>Natural History Museum London, London, U.K., <sup>4</sup>Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China, <sup>5</sup>Natuurhistorisch Museum Rotterdam, Rotterdam, Netherlands

Over the past decades, an increasing number of mostly marine reptiles have been described from the Triassic of southern China. Many of these taxa had a Tethys-wide distribution, whereas terrestrial reptile taxa known from both western and eastern margins of the Tethys are exceptionally rare. One such terrestrial animal is the small to medium sized tanystropheid archosauromorph *Macrocnemus* from the Middle Triassic. The genus is represented by two European species, the well-known *M. bassanii* and *M. obristi*, known only from posterior postcranial remains, and the slightly younger *M. fuyuanensis*, known from two complete specimens from southwestern China. Species recognition in the genus classically relied on proportional differences of the limb bones. *M. fuyuanensis* was recently tentatively proposed to

be present also in Europe, based on a single specimen from the Besano Formation of Monte San Giorgio, southern Switzerland/northern Italy. Further analysis, however, was hampered due to limited original description of the holotype specimen of *M. fuyuanensis* and insufficient understanding of the cranial anatomy of *M. bassanii*, despite being known from several complete and well-preserved specimens in European collections. To clarify the relationships among *Macrocnemus* species, we re-described both the holotype of *M. fuyuanensis* and a well-preserved skull of *M. bassanii*, the latter using high-resolution synchrotron micro-computed tomography, which allowed us to reconstruct and describe the configuration of the skull, including the braincase for the first time, in high detail. Our findings reveal that the osteology of both species is very similar and no clear differences were found in the cranium. The skull of *Macrocnemus* has a rigid, tightly fitting squamosal-quadrato joint allowing little, if any, cranial kinesis. The configuration of the palatal bones with the tooth-bearing pterygoids, palatines and vomers could be reconstructed for the first time. In the postcranium, besides the limb ratios, we confirmed the identification of the interclavicle as the most important bone for species recognition. The interclavicle of *M. fuyuanensis* can be distinguished from *M. bassanii*, among other features, by its short and fusiform posterior process and anterior facing rod-like processes that extend from a common base enclosing a narrow 'V'-shaped median notch. The presence of *M. fuyuanensis* at Monte San Giorgio confirms its widespread distribution over the entire Tethys realm.

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### Fishes & Chondrichthyans: Evolution & Distribution

#### SKELETAL AND SOFT TISSUE COMPLETENESS OF THE ACANTHODIAN FOSSIL RECORD THROUGH TIME

Schnetz, Lisa<sup>1</sup>, Butler, Richard J.<sup>1</sup>, Coates, Michael I.<sup>2</sup>, Sansom, Ivan J.<sup>1</sup>

<sup>1</sup>Earth Sciences, University of Birmingham, Birmingham, U.K., <sup>2</sup>Organismal Biology and Anatomy, University of Chicago, Chicago, Illinois, U.S.A.

Acanthodians are a poorly understood paraphyletic group of extinct fishes from the Paleozoic. While they show comparatively little diversity in lifestyle and range of body shape, they play a prominent part in our understanding of vertebrate evolution as part of the chondrichthyan stem-group. Their evolutionary history, however, is poorly understood, largely due to the limited preservation of their

mostly cartilaginous skeleton that results in a bias towards isolated remains such as fin spines and scales. Thus, considerable uncertainties remain in how the completeness of acanthodian fossils impact on the phylogenetic narrative of both chondrichthyans and other vertebrates. Here, we address these issues by using a variation of the previously defined Skeletal Completeness Metric (SCM), an approach that calculates how complete the skeletons of individuals are compared to their theoretical complete skeleton, to quantify the quality of the acanthodian fossil record. A novel Soft Tissue Completeness Metric (STCM) is introduced to estimate the percentage of soft body tissue preserved as an alternate measurement of completeness. A database of >1600 specimens comprising >300 taxa from museum collection visits and literature has been compiled. Acanthodian completeness peaks in the Lochkovian, Givetian, Bashkirian-Moscovian, and again in the Asselian, with lowest scores in the Llandovery. Changes in SCM and STCM of acanthodians show a significant correlation through time with higher completeness in the later stages of the Paleozoic. There is no correlation between acanthodian taxonomic richness and completeness but there is a weak trend towards lower richness through time. Acanthodians show a significantly lower completeness distribution than many tetrapods, including theropods, plesiosaurs, sauropodomorphs, ichthyosaurs, pelycosaur and parareptiles, but a similarly low distribution to bats. Analysis of completeness distribution between acanthodian orders reveals significant differences, with the Acanthodiformes and Diplacanthiformes showing highest overall completeness. Our assessment of completeness reveals only weak spatial biases influencing the acanthodian fossil record while temporal biases are much higher. Variation in completeness will have an impact on the utility of characters in assessing the phylogenetic positioning and limits of the various acanthodian groups.

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## Mesozoic & Early Cenozoic Mammalian Evolution

### THE ROLE OF CLIMATE CHANGE ON THE DENTAL EVOLUTION OF LATE PALEOCENE AND EARLY EOCENE *PHENACOLEMUR*

Schottenstein, Naava<sup>1</sup>, Hunter, John<sup>3</sup>, Hubbe, Mark<sup>2</sup>

<sup>1</sup>Evolution, Ecology, and Organismal Biology, The Ohio State University, Columbus, Ohio, U.S.A., <sup>2</sup>Department of Anthropology, The Ohio State University, Columbus, Ohio, U.S.A., <sup>3</sup>Evolution, Ecology, and Organismal Biology, The Ohio State University, Newark, Ohio, U.S.A.

The Paromomyidae is a family of plesiadapiform primates that appeared near the Cretaceous–Paleogene boundary

and persisted until the middle Eocene in North America. The paromomyids were stem primates that evolved during the first major primate radiation. A nearly continuous record exists in the Bighorn Basin, Wyoming for the late Paleocene and early Eocene paromomyids in the *Phenacolemur archus*–*Phenacolemur citatus* lineage, consisting of six named species and intermediates, spanning multiple dietary shifts. Paleoclimatic conditions previously reconstructed through leaf margin analyses show temperatures reached as high as 20°C at the Paleocene–Eocene Thermal Maximum (PETM), which occurred about 55.8 Ma. Temperatures decreased after that, falling to 11°C by 54.38 Ma, and increased dramatically again reaching 22°C during the Early Eocene Climatic Optimum (53 Ma). Changes in the lengths and widths of the p4, m1, m2, and m3 teeth, and the protoconid height and crown height of the p4 in the *P. archus*–*P. citatus* lineage appear to track changes in MAT positively through time, not negatively as predicted by Bergmann's rule. Although others have observed a decrease in size in several mammalian lineages across the PETM, no prior studies have attempted to assess how closely these paradoxical changes in *Phenacolemur* tooth metrics track changing paleotemperatures. We test the following hypotheses: (1) the *P. archus*–*P. citatus* lineage responded with increasing tooth sizes during intervals of climate warming, and (2) the *P. archus*–*P. citatus* lineage responded with decreasing tooth sizes during the interval of climate cooling. We compare the magnitude and timing of dental changes to the paleotemperature curve and found significant positive correlations with temperature over the entire lineage for all tooth measurements and during both warming periods for most tooth measurements. During the cooling period following the PETM, we observed a complex series of positive and negative correlations. However, the negative correlations all indicate a lowering and widening of the p4 and m1 during a dietary shift from omnivory to frugivory. These findings suggest that paleotemperature played an important but complex role, along with diet and other factors, in the dental evolution of *Phenacolemur*, beyond the predictions of Bergmann's rule.

## Evolution & Biology of Non-Avian Theropods

### MIND THE GAP: THE IMPACT OF JUVENILE MEGATHEROPODS ON DINOSAUR BODY SIZE DISTRIBUTIONS AND GLOBAL DIVERSITY

Schroeder, Katlin M.<sup>2</sup>, Lyons, S.K.<sup>1</sup>, Smith, Felisa A.<sup>2</sup>  
<sup>1</sup>Biology, University of Nebraska-Lincoln, Lincoln, NE, U.S.A., <sup>2</sup>Biology, University of New Mexico, Edgewood, New Mexico, U.S.A.

Non-avian dinosaurs were the dominant terrestrial vertebrates for over 150 million years, yet were never particularly speciose. Low diversity in small dinosaurs is particularly unusual when compared to modern and fossil

vertebrates, which due to increased resource partitioning and turnover between habitats reach their highest diversity in small species. Dinosaur ovipary and gigantism resulted in rapid growth through multiple morphological stages, from disproportionately small infants to extremely large adults. Interspecific competition from juveniles of large dinosaurs may have excluded smaller dinosaurs from communities. Mass death assemblages confirm the relatively large standing crop of juveniles in the fossil record, yet their impact on taxonomic diversity and body size distributions has yet to be determined. Did community-level interactions effect global dinosaur diversity, and did juveniles have a significant impact on their community structure? Here we examine the impact of ontogenetic niche shift on community structure and overall dinosaur diversity. We compiled 39 non-avian dinosaur communities containing over 240 unique species, spanning five continents and 136 million years, using the Paleobiology Database with mass estimates from the primary literature. To assess the impact of community-level interactions we compared the shape of local-scale mass distributions against the published global. In local assemblages showing divergence from the global pattern, we quantified species-mass likelihood in relation to the presence of larger species and added juveniles as morphospecies within their communities. We find carnivorous theropods diverge significantly from the global trend, indicating local ecology played a significant role in their mass distributions. Carnivorous theropods follow a bimodal trend, with communities containing a pervasive gap in species between 100–1,000 kg. The prevalence of this gap is significantly correlated with the presence of carnivorous species greater than 1,000 kg. Juveniles of these large megatheropods represent a significant proportion of dinosaur biomass, consistently falling within the carnivore body size gap in communities. These juveniles filled mesocarnivore niches, deflating taxonomic diversity in communities. The persistence of these trends through time and space suggest dinosaurs' use of multiple niches through ontogeny is an important biological factor in community structure and low overall dinosaur diversity.

### **Symposium: Dietary Reconstruction**

#### **DIET AND RESOURCE PARTITIONING IN MOSASAURS - THE NECESSITY OF A MULTI-PROXY APPROACH**

Schulp, Anne S.<sup>1</sup>, Giltaij, Tom J.<sup>3</sup>, Holwerda, Femke M.<sup>2</sup>  
<sup>1</sup>Naturalis Biodiversity Center, Leiden, Netherlands,  
<sup>2</sup>Royal Tyrrell Museum, Drumheller, Alberta, Canada,  
<sup>3</sup>Geosciences, Utrecht University, Utrecht, Netherlands

A wide diversity of analytical techniques can inform us about the diet of extinct animals. Ideally, multiple, independent lines of evidence converge to bolster the argument. In reconstructing diet, niche partitioning and the ecology of mosasaurs, their tooth morphology, biting and swimming biomechanics, eye morphology, neurosensory adaptations, dental microwear, geochemical signatures and stomach contents can all provide independent clues as to the feeding biology of these extinct marine squamates.

Analyses performed over the last decade, exploring the  $\delta^{13}\text{C}$  stable isotope signature of various mosasaur faunas, interestingly showed larger mosasaurs to generally exhibit more depleted  $\delta^{13}\text{C}$  values than smaller ones. In extant marine ecosystems, the trophic effect alone can be seen to drive  $\delta^{13}\text{C}$  values up to about 1‰ less depleted values with every step up the food chain, so this does not account for such a difference between macropredators in the same ecosystem. This underscores that diet is not the only determining factor in  $\delta^{13}\text{C}$  signature, and is likely to be overprinted by other factors, including diving behavior (Bohr effect) and a nearshore-offshore gradient.

We recently expanded our analyses with a new dataset covering the Maastrichtian mosasaur fauna from Denmark (c. 44°N paleolatitude) and generally arrive at a similar pattern to that observed earlier in the roughly coeval but different latitude faunas of the Netherlands, Angola and the U.S.A., with larger mosasaurs exhibiting more depleted values. The mosasaur fauna of Denmark, as recognized so far, is very similar to that of the type Maastrichtian of the Netherlands and Belgium, and includes *Mosasaurus*, *Plioplatecarpus*, *Carinodens*, and - newly-recognized in Denmark - *Prognathodon*.

We contextualize the  $\delta^{13}\text{C}$  stable isotope record in mosasaur teeth against a series of dental microwear analyses. Indeed, type Maastrichtian mosasaur dental microwear analysis shows the larger taxa to be more generalist, whereas the smaller mosasaurs yield a more specialist dental microwear signal, which may well provide an additional explanation for the  $\delta^{13}\text{C}$  values differing between larger apex predators and smaller mosasaurs, beyond trophic level and diving depth.

This elucidation of influencing factors in the context of this system clearly demonstrates the importance of applying multiple proxies in reconstructing the complexities of mosasaur feeding paleobiology.

### **Symposium: Paleoneurology**

#### **VESTIBULAR MORPHOLOGY REVEALS ECOMORPHOLOGICAL TRENDS AND ONTOGENETIC CHANGES IN CROCODYLOMORPHS**

Schwab, Julia A.<sup>1</sup>, Young, Mark T.<sup>1</sup>, Neenan, James M.<sup>2</sup>, Walsh, Stig<sup>3</sup>, Herrera, Yanina<sup>4</sup>, Witmer, Lawrence<sup>5</sup>,

Brochu, Christopher A.<sup>6</sup>, Choiniere, Jonah N.<sup>7</sup>, Turner, Alan H.<sup>8</sup>, Brusatte, Stephen<sup>1</sup>

<sup>1</sup>University of Edinburgh, Edinburgh, U.K., <sup>2</sup>Oxford University Museum of Natural History, Oxford, U.K.,

<sup>3</sup>National Museum of Scotland, Edinburgh, U.K.,

<sup>4</sup>CONICET. División Paleontología Vertebrados, Museo de La Plata, La Plata, Argentina, <sup>5</sup>Ohio University, Athens, Ohio, U.S.A., <sup>6</sup>University of Iowa, Iowa City, Iowa, U.S.A., <sup>7</sup>University of the Witwatersrand, Johannesburg, South Africa, <sup>8</sup>Stony Brook University, Stony Brook, New York, U.S.A.

One prime example of a major evolutionary transition is thalattosuchian crocodylomorphs, which evolved from terrestrial ancestors and moved into the open ocean. Their transition began in the Early Jurassic in semiaquatic environments, before they became the only group of archosaurs that fully adapted to a pelagic lifestyle, with paddle shaped limbs, a hypocercal tail and a streamlined body. Sensory systems, such as the inner ear, are key to understanding such transitions, and can reveal how ecology changed over long time scales. The bony labyrinth, the cavity housing the membranous system of the inner ear, has previously been linked to ecomorphological adaptations, such as locomotor behavior and habitat preferences, and can also be used to study developmental changes. Due to its involvement in orientation this system needs to change and adapt when animals transition into new environments. Using CT scans and geometric morphometrics we examined the bony labyrinths of a broad sample of taxa, including 14 extant and 18 fossil crocodylomorphs (adults and subadults) of different habitats, and an additional six hatchlings and seven juveniles of extant species to study ontogenetic differences in the labyrinth morphology. Our results show that there are both ecomorphological and ontogenetic differences. Pelagic metriorhynchids developed a dorsoventrally short labyrinth with thicker semicircular canals compared to their terrestrial ancestors, with the most extreme pelagic morphology present in the derived metriorhynchids *Cricosaurus* and *Torvoneustes*. Similar adaptations have previously been noted in other secondarily aquatic vertebrates such as pliosaurus, turtles and cetaceans. In thalattosuchians this pelagic labyrinth evolved after major osteological changes that permitted swimming (e.g., flippers, loss of osteoderms, tail fluke). Modern hatchling and juvenile crocodylians, compared to adults have a more compact labyrinth with smaller semicircular canals and a particularly reduced lateral canal. This is somewhat similar to the pelagic metriorhynchid labyrinth morphology, indicating possible heterochrony. Changes in developmental timing therefore, may have helped thalattosuchians adapt their sensory systems to the water.

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## Holocene & Pleistocene Mammalian Macroecology & Faunal Studies

### DEMOGRAPHY OF LATE PLEISTOCENE *EQUUS OCCIDENTALIS* FROM RANCHO LA BREA, CALIFORNIA, BASED UPON DENTAL AND PELVIC DATA

Scott, Eric, Gust, Sherri M.

Paleontology, Cogstone Resource Management, Inc., Orange, California, U.S.A.

The large horse species *Equus occidentalis* is the second most common large mammal herbivore at the Rancho La Brea (RLB) asphalt deposits in Los Angeles, California, represented by thousands of skeletal elements representing hundreds of individuals. The present study employs teeth and pelvic bones of *E. occidentalis* at RLB to determine the minimum number of individuals, the distribution of ontogenetic age classes, and (where possible) the distribution of males and females within the sample.

Based upon teeth, more than 250 individuals of *Equus occidentalis* are present in the sample. Almost 50% of this sample consists of individuals younger than approximately 1.2 years in age; this age distribution is consistent across most individual localities ('pits') with the exception of Pit 77, where dentally adult animals are unusually abundant. Of 42 crania, 29 (69%) had large canines and are considered male. In mandibular or dentary portions, 22 of 34 adult specimens (65%) exhibited large canines. Combining upper and lower adult dental samples yields a proportion of 29 adult males (71%, upper teeth) to 12 adult females (29%, lower teeth). In subadults (2.5–4 years, N = 14), 8 specimens (57%) had large unerupted or erupting canines and are presumed male. This proportion is not significantly different from a 1:1 sex ratio.

Pelvic data derive from individual pits with published radiometric dates. This sample size is smaller (N = 120), but the ontogenetic distribution is similar; juveniles comprise 45% of the sample, subadults 39%, and adults 16%. Sex ratios based upon pelvises show a ratio of adult (> 5 years) males to females of 1:1.3 (N = 19). The combined adult/subadult pelvic sample yielded a male-female ratio of 1.8:1 (N = 66). Observed differences in male-female ratios between teeth and pelvises are likely due to: (1) differences in the samples examined (entire sample for dentitions, only radiometrically-dated pits for pelvises); (2) different age classifications in each sample (a dental adult is not the same as a pelvic adult); and (3) differences in the number of age classes examined for sex (i.e., pelvic data enabled interpretation of younger age classes than was possible in the dental sample).

Results suggest that bands of *Equus occidentalis* inhabited the region during the late Pleistocene. Family units consisted of a male (whether territorial or not) and females

with young. Male bachelor groups were also likely present in the area.

### Taphonomy & Stratigraphy

#### A TAPHONOMIC ANALYSIS OF A MONODOMINANT *WENDICERATOPS PINHORNENSIS* BONEBED FROM THE OLDMAN FORMATION (CAMPANIAN) OF ALBERTA REPRESENTING THE OLDEST EVIDENCE OF HERDING BEHAVIOR IN CERATOPSIDS

Scott, Sebastian H.<sup>1</sup>, Ryan, Michael J.<sup>2</sup>, Evans, David<sup>3</sup>  
<sup>1</sup>Ecology and Evolutionary Biology, University of Toronto, Kingston, Ontario, Canada, <sup>2</sup>Earth Sciences, Carleton University, Ottawa, Ontario, Canada, <sup>3</sup>Royal Ontario Museum, Toronto, Ontario, Canada

Despite the abundance and diversity of ceratopsid dinosaurs in the latest Cretaceous of North America, research has primarily focused on cranial anatomy with few detailed studies of the postcranial skeleton. This has led to a gap in the understanding of the evolution of the ceratopsid postcranial skeleton. The early centrosaurine ceratopsid, *Wendiceratops pinhornensis*, was discovered in Alberta, Canada, in a medium density, monodominant bonebed from the lowermost strata of the Oldman Formation (mid-Campanian, ~79 Ma). The bonebed contains abundant, well-preserved postcranial material, allowing for a taphonomic analysis of the site and the first detailed description of the postcranium in an early ceratopsid. The material confirms that the shape of the curved and elongated distal terminus of the ischium is an apomorphic character of *Wendiceratops pinhornensis*.

The bonebed lithosome is hosted within an approximately 40 cm thick, organic-fragment-rich clayey, sandy mudstone that has abundant horizontal and vertical coalified root traces, suggesting a water-logged anoxic deposit. This interpretation is supported by a large number of bones exhibiting wet rot and green fractures.

Over 200 bones assignable to *Wendiceratops* have been collected from the bonebed to date, and all parts of the skull and skeleton are present except for manual and pedal elements. The assemblage contains multiple individuals (MNI = 4) from multiple age classes. Extrapolation from the approximately 12 m<sup>2</sup> of the bonebed excavated to the exposed lateral extent of the bonebed suggests the total deposit contains over 50 individuals. The bonebed contains over 95% ceratopsid remains, and all identifiable elements are referred to *Wendiceratops*. The elements are completely disarticulated, but have undergone little abrasion or weathering (both Stage 0), exhibit extensive breakage, but lack signs of scavenging; all these factors are indicative of a mass death assemblage with moderate hydrological reworking. The *Wendiceratops* bonebed is ~2

million years older than other well documented ceratopsid bonebeds that have been rigorously taphonomically analyzed and interpreted as preserving evidence of gregarious behavior. These all suggest a catastrophic mass death of a large social group. The taphonomic evidence presented here is consistent with other inferred ceratopsid mass death assemblages, suggesting that the *Wendiceratops* bonebed is the oldest evidence of herding behavior in a ceratopsid.

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### Mesozoic & Early Cenozoic Mammalian Evolution

#### PATTERNS OF INTRASPECIFIC VARIATION IN THE DIET OF *MICROSYOPS LATIDENS* (MAMMALIA, PRIMATES) OVER TIME: INSIGHT INTO ECOLOGICAL AND CLIMATIC CHANGE USING DENTAL TOPOGRAPHIC ANALYSIS

Selig, Keegan R., Silcox, Mary T.  
Anthropology, University of Toronto Scarborough, Toronto, Ontario, Canada

Intraspecific variation in the dentition has long been studied in the context of taxonomy. However, ecological signals like diet have largely been overlooked when considering how teeth vary within a species. Such studies also typically use linear measurements or non-metric traits to quantify levels of variation, meaning complex, three-dimensional (3D) form is unaccounted for. Dental topographic analysis (DTA) provides means for quantifying the curvature, complexity, and relief of 3D occlusal morphology. These metrics are known to vary interspecifically with diet in extant euarchontans, but less is known about the relationship between intraspecific variation and diet. We used DTA to quantify lower molar form in a sample of early Eocene plesiadapiforms (*Microsyops latidens*) from the southern Bighorn Basin of Wyoming to study intraspecific variation over time and its relationship to diet and climate. *Microsyops latidens* is an ideal taxon for examining change over time as it was relatively short-lived (~500,000) yet known from a large, stratigraphically controlled sample spanning a period of climatic change. We compared variation in occlusal morphology in *M. latidens* (n >20) with 20 extant euarchontan taxa (n = 94) by calculating coefficients of variation (CVs) with and without a correction factor that accounts for sample sizes.

Our results show that although *M. latidens* spans ~500,000 years, this taxon exhibits little variation compared to the modern sample. Uncorrected CVs range from 3.7–20.9 (curvature), 3.0–18.9 (complexity), and 2.3–12.2 (relief) among extant taxa, whereas *M. latidens* has CVs of 8.3 (curvature), 8.6 (complexity), and 6.1 (relief). Extant taxa such as *Tupaia palawanensis* (n = 6) and *Eulemur fulvus* (n

= 7) consistently show higher CVs (corrected and uncorrected) for all three metrics. Although *M. latidens* does not vary greatly over time, it shows increased topographic values (consistent with increased insectivory) during a previously identified period of decreased local temperature. Our results, therefore, suggest that local climate had an impact on the diet of *M. latidens*. The degree of change is within the range of variation of modern taxa, suggesting that the inferred temporal variation we see in the diet of *M. latidens* falls within the scope of variation we see in extant species. These results show there may be a signal for dietary change relating to rapid pulses of climate change even within the context of intraspecific variation.

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### Romer Prize

#### JAW MUSCLES, JAW JOINTS, AND THE STEPWISE ACQUISITION OF HIGH BITE FORCE PERFORMANCE OF MODERN CROCODYLIA

Sellers, Kaleb

University of Missouri, Columbia, Missouri, U.S.A.

Crocodyliforms have been key components of vertebrate faunas for 200 million years, but their evolutionary success is a biomechanical paradox: How do flat-headed animals bite with such high force? Many crocodyliform traits involved in generating and resisting high forces are not found in their ancestors, such as a quadrate and palate that are sutured to the braincase, a pterygomandibular joint (PMJ), and expanded jaw muscles. With this suite of features, crocodyliforms radiated into forms with diverse diets and derived craniodental adaptations. However, the effects of these shifts on feeding performance have not been evaluated, obscuring coevolutionary patterns of morphology and function. Here, I reconstruct musculoskeletal anatomy and evaluate biomechanical performance in key fossil suchians. I hypothesize that joint changes will precede muscular changes in suchian evolution, and that joint loading magnitude and orientation in crocodylians will correlate with joint surface anatomy and size. Along with observations from many extant and fossil suchians, I used CT data to create high fidelity 3D models of twelve taxa, with emphasis on the origin of Crocodyliformes. I used osteological correlates to reconstruct jaw muscles and used the computational package Boneload to distribute forces across bony surfaces for finite element analysis. I adapted geographic information systems (GIS) techniques and developed novel morphometrics to characterize joint surface anatomy. These results show a feeding apparatus that defies

traditional understanding. The combination of dual craniomandibular joints and jaw joints loaded in tension is unknown in other tetrapods. I found that joint force orientation tracks with articular surface metrics. Coordinated changes in cranial joints took place near the base of Crocodyliformes: kinetic joints were immobilized first, followed the acquisition of the PMJ and a flat jaw joint articular surface. In Mesoeucrocodylia, jaw muscles became more mediolateral as the skull flattened, pterygoideus ventralis inserted on the lateral mandible, and depressor mandibulae expanded its ventral attachment. Despite variable joint loading conditions, joints maintain remarkably consistent joint pressures. These results suggest the coordinated evolution of anatomical and functional systems in one of the great transitions in vertebrate evolution, the crocodylian skull.

**Funding Sources** NSF EAR 163753.

### Dinosaur Systematics, Diversity & Ecology

#### NEW REMAINS OF *PARARHABDODON ISONENSIS* (DINOSAURIA: LAMBEOSAURINAE): IMPLICATIONS FOR THE LIFE HISTORY AND PALEOECOLOGY OF IBERO-ARMORICAN HADROSAURIDS

Serrano, Jesus F., Selles, Albert G., Vila, Bernat, Galobart Lorente, Angel, Prieto-Marquez, Albert  
Dinosaur Ecosystems, Institut Catala de Paleontologia, Sabadell, Catalunya, Spain

*Pararhabdodon isonensis* was the first species of lambeosaurine hadrosaurid described in Europe and represents one of the last non-avian dinosaurs that lived before the K-Pg extinction. Yet, its relationship with other European lambeosaurines has reminded controversial due to the lack of overlapping diagnostic material among taxa. Newfound hindlimb elements from the type locality of *P. isonensis* reveal an autapomorphic swelling in the proximal region of the femur. This character reinforces the distinction of *P. isonensis* from other European lambeosaurines and its postulated close relationship with *Tsintaosaurus spinorhinus*. *P. isonensis* becomes restricted to the upper Maastrichtian Tarn Formation in the south-central Pyrenees of NE Spain.

Our osteohistological analysis indicates that *Pararhabdodon isonensis* probably reached adult body sizes comparable to those of other lambeosaurines from the Iberian Peninsula and nearing the body sizes of large North American and Asian species. Its osteohistological structure indicates a relatively low growth rate, suggesting the achievement of larger body sizes over longer time periods, perhaps facilitated by a relatively low predation pressure. Unlike other coeval dinosaurian clades of the Late Cretaceous of Europe, *P. isonensis* and at least some of the

other lambeosaurines from the Iberian region such as *Adynomosaurus arcanus*, reached similarly large body sizes that represent exceptions to the 'island rule'.

**Funding Sources** Governments of Spain (grants RyC-2015-17388 and CGL2016-73230-P from MINECO) and Catalonia (grant CLT/903/2018/67 and CERCA program).

### **Fishes & Chondrichthyans: Evolution & Distribution**

#### **COMPOSITION OF MARINE FISH COMMUNITIES DURING THE EARLY PERMIAN PERIOD IN CENTRAL NORTH AMERICA**

Shell, Ryan, Ciampaglio, Charles  
Earth and Environmental Sciences, Wright State University, Dayton, Ohio, U.S.A.

Marine vertebrates from the early Permian-aged Cisuralian Epoch are rare in the global fossil record. Species-rich faunas from individual localities are especially poorly understood, and single occurrence localities fail to properly illustrate faunal trends in marine vertebrate ecology during this interval. Here we report marine vertebrate faunas from seven fossil localities across central North America, each containing 4–15 unequivocal vertebrate taxa. This survey includes representatives from each of the Cisuralian Epoch's faunal stages, and is the result of previously published reports as well as new field investigations. An analysis of the number and identity of these fossils at the ordinal level indicates marine vertebrate communities during this interval of time were likely dominated by hybodontiform and ctenacanthiform sharks. Other groups such as the Petalodontiformes, Symmoriiformes, Eugeneodontiformes, and Osteichthyes were major components to these many of these assemblages as well, and orodontiforms, neoselachians, bransonelliforms, and cochliodontiforms, also occurred in smaller numbers at various points during the Cisuralian Epoch.

**Funding Sources** Wright State University, Benjamin Richards Memorial Grant.

### **Taphonomy & Stratigraphy**

#### **TAPHONOMIC BIAS IN HORSE PHALANGES FROM THE BARSTOW FORMATION (MIOCENE) AND LA BREA TAR PITS (PLEISTOCENE) OF CALIFORNIA, U.S.A.**

Shi, Yaoran<sup>2</sup>, Gu, Victoria W.<sup>2</sup>, Farke, Andrew A.<sup>1</sup>  
<sup>1</sup>Raymond M. Alf Museum of Paleontology at The Webb Schools, Claremont, California, U.S.A., <sup>2</sup>The Webb Schools, Claremont, California, U.S.A.

Horses are the most common vertebrate taxa in the Barstow Formation (Miocene) of southern California, representing

at least six different species of varying size and ecology. As such, their fossils are also important for understanding the taphonomy of the formation. Based on anecdotal observations from collections made over 80 years of field work by the Alf Museum, proximal (P1) and middle (P2) phalanges are far more common than ungual (P3) phalanges for digit III. Here, we examined these patterns quantitatively and compared the sample from Barstow (housed at the Raymond M. Alf Museum of Paleontology, Claremont, California) with that of Pleistocene equids from the La Brea Tar Pits (Los Angeles, California). Phalanges were identified to position within the manus/pes, and frequencies were compared using a chi-square test. The sample from the Barstow Formation had 229 proximal, 152 middle, and 37 distal phalanges. The chi-square test was significant ( $p < 0.001$ ), consistent with preservation bias between phalanx types. Two samples from La Brea were analyzed. The sample from Pit 3 (164 proximal, 145 middle, 104 distal) was biased in phalangeal preservation as determined by a chi-square test ( $p < 0.001$ ), but middle and proximal phalanges did not differ significantly in preservation frequency ( $p = 0.280$ ). The sample from Pit 77 showed equal preservation of all phalangeal positions (54 proximal, 55 middle, 51 distal;  $p = 0.922$ ). We hypothesize that depositional environment may influence preservation of particular phalangeal positions. Unguals are relatively less dense, and so could be more susceptible to damage either before burial or after exposure and prior to collection. Furthermore, relative size differences may explain why proximal phalanges are often more commonly preserved than middle phalanges. Differences in the rate of preservation/collection for certain elements highlights how taphonomy affects calculations of minimum number of individuals (MNI) and other common metrics.

**Funding Sources** David B. Jones Foundation; Augustyn Family Research Fund; Mary Stuart Rogers Foundation.

### **Fishes & Chondrichthyans: Evolution & Distribution**

#### **A NEW EDENTULOUS ICHTHYODECTIFORM FISH (OSTEICHTHYES: ACTINOPTERYGII) FROM THE UPPER CRETACEOUS OF TEXAS, U.S.A., AND ITS SYSTEMATIC POSITION**

Shimada, Kenshu<sup>1</sup>, Hacker, Riley<sup>2</sup>  
<sup>1</sup>Biology & Environmental Science, DePaul University, Chicago, Illinois, U.S.A., <sup>2</sup>Biology, DePaul University, Chicago, Illinois, U.S.A.

DMNH 20149 housed in the Perot Museum of Nature and Science, Dallas, Texas, U.S.A., is an ichthyodectiform fish from the Arlington Member (mid-Cenomanian) of the Upper Cretaceous Woodbine Formation in Denton County,

Texas, U.S.A. The fossil fish is represented by a nearly complete skeleton measuring about 50 cm in total length and 11 cm in maximum body depth. Whereas the specimen preserves the soft tissue outline of the asymmetrical forked caudal fin with the longer ventral lobe relative to the dorsal lobe, a notable aspect of this fish is its edentulous triangular jaws along with a mosaic of characters not seen in any previously known ichthyodectiforms. In order to examine its systematic position within the order Ichthyodectiformes, two sets of phylogenetic analyses were conducted based on the combination of two previously published character matrices. The first set used the original character matrices with three outgroups (*Amia calva*, *Elops hawaiiensis*, and *Leptolepis coryphaenoides*), 30 ingroup taxa, and 72 characters. The second set used *E. hawaiiensis* as the only outgroup but with the same ingroup taxa and characters where the polarity of 16 characters were recoded or modified as their state exhibited by *E. hawaiiensis* was considered to be plesiomorphic. For each set, a strict consensus tree and a 50% majority-rule consensus tree were constructed. Our analyses reveal that the topological arrangements of the four trees are relatively consistent, where DMNH 20149 is clustered with *Amakusaichthys goshouraensis* and *Heckelichthys* spp. in all four trees. The highest topological resolution was achieved by the 50% majority-rule consensus tree of the second set with a clade '[DMNH 20149 + [*Amakusaichthys* + *Heckelichthys*]]', although the 50% majority-rule consensus tree of the first set yielded '[[DMNH 20149 + *Amakusaichthys*] + *Heckelichthys*]'. Among the species within the specific clade, the overall cranial morphology superficially resembles that of *H. vexillifer*. However, the fact that none of the trees shows an immediate sister relationship between DMNH 20149 and *H. vexillifer*, combined with the lack of any decisive synapomorphy for the well-supported clade consisting of DMNH 20149, *Amakusaichthys*, and *Heckelichthys*, suggests that these and many other ichthyodectiform taxa are indeed manifested with a mosaic of characters. In particular, the aforementioned jaw and caudal fin characteristics in DMNH 20149 are designs seen in some Jurassic ichthyodectiforms.

### Macroecology & Macroevolution

#### PATTERNS OF BODY SIZE DISTRIBUTION ALONG PALEOLATITUDE OF EXTINCT ARCHOSAURS DURING THE LATE CRETACEOUS

Shimizu, Shuhei, Kobayashi, Yoshitsugu  
Hokkaido University, Sapporo, Hokkaido, Japan

Bergmann's Rule is one of the most notable ecogeographical rules. Previous studies noted that the body masses of birds and mammals generally increase towards

higher latitudes, suggesting that this rule agrees with the overall distributions of endotherms (birds and mammals). On the other hand, the body size distributions of other vertebrates do not follow this rule. For example, squamates and crocodylians reduce body mass at higher latitudes, and turtles show no trend. Here we test whether the body mass distribution of non-avian dinosaurs along paleolatitude shows 'endothermic' distribution, and, if not, which non-avian dinosaur groups show this distribution, or do not. In this study, a dataset of 258 body masses of non-avian dinosaurs and crocodylians from the latest Cretaceous (Campanian-Maastrichtian) was compiled.

Regression analysis shows that extinct crocodylians have a negative correlation as in modern crocodylians, however, all data of non-avian dinosaurs have no specific trend. Regression analysis of different groups of non-avian dinosaurs results in a negative trend in ceratopsians and a positive trend in hadrosaurs, tyrannosaurs, and ankylosaurs. No trend was found in titanosaurs and some theropods (dromaeosaurs, troodontids, ornithomimosaurs, and oviraptorosaurs). It is noteworthy that those theropods with no trend show no significant change in body masses with different paleolatitudes, but a latitudinal range of collected data is wide in ornithomimosaurs and oviraptorosaurs (25° to 30°) and narrow in troodontids and dromaeosaurids (~15°).

Supposing that these body mass distributions are reflections of endothermy and ectothermy, our result is discordant with the idea that the endothermy evolved in non-avian theropod dinosaurs. Rather, our result may suggest that non-avian dinosaurs were not endotherms like modern birds and mammals, but mesotherms instead, which may have been influenced more by other environmental factors such as the size of landmasses and food resources.

### Permo-Triassic Tetrapods

#### THE FIRST VERTEBRATE ASSEMBLAGE FROM THE MIDDLE FREMOUW FORMATION (TRIASSIC) OF ANTARCTICA.

Sidor, Christian A.<sup>1</sup>, Gee, Bryan M.<sup>1</sup>, Kulik, Zoe T.<sup>1</sup>, Makovicky, Peter J.<sup>6</sup>, McIntosh, Julia<sup>3</sup>, Smith, Nathan D.<sup>5</sup>, Smith, Roger M.<sup>4</sup>, Tabor, Neil J.<sup>3</sup>, Whitney, Megan<sup>2</sup>

<sup>1</sup>University of Washington, Seattle, Washington, U.S.A.,

<sup>2</sup>Harvard University, Cambridge, Massachusetts, U.S.A.,

<sup>3</sup>Southern Methodist University, Dallas, Texas, U.S.A.,

<sup>4</sup>University of the Witwatersrand, Johannesburg, South Africa,

<sup>5</sup>Natural History Museum of Los Angeles County, Los Angeles, California, U.S.A.,

<sup>6</sup>University of Minnesota, Minneapolis, Minnesota, U.S.A.

Rocks of the Beacon Group in the Transantarctic Mountains were first investigated by vertebrate paleontologists during the 1970–1971 austral summer. Tetrapods such as *Lystrosaurus*, *Procolophon*, and *Thrinaxodon* that were recovered from the lower member of the Fremouw Formation provided a critical link to the Lower Triassic *Lystrosaurus* biozone of the Beaufort Group of South Africa and afforded compelling evidence that Antarctica once formed part of Pangea. Near the end of the 1985–1986 field season, a second vertebrate-bearing horizon was discovered at the base of the upper member of the Fremouw Formation. Fossils of large capitosauroid temnospondyls as well as diademodontids and *Cynognathus* linked this stratigraphic interval to the *Cynognathus* Assemblage Zone of South Africa, which has been interpreted as either Middle or Late Triassic in age. Until now, no identifiable vertebrate fossils have been recovered from the middle member of the Fremouw Formation.

Our geologic work at McIntosh Ridge in 2017–2018 demonstrates that the middle Fremouw measures 70 meters thick and that vertebrate fossils primarily occur ~20 meters above the lower-middle Fremouw contact. Fossiliferous horizons are lithologically characterized by root-bearing grey sandy-siltstone between thin ( $\leq 2$  meter) laterally continuous horizontally-bedded fine-grained sandstone sheets suggesting a humid proximal floodplain paleoenvironment. Small-bodied temnospondyls are an important component of the middle Fremouw assemblage and likely include a new species that is a member of the Lapillopsidae, an enigmatic clade represented by material from the Lower Triassic of Australia and India. Amniotes specimens from the middle Fremouw include scattered gracile elements likely pertaining to a diapsid as well as partially articulated postcranial skeletons with anatomy similar to that of *Procolophon*. Importantly, *Lystrosaurus* was not recovered. Most interestingly, a nearly complete and three-dimensionally preserved skull represents the most phylogenetically informative theriocephalian fossil yet recovered from Antarctica. The presence of a broad bony connection between the palatal processes of the maxilla and the vomer forming a secondary palate and a long, low rostrum with numerous postcanine teeth indicate it represents a non-bauriid baurioid similar to *Lycideops*. The middle Fremouw fossil assemblage suggests a continuous inhabitation of the Antarctic portion of southern Pangea during Early Triassic times.

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### Quantitative Methods

### RECONSTRUCTING MAMMALIAN PHYLOGENY USING MORPHOMETRIC DATA: INSIGHTS FROM A PRELIMINARY CLADISTIC ANALYSIS

### OF HORSES (PERISSODACTYLA, EQUIDAE, EQUINI, EQUUS)

Silviria, J. S.

La Brea Tar Pits & Museum, Los Angeles, California, U.S.A.

An increasing number of phylogenetic studies on placental mammals have focused on expanding datasets to include postcranial as well as craniodental morphology, but most still rely on matrices with discretely coded characters. Utilization of linear and geometric morphometric data for maximum parsimony cladistic analyses has long been possible through continuous character functions in TNT, but these tools remain largely ignored by systematic paleomammalogists.

Here I present preliminary results from a morphometric cladistic analysis of horses in the genus *Equus*. A new character matrix was constructed from an online open-access database (<https://vera-eisenmann.com>), based on a standardized system of 260 linear measurements (97 craniodental, 162 postcranial) described by Eisenmann and colleagues in 1988. Characters were coded as continuous ranges to account for intraspecific polymorphism. As of May 2020, the matrix includes 12 extant OTUs and 32 proposed extinct taxa. Analyses of the matrix were done in TNT 1.5 using maximum parsimony with extended implied weighting at  $3 \leq K \leq 12$ , both with and without a constraint based on recent studies of *Equus* mitochondrial DNA.

In preliminary results, the most robustly resolved subclade of *Equus* in majority consensus and strict consensus trees, for both unconstrained and constrained analyses, comprises most extant wild asses and zebras, as well as some extinct asses (*E. hydruntinus*, *E. melkiensis*, *E. tabeti*). This clade may be diagnosed by decreased medial tibial length, as well as decreased dorsal length of the posterior distal phalanx. Additionally, most late Pliocene–early Pleistocene 'plesippine' and 'stenonine' horses, along with middle Pleistocene 'suessemionines' and the 'caballine' *E. mosbachensis*, comprise an extinct clade united by increased basilar length of the cranium, and an extremely long anterior ocular line between the premaxilla tip and the posterior supraorbital margin. However, most other nodes are poorly supported and collapse in the unconstrained strict consensus tree.

Ongoing work involves expanding taxon sampling to include all potentially valid extinct species of Equini; and expanding character sampling to include non-appendicular postcranial measurements, as well as craniodental ratios proposed by Eisenmann and Barclay in 2000 and Eisenmann in 2006 to be synapomorphies of 'caballine', 'stenonine', and 'plesippine' subclades of *Equus*.

### Mesozoic Herpetology

## SPHENODONTIAN PHYLOGENY AND THE IMPACT OF MODEL CHOICE ON DIVERGENCE TIMES AND EVOLUTIONARY RATES

Simoes, Tiago R.<sup>1</sup>, Caldwell, Michael<sup>2</sup>, Pierce, Stephanie E.<sup>1</sup>

<sup>1</sup>Museum of Comparative Zoology & Dpt. Organismic and Evolution Biology, Harvard University, Cambridge, Massachusetts, U.S.A., <sup>2</sup>Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada

Sphenodontians are an extremely long-lived lineage of lepidosaurian reptiles with a fossil record of at least 230 million years. However, there have been comparatively much fewer studies on sphenodontian phylogeny and evolution compared to squamates. As a result, all previous studies on sphenodontian phylogeny and macroevolution stem from additions and modifications from a single morphological data set published over 30 years ago. Here, we provide a new morphological data matrix to investigate sphenodontian evolutionary relationships, following several advances from the last two decades towards the construction of morphological data sets. Such advances include assessment of character dependencies, appropriate coding of states to avoid biases by missing/inapplicable data and scoring of autapomorphies for methods taking branch lengths into account. The final data set includes 36 taxa and 131 characters. We implemented different optimality criteria to analyze this data set, including maximum parsimony, non-clock Bayesian inference, and relaxed clock Bayesian inference with tip dating. Further, in order to investigate divergence times and evolutionary rates in the group using morphological clocks, we performed a thorough investigation of the differential impact of different clock models, taxon sampling strategies, the assumption of sampling for ancestors, and variations on the fossilized birth-death (FBD) models. In our results, we find a new hypothesis of sphenodontian relationships, and a strong negative impact on divergence time estimates and background clock rates when sampling for ancestors and using least-fit clock models. In particular, we find considerable improvement on divergence times when not sampling for ancestors and implementing the skyline FBD model, thus indicating the necessity to perform systematic tests of models and search strategies when implementing morphological clocks. Our results indicate high evolutionary rates and the divergence of most of the major sphenodontian lineages during the Triassic and Early Jurassic. This is subsequently followed by a continuous and sustained decrease in rates of morphological evolution across time in sphenodontians, reaching its lowest levels in the lineage leading to the modern tuatara (*Sphenodon punctatus*).

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## Quantitative Methods

### TESTING A NON-DESTRUCTIVE METHOD FOR ANALYZING PRESERVATION OF VERTEBRATE REMAINS

Simpson, Emily M., Crowley, Brooke, Sturmer, Dan  
Geology, University of Cincinnati, Cincinnati, Ohio, U.S.A.

Fossils preserve irreplaceable information about our planet's past climate, ecosystems, and organisms. Unfortunately, many of the types of analyses that reveal this information are destructive, and only provide viable data if the chemical composition is unaltered. Methods frequently used to determine alteration, such as scanning electron microscopy with Energy Dispersive X-Ray Spectroscopy (SEM-EDX), X-ray diffraction (XRD), benchtop X-ray fluorescence (XRF), and Fourier Transform Infrared Spectrometer (FTIR), are in themselves normally destructive, expensive, or both. FTIR measures crystallinity, whereas SEM-EDX, XRD, and XRF measure relative elemental abundances (e.g., the ratio of calcium to phosphorous; Ca/P). We conducted a pilot study to assess if handheld XRF, which is relatively inexpensive, portable, and non-destructive, produces results similar to other methods. We further investigated variability in Ca/P: (1) among mammalian taxa, (2) between tooth enamel and bone, and (3) in modern, sub-fossil, and fossil specimens. The use of the mass ratio Ca/P as a proxy for preservation has largely been limited to archaeological studies. Bone and tooth mineral is mainly composed of hydroxyapatite ( $\text{Ca}_{10}(\text{PO}_4)_6(\text{OH})_2$ ), with other immature phases of hydroxyapatites present. Theoretically, the mass ratio Ca/P should be 2.2, although reported values for modern human bone range from 1.3 to 2.3. This should be consistent regardless of taxon and tissue, but this has not been established systematically. Depending on the availability of soluble ions and pH in the environment, Ca/P in fossil and historic specimens may increase or decrease. However, data from poorly preserved material have not been reported, making it challenging to build expectations for altered material. We combined published data collected from an extensive literature search that included multiple methods, taxa, tissues, and specimen ages with new data from a selection of modern mammalian taxa analyzed using a Bruker Tracer 5i handheld XRF. Results are largely consistent, regardless of analytical method, taxon, element, or specimen age, although there may be a few exceptions. Further research, including analysis of the same material using multiple methods, will

help validate these preliminary findings, as well as expectations for altered material.

### Taphonomy & Stratigraphy

#### IDENTIFICATION OF TOOTH TRACES FROM AN *EDMONTOSAURUS ANNECTENS* BONEBED WITHIN THE LANCE FORMATION (MAASTRICHTIAN), WYOMING

Siviero, Bethania C.<sup>1</sup>, Rega, Elizabeth<sup>2</sup>, McLain, Matthew<sup>3</sup>, Brand, Leonard<sup>1</sup>, Chadwick, Art<sup>4</sup>, Nelson, David<sup>5</sup>

<sup>1</sup>Loma Linda University, Loma Linda, California, U.S.A., <sup>2</sup>Western University of Health Sciences, Pomona, California, U.S.A., <sup>3</sup>The Master's University, Santa Clarita, California, U.S.A., <sup>4</sup>Southwestern Adventist University, Keene, Texas, U.S.A., <sup>5</sup>Southern Adventist University, Collegedale, Tennessee, U.S.A.

Identifying the origin of perforating lesions on fossil bone is often difficult, and many are considered tooth traces in spite of more likely and more parsimonious etiologies. Much of this confusion stems from tooth trace criteria that are often ambiguous when the context for the lesions is not considered. Mistaken identification of biogenic and diagenetic taphonomic factors as tooth traces has led to misleading interpretations of animal behavior. This study of tooth traces on fossil bones critically reviews previous criteria and applies them to assessing bones from an *Edmontosaurus annectens* bone bed within the Lance Formation, Wyoming, U.S.A. Of the 3,013 bones examined by the first author, approximately 25 bones had superficially lytic lesions with 15 bones possessing features indicative of tooth traces based on gross appearance. Of these 15, three bones had lesions that were determined to have other causes, including normal foramina, infection, and degenerative joint disease. Twelve bones with different types of traces were attributed to tooth marks, including four bones with *Knethichnus parallelum* and *Linichnus serratus* ichnotaxa. *Tyrannosaurus rex* was identified as the likely inflictor of traces attributable to both ichnotaxa, by comparison of denticle density of carnivore teeth within the bonebed with striation/serration density of the traces. Including the context in the analysis revealed its importance to the identification of other types of features. Nutrient and neural foramina and lesions associated with pathology are examples that had the potential to be mistaken for tooth traces, if context was not considered. The application of refined criteria was useful in correctly labeling bone tooth traces, which will add to the literature on animal biting behavior in fossil taxa and stimulate further research.

### Permo-Triassic Tetrapods

#### FIRST OCCURRENCE OF THE PALEOZOIC VERTEBRATE ICHNOTAXON *ICHNIOOTHERIUM COTTAE* FROM THE TYPE SECTION OF THE CUTLER FORMATION: EVIDENCE FOR UPLAND HABITAT PREFERENCE BY DIAECTIDS (REPTILIOMORPHA)

Small, Bryan J.<sup>1</sup>, Huttenlocker, Adam<sup>2</sup>, Henrici, Amy C.<sup>3</sup>, Douglass, Robert<sup>4</sup>, Voigt, Sebastian<sup>5</sup>, Rasmussen, Donald<sup>6</sup>  
<sup>1</sup>The Museum, Texas Tech University, Aurora, Colorado, U.S.A., <sup>2</sup>University of Southern California, Los Angeles, California, U.S.A., <sup>3</sup>Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A., <sup>4</sup>Natural History Museum of Utah, Salt Lake City, Utah, U.S.A., <sup>5</sup>Umweltmuseum GEOSKOP, Burg Lichtenberg, Germany, <sup>6</sup>Biodiversity Institute, University of Kansas, Lawrence, Kansas, U.S.A.

The Carboniferous–Permian (C–P) Cutler Formation was deposited as a continental sequence of interbedded fluvial, lacustrine and eolian sediments within a vast depositional area of what is now the western U.S.A. During the Permian, the type section at Cutler Creek, Ouray, Colorado, would have been situated near the southwestern slope of the ancestral Uncompahgre highlands. During field work at Cutler Creek, a footprint of the Paleozoic vertebrate ichnotaxon *Ichniotherium cotta* (Reptiliomorpha) and other trace fossils were observed, and follow-up work resulted in additional footprint discoveries. These *Ichniotherium cotta* and *I. sp.* discoveries are the first in the Cutler and provide a datum that ties the ichnotaxon to the formational type section while making novel interbasinal comparisons of C–P vertebrate communities possible.

*Ichniotherium* is known from C–P of Europe, Morocco, Canada, and U.S.A. by two species, *I. cotta* and *I. sphaerodactylum*. In U.S.A., *I. cotta* now occurs in the Cutler and Maroon formations of Colorado and the Sangre de Cristo and Abo formations of New Mexico, and *I. sphaerodactylum* is known from the Leonardian Coconino Sandstone of Arizona. *Ichniotherium cotta* has been conclusively associated with the herbivorous diadectid *Diadectes*, which, based on their track and body fossil occurrences, inhabited inland/upland habitats and were less common components of coastal lowlands. The Maroon Formation of Colorado has the most numerous occurrences of *Ichniotherium cotta* in U.S.A. where they outnumber other known track species. They occur in the Eagle Basin, a subsiding basin between the western slope of the Ancestral Front Range and eastern slope of the Uncompahgre highlands. Our discovery of *I. cotta* from the Cutler type locality adds to the record of the herbivorous *Diadectes* inhabiting an inland/upland paleoenvironment and reinforces the theory that the herbivorous *Diadectes* preferred upland environments as

has been documented elsewhere in the Tambach Formation, Germany. Though a small sample size, the Cutler *I. cotta* hints at another example of the earliest herbivore-dominated vertebrate assemblages, as recorded in the Tambach Formation (Germany) and Maroon Formation (Colorado).

### Biomechanics & Functional Morphology

#### RECONSTRUCTED HINDLIMB MUSCULATURE AND FUNCTION IN THE THERIZINOSAUR *NOTHRONYCHUS* WITH IMPLICATIONS FOR THE OPISTHOPUBIC PELVIS IN MANIRAPTORAN THEROPODS

Smith, David<sup>1</sup>, Gillette, David<sup>2</sup>

<sup>1</sup>Biology, Northland Pioneer College, Holbrook, Arizona, U.S.A., <sup>2</sup>Geology, Museum of Northern Arizona, Flagstaff, Arizona, U.S.A.

The maniraptoran theropod *Nothronychus* is characterized by a reduced tail, an incipiently opisthopic pelvis, and long tibia relative to the femur. The opisthopic morphology evolved more than once and can be considered convergent with the hip of ornithischians. It is associated with reorganization of the musculature leading to the avian condition. This project involves reconstruction of the hindlimb muscles and function in *Nothronychus*. It incorporates a model of the range of motion in the pes. Important muscles include m. caudifemoralis longus, mm. obturatorius, mm. iliofemoralis, m. iliotrochantericus caudalis, m. tibialis anterior, and m. gastrocnemius. In *Nothronychus*, the tail is reduced, concomitant with a reduced m. caudifemoralis longus origin and associated function. Its retractive function is largely transferred to mm. obturatorius, but this insertion is on the more proximal femur. The protractive function of mm. iliofemoralis is transferred to m. iliotrochantericus caudalis. As the tail is reduced, the center of mass is transferred anteriorly in front of the acetabulum. This change requires rotation of the femur anteroventrally from a more ventral orientation at rest. Muscle scars indicate an avian topology for m. gastrocnemius and m. tibialis anterior along with the overall convergence with birds. Range of motion study in *Nothronychus* assuming minimal soft tissue within the pedal phalanges indicate a typical theropod foot, but the acquisition of a raptorial digit II convergent with dromaeosaurs.

The *Nothronychus* hindlimb can be used as a model for the evolution of the avian hindlimb, as it is incipiently convergent with later maniraptoran theropods. With the development of the opisthopic pelvis, the musculature attains a nearly avian topology and function. The acquisition of a raptorial pedal digit II indicates that this character evolved multiple times within maniraptorans. As

the adult *Nothronychus* is not modeled as particularly mobile, this character may have been more useful in juveniles and smaller taxa.

### Holocene & Pleistocene Mammalian Macroecology & Faunal Studies

#### THE MISSING PIECE: LATE PLEISTOCENE CHANGES IN THE ECOLOGICAL FUNCTION OF A MAMMAL COMMUNITY IN NORTH AMERICA

Smith, Felisa A.<sup>1</sup>, Villasenor, Amelia<sup>2</sup>, Elliott Smith, Emma A.<sup>3</sup>, Tomé, Catalina<sup>4</sup>, Lyons, S. K.<sup>4</sup>, Newsome, Seth<sup>1</sup>

<sup>1</sup>Biology, University of New Mexico, Albuquerque, New Mexico, U.S.A., <sup>2</sup>Anthropology, University of Arkansas, Little Rock, Arkansas, U.S.A., <sup>3</sup>Smithsonian, National Museum of Natural History, Washington D.C., District of Columbia, U.S.A., <sup>4</sup>Biological Sciences, University of Nebraska, Lincoln, Nebraska, U.S.A.

By the late Pleistocene, hominins were actively exploiting other mammals for food and resources. As they became increasingly abundant and dispersed across the globe, a temporally and spatially transgressive extinction of large-bodied mammals followed; the selectivity was unprecedented in the Cenozoic fossil record. Extinction rates have only increased since; the current conservation status of the largest mammals is precarious owing to a disastrous combination of hunting, habitat loss, and conflict with humans.

Large-bodied species perform many essential ecosystem services. Because threats are ongoing, conservation biologists cannot wait for results of long-term studies before proposing potential mitigation strategies. Yet, understanding the functional role of large-bodied mammals is essential for effective management of the remaining wild areas on Earth. Thus, a paleoperspective is essential; studying the consequences of the catastrophic biodiversity loss at the terminal Pleistocene can yield insights into the long-term ecological effects of biodiversity loss.

Here, we focus on morphological and isotopic dietary space as a proxy for functional space. We characterized changes in size and diet of the mammal community in the Edwards Plateau, Texas before and after the megafauna extinction. Body size was estimated from molars or postcranial material; carbon ( $\delta^{13}\text{C}$ ), nitrogen ( $\delta^{15}\text{N}$ ) and/or oxygen isotope values were derived from analysis of collagen or apatite extracted from fossils. Prior to the extinction, we find a diversity of C4 grazers, C3 browsers, and mixed-feeders, with specialization among felid hypercarnivores for C4 grazers, similar to their counterparts in modern African systems. The ursids (*Arctodus* and *Ursus*) fell into mixed C3–C4 to pure C3 isotopic ranges; *Arctodus* was more omnivorous (average  $\delta^{15}\text{N} = 7.6\text{‰}$ ) than

hypercarnivores (average  $\delta^{15}\text{N} = 13.9\text{‰}$ ). *Ursus* remained low in  $\delta^{15}\text{N}$  space through time (average  $\delta^{15}\text{N} = 4.4\text{‰}$ ). Post-extinction, the  $\delta^{13}\text{C}$  niche space of several surviving browsers and carnivores (*Odocoileus* and *Ursus*) did not change. However, Pleistocene herbivores show a significant increase in  $\delta^{15}\text{N}$  values near the Pleistocene–Holocene transition that decreased again in the Holocene, suggesting a change in biogeochemical cycling. Overall, the extinction led to losses in body size and feeding diversity, suggesting that, without major conservation efforts, future extinctions will lead to missing pieces across modern mammal communities.

**Funding Sources** This research is supported by the National Science Foundation Division of Environmental Biology (DEB 1555525; FA Smith PI; SK Lyons and SD Newsome, co-PIs).

## Taphonomy & Stratigraphy

### A TAPHONOMIC ANALYSIS OF VERTEBRATE-BEARING CAVE BRECCIA IN SOUTHEAST ASIA

Smith, Holly E.<sup>1</sup>, Morley, Mike<sup>5</sup>, Bevitt, Joseph<sup>4</sup>, Garbe, Ulf<sup>4</sup>, Rizal, Yan<sup>3</sup>, Zaim, Jahdi<sup>3</sup>, Rizki Puspaningrum, Mika<sup>3</sup>, -, Aswan<sup>3</sup>, Trihascaryo, Agus<sup>3</sup>, Price, Gilbert<sup>2</sup>, Louys, Julien<sup>1</sup>

<sup>1</sup>Australian Research Centre for Human Evolution, Griffith University, Nathan, Queensland, Australia, <sup>2</sup>School of Earth and Environmental Sciences, University of Queensland, Brisbane, Queensland, Australia, <sup>3</sup>Geology Study Program, Institut Teknologi Bandung, Bandung, Java, Indonesia, <sup>4</sup>DINGO neutron imaging station, Australian Nuclear Science and Technology Organisation, Sydney, New South Wales, Australia, <sup>5</sup>College of Humanities, Flinders University, Adelaide, South Australia, Australia

Southeast Asia has a rich and interesting paleohistory; however, it can be incredibly difficult to discern the mechanisms of fossil site formation, depositional history, and faunal accumulation. This is in part due to dating complexities and poor preservation potential in tropical environments. Calcareous fossil-bearing breccia deposits that accumulate in limestone caves may hold the key to resolving this issue. These deposits are often overlooked as they appear homogenous and are often considered too difficult to work with. Our research develops a method for using breccia to establish the dominant factors responsible for accumulation and preservation of the vertebrate remains. Field work was undertaken in the Padang Highlands of western Sumatra, in three key cave localities: Lida Ajer, Ngalau Gupin, and Ngalau Sampit. Rapid thermal neutron tomographic imaging, micromorphology, and a paleontological review of the excavated faunal assemblages was undertaken. Tomographic imaging

provides a macro-taphonomic approach for revealing the internal composition of consolidated breccia deposits before any destructive preparation. Tomographic imaging has thus far revealed a high-resolution chronology of site formation. These seemingly homogeneous breccias formed during several depositional phases determined by cyclic water influx events. Micromorphology provides a micro-taphonomic approach to determine the alteration processes of fossils during burial or post-deposition. Our research reveals species composition, chronology, and paleogeographic affinities; evidence informing the taphonomic events that transpired at each cave site. Understanding the stratigraphical progression of the cave has revealed principal evidence of a rich, diverse late Pleistocene mammalian assemblage altered by two very different taphonomic histories: large carnivore attrition, prolific scavenging of porcupines, and alteration by water action of large mammal remains; and small carnivore attrition of small mammal remains. This study highlights the potential for analyses of complex breccia deposits in anthropological and paleontological studies in the caves of Southeast Asia.

**Funding Sources** ARCHE Department, Griffith University; ARC Future Fellowship FT160100450; Australian Nuclear Science and Technology Organisation grant; Winifred Violet Scott Estate Fund.

## Preparators

### SCREENWASHING, MICROPREPARATION, AND MICRO CT: A CASE STUDY OF HOW PREPARATION WORKFLOW FACILITATES RESEARCH ON MICROFOSSIL LOCALITIES AT PETRIFIED FOREST NATIONAL PARK

Smith, Matthew E.<sup>1</sup>, Kligman, Ben<sup>2</sup>, Yarborough, Viki<sup>2</sup>, Marsh, Adam D.<sup>1</sup>

<sup>1</sup>Petrified Forest National Park, Holbrook, Arizona, U.S.A., <sup>2</sup>Department of Geosciences, Virginia Tech, Blacksburg, Virginia, U.S.A.

Microvertebrate bonebeds are important proxies for diversity and ecological structure in the fossil record, but how microvertebrate field collection and preparation methods bias our interpretation of the fossil record remain largely unevaluated. This is largely due to a lack of published preparation techniques in the scientific literature which leaves no way to adequately evaluate past and current biases in the field and laboratory. Recent work at several new and well-known sites in Petrified Forest National Park, Arizona (PEFO) suggest that collection and

preparation technique can have a significant effect on interpretation of species diversity.

Recently we developed a methodological protocol that we believe maximizes recovery of small, delicate, diagnostic skeletal elements from Late Triassic microvertebrate bonebeds in PEFO. Paleocological data loss is minimized, resulting in recovery of unparalleled levels of lissamphibian and lepidosaur diversity for the Triassic. Therefore, we have adopted this protocol in house as a best practice.

The workflow involves two sub-paths. 1) Bones visible to the naked eye while quarrying are collected as hand samples and mechanically prepared in the round, often only exposing one diagnostic surface if the fossil is overly fragile. 2) All fossiliferous matrix without visible fossils is mapped, collected as blocks, and then systematically screen-washed with a minimum screen size of 0.446 mm in separate 2.25 kg batches. Batches of concentrate are individually sorted, and elements which fragmented into pieces during screen washing including jaws and limbs are re-associated and reassembled using a novel inexpensive jig similar to a jeweler's ball vise. Resulting bones from both sub-paths are  $\mu$ -CT scanned and 3D printed at a large scale to reduce handling of specimens.

The re-assembly of associated skeletal elements from screen washing has yielded many scientifically important specimens, producing a more accurate picture of total diversity and ecology for sampled sites compared to past studies at similar localities within PEFO. Implications of this new methodology allow reconstruction of past ecosystems with less bias allowing for robust studies of how and why they change through time; and recovery of bones from scientifically important clades with poor fossil records due to their minute and fragile bones.

**Funding Sources** Additional funding for this work was provided by the Petrified Forest Museum Association and Friends of Petrified Forest.

## Permo-Triassic Tetrapods

### A KANNEMEYERIIFORM (SYNAPSIDA: DICYNODONTIA) OCCIPITAL PLATE FROM THE MIDDLE TRIASSIC UPPER FREMOUW FORMATION OF ANTARCTICA

Smith, Nathan D.<sup>1</sup>, Makovicky, Peter J.<sup>2</sup>, Sidor, Christian A.<sup>3</sup>, Hammer, William R.<sup>4</sup>

<sup>1</sup>Dinosaur Institute, Natural History Museum of Los Angeles County, Los Angeles, California, U.S.A., <sup>2</sup>Earth and Environmental Sciences, University of Minnesota, Minneapolis, Minnesota, U.S.A., <sup>3</sup>Biology, University of Washington, Seattle, Washington, U.S.A., <sup>4</sup>Geology, Augustana College, Rock Island, Illinois, U.S.A.

Three terrestrial vertebrate faunas have been described from the early Mesozoic of Antarctica, representing Early Triassic, Middle Triassic, and Early Jurassic assemblages. Middle Triassic vertebrate fossils from the upper Fremouw Formation were first discovered during the 1985–86 Beardmore Glacier expedition, and are known from sites at both Gordon Valley and Fremouw Peak. At approximately 75 degrees South paleolatitude, the upper Fremouw Formation represents the highest paleolatitudinal setting for any Middle Triassic tetrapod assemblage. A total of 10 distinct tetrapod taxa can be recognized from the upper Fremouw Formation, including two endemic temnospondyls. Here, we describe a new specimen of kannemeyeriiform dicynodont from the upper Fremouw Formation. The specimen is from a quartzose conglomeratic sandstone unit that contains logs and siltstone clasts and crops out at both Gordon Valley and Fremouw Peak. The specimen comprises the occipital plate, including portions of the supraoccipital, exoccipitals, opisthotics, and basioccipital, which have been fused into a periotic element, as in most dicynodonts. The Antarctic specimen is comparable in size to *Kannemeyeria simocephalus* from the well-known *Cynognathus* Assemblage Zone of the Beaufort Group of South Africa, and represents the largest therapsid currently known from the upper Fremouw Formation. The presence of an occipital condyle with distinct contributions from the exoccipital and basioccipital; a wide, tri-radiate occipital condyle; and a well-developed tympanic process of the paroccipital represent a combination of character states hitherto unknown among Kannemeyeriiformes. Combined with the possible autapomorphic feature of slender, dorsoventrally elongate basal tubera, this may suggest the Antarctic specimen represents a new taxon. This material represents the most complete, and only the third definitive, dicynodont specimen from the upper Fremouw Formation, and the contradictory phylogenetic character data from these three specimens adds support for the presence of at least two co-occurring kannemeyeriiform taxa within the Antarctic tetrapod fauna. Coupled with new radiometric age data for the Fremouw Formation, these kannemeyeriiform specimens provide additional support for a correlation with the *Cynognathus* Assemblage Zone (particularly subzones B or C), as well as an Anisian or younger age for the upper Fremouw tetrapod fauna.

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## Permo-Triassic Tetrapods

### NEONATE AGGREGATION IN THE PERMIAN THERAPSID *DIICTODON*: EVIDENCE FOR A REPRODUCTIVE FUNCTION FOR BURROWS?

Smith, Roger M.

Dept. Geological Sciences, University of the Witwatersrand, Cape Town, South Africa

Despite over 150 years of fossil prospecting in the South African Karoo there is no direct evidence that therapsids laid eggs. In the late 1980's the discovery of late Permian helical burrow casts containing articulated skeletons of the small herbivorous therapsid *Diictodon* led to the conjecture that their primary reason for going underground was to give birth and provide shelter for infants. Here we present new fossil evidence to support the brood chamber hypothesis.

Re-investigation of the original helical burrow site led to the discovery of several more mudrock-filled burrow casts containing mostly scattered yet still-associated skeletons of *Diictodon*. Mechanical preparation of one of the complete terminal chambers revealed a disarticulated but anatomically-associated adult *Diictodon* skeleton along with a single tiny (5 mm long) humerus of an infant dicynodont.

A nearby outcrop of proximal floodplain mudrocks yielded a block containing a close association of an adult *Diictodon* skull in the process of erupting tusks (skull length 84mm), a tiny semi-articulated *Diictodon* skeleton (skull 19 mm, mandible 10.5mm long), a second incomplete mandible of the same size and an articulated skeleton of the diapsid *Youngina*. Synchrotron X-ray Computed Tomography of the infant skeleton confirmed that the size and humeral morphology closely matches that of the isolated bone in the *Diictodon* burrow cast. Despite this behaviorally-arranged taphonomic mode, no burrow structure was evident in the massive grey siltstone surrounding the bones. Yet, the spatial and stratigraphic proximity of these four specimens with clusters of helical and straight or slightly sinuous decline burrow casts is strong evidence that the animals were in a confined underground chamber before death.

The consistent association of *Diictodon* with these burrow structures, combined with forelimb and hindlimb specializations for digging, implicate *Diictodon* as the excavator of the burrows. The association of neonates and adults within the structures leads us to hypothesize that terminal portions of the burrows served as brood chambers. The stable temperature environment within a burrow could explain histological data indicating uninterrupted growth to ca. 70% of adult size in *Diictodon*. As opposed to a shelter-sharing scenario, the fully-articulated *Youngina* lying alongside the neonates likely arrived after the *Diictodon* had died and was using their inactive burrow as an aestivation refuge.

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## Evolution & Biology of Non-Avian Theropods

### GROWTH AND REMODELING IN AN ONTOGENETIC SERIES OF *GORGOSAURUS LIBRATUS* (DINOSAUR PROVINCIAL PARK, ALBERTA) METATARSALS REVEALED THROUGH 3D VASCULAR HISTOLOGY

Snively, Eric<sup>1</sup>, Longrich, Nicholas<sup>2</sup>, Barta, Daniel E.<sup>1</sup>, Woodward, Holly<sup>1</sup>, Cooper, David M.<sup>3</sup>, Burns, Michael M.<sup>4</sup>, Surring, Lara<sup>5</sup>, Currie, Philip J.<sup>6</sup>

<sup>1</sup>Anatomy and Cell Biology, Oklahoma State University College of Osteopathic Medicine, Tulsa, Oklahoma, U.S.A., <sup>2</sup>University of Bath, Bath, U.K., <sup>3</sup>Anatomy Physiology and Pharmacology, University of Saskatchewan, Saskatoon, Saskatchewan, Canada, <sup>4</sup>Jacksonville State University, Jacksonville, Alabama, U.S.A., <sup>5</sup>Independent, Calgary, Alberta, Canada, <sup>6</sup>Biological Sciences, University of Alberta, Edmonton, Alberta, Canada

Bone histology shows active processes of growth, remodeling, and external loading in dinosaurs and other vertebrates. For investigating these phenomena, histological thin sections reveal details of bone tissues to the cellular level, and microCT enables 3D reconstruction at the cost of tradeoffs between resolution and the sizes of scanned samples. Phase contrast microCT partially bridges the gap between traditional thin sections and microCT, by resolving edge details below the nominal resolution of the X-ray detector.

We applied phase contrast synchrotron microCT to investigate growth in an ontogenetic series of metatarsals (MT) attributable to the Campanian tyrannosaurid *Gorgosaurus libratus* from Dinosaur Provincial Park, Alberta. Protocols for large and small samples were developed and applied on the Biomedical Imaging and Therapy beam line of the Canadian Light Source synchrotron. Scanning encompassed MT III of one juvenile and drill cores of an adult at 4.3  $\mu$  voxel size, and large longitudinal transects of mid-size juvenile elements at 9.2  $\mu$ . Anatomical resolutions of CT slices were compared with details evident in histological thin sections of tyrannosaurid specimens. 3D reconstruction of vascular networks enabled visualization and color-indexed diameters of primary and remodeling canals.

The *Gorgosaurus* metatarsals showed, with growth, expected shifts from predominance of primary osteons to exclusively Haversian bone in the superficial cortex of the large adult. The mid-sized juvenile specimens possess localized remodeling by Basic Multicellular Units (active remodeling systems), likely induced by locomotor loadings. Notably, the 9.2  $\mu$  resolution for the larger

juveniles reveals details close to those of the higher-resolution scans of the smaller samples, including inferred osteon cement lines. Clear bands of arrested growth in these specimens indicate an age of 3–4 years at mortality, when the individuals were human-sized.

These results are consistent with growth rates determined for *Albertosaurus sarcophagus* (early Maastrichtian, Horseshoe Canyon Formation, Alberta), indicating similar rates in *Gorgosaurus* and *Albertosaurus*. Growth in these tyrannosaurids was substantially slower than in ornithischians such as *Maiasaura*, heuristic for ecological interplay and differing population structures in contemporaneous tyrannosaurids and hadrosaurs.

**Funding Sources** National Science and Engineering Research Council, Canada Foundation for Innovation, Canadian Light Source, Oklahoma State University, University of Wisconsin-La Crosse.

### Symposium: Paleoneurology

#### NEUROSENSORY EVOLUTION IN REPTILES AND THE FULL TRANSITION TO LAND

Sobral, Gabriela  
Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Baden-Württemberg, Germany

Reptiles are the most diverse group of living tetrapods, and primarily terrestrial. However, rather than an event, terrestrialization was a process, and one that is not yet fully understood. Given the quite different environments represented by water and land, and the connection between habitat exploitation and sensory perception, fossils provide us valuable information on the evolution of neurosensory features and the full transition to land. The goal is to explore some morphological trends and indicate future directions. Analysis of the ear of stem-reptiles like *Captorhinus* and *Youngina* shows the stepwise acquisition of traits specialised for terrestrial hearing, such as the increasing sound-transmitting function of the stapes and the gradual shift from low-frequency hearing ranges. During reptile evolution, the stapes becomes slender and more mobile, facilitating sound transmission by means other than intra-bone sound conduction. Coupled with the tympanic membrane, this increases the impedance-matching function of the ear and enables the detection of high-frequency sounds. In archosauriforms, such as *Mesosuchus* and *Euparkeria*, the structural separation of the inner ear from the brain through the ossification of the otic capsule and the development of a pressure-relief mechanism further enhances these features. These processes were first inferred through anatomical analyses, but later confirmed by CT scans. Nonetheless, it still remains unknown when the tympanum first appeared in reptiles. While the hearing sense has been more extensively explored, other aspects of reptile neurology remain poorly

known because both cranial endocasts and anatomical approaches to the braincase of early reptiles are virtually absent. For instance, the relative proportion of the (para)basisphenoid and the basioccipital on the braincase floor indicate the relative sizes of the cerebellum and medulla and, where present, sphenoid ossifications show the relative position of the forebrain. These relationships change during reptile evolution, indicating a rearrangement of the brain. It results in the verticalization of the braincase and incorporation of embryonic structures like the pila antotica to the ossification process of the prootic. While it is difficult to directly link form and function in extinct taxa, these changes presumably represent a refinement in dealing with the stimuli of the environment, and may be indicative of a specialization to a more terrestrial habitat.

### Colbert Poster Prize/Permo-Triassic Tetrapods

#### UNIQUE INTERNAL AND EXTERNAL MORPHOLOGIES OF MANUAL UNGUALS OF DREPANOSAURIFORMS HELP IDENTIFY ISOLATED SKELETAL ELEMENTS AND GEOGRAPHIC DISTRIBUTION OF THE CLADE IN THE WESTERN U.S.A. DURING THE LATE TRIASSIC AND BEYOND.

Sodano, Megan P.<sup>1</sup>, Kligman, Ben<sup>1</sup>, Stocker, Michelle R.<sup>1</sup>, Marsh, Adam D.<sup>2</sup>, Parker, William<sup>2</sup>, Pritchard, Adam C.<sup>3</sup>, Nesbitt, Sterling J.<sup>1</sup>

<sup>1</sup>Geosciences, Virginia Tech, Blacksburg, Virginia, U.S.A., <sup>2</sup>Division of Science and Resource Management, Petrified Forest National Park, Holbrook, Arizona, U.S.A., <sup>3</sup>Paleontology, Virginia Museum of Natural History, Martinsville, Virginia, U.S.A.

Drepanosauromorphs are small (>45 cm in length) and possibly arboreal diapsid reptiles, known for their claw-tipped prehensile tails, bird-like heads, and specialized forelimb anatomy, that lived in current-day central Asia, western Europe, and the southwestern U.S.A. during the Late Triassic. One of the most bizarre features of the largest drepanosauromorphs is their enlarged manual unguals (most well-known from *Drepanosaurus unguicaudatus*). Unfortunately, details of the external and internal features of the ungual cannot be determined for *D. unguicaudatus* because of the two-dimensional taphonomic compression of the skeleton. Using micro-computed tomography, we evaluated the external and internal anatomy of three-dimensionally preserved drepanosauromorph unguals from several fossil localities in the Chinle Formation within and around Petrified Forest National Park, Arizona, and the Hayden Quarry at Ghost Ranch, New Mexico. The largest unguals are mediolaterally slender, have little to no distinct grooves and furrows, and possess a thin dorsal margin that

thickens ventrally. The smaller unguals are wider, possess grooves, and have rounded dorsal edges. All of the unguals have a strong and consistent convexity from the proximal end to the distal tip on the dorsal margin (~160 degrees of curvature). In ventral view, the curve is segmented into three sections: a proximal triangular fossa (1/3 the length), a middle rounded tubercle, and a distal tapering tip. The deep articulation surfaces with the penultimate phalanx are situated ventrally on the proximal surface. Internally, the thin (~1 mm) and finely-laminated cortex surrounds a largely hollow internal space with sporadic trabeculae, whereas the tips are solid compacta. This combination of internal and external morphologies of drepanosauromorphs is distinct among reptiles and allows isolated unguals to be assigned to the clade and new records of drepanosauromorph unguals to be identified from other Chinle Formation microvertebrate localities (e.g., 'Green locality'), thus indicating the presence of this clade in nearly all Chinle Formation paleocommunities. Additionally, our novel morphological characterization may open the door to identification of drepanosauromorph unguals from Triassic-aged microvertebrate assemblages worldwide, improving our understanding of this enigmatic clade.

### Mammalian Skeletal Morphology

#### FIVE IN TWO: PENTADACTYLLY IN GIRAFFIDAE

Solounias, Nikos<sup>2</sup>, Yohe, Laurel R.<sup>1</sup>

<sup>1</sup>Earth and Planetary Sciences, Yale University, New Haven, Connecticut, U.S.A., <sup>2</sup>Anatomy, New York Institute of Technology, Old Westbury, New York, U.S.A.

In ruminants, the metatarsal is the fusion of digits three and four. This is clearly obvious in the adult where there are two medullary cavities inside the metatarsal and the fusion line is observable on the dorsal surface. While this is characteristic of bovids and cervids, the Giraffidae are different. We found that all five digits are present in the adult giraffe; giraffids, unlike bovids and cervids, are pentadactylus. This is true for two key fossil taxa where the genus is unknown, and also for *Giraffokeryx*, *Helladotherium*, *Bramatherium*, *Samotherium*, *Palaeotragus*, *Bohlinia*, and *Giraffa*. The evidence for this does not derive solely from the presence of the four proximal articular facets, which are also present in Bovidae and Cervidae. In the outgroup *Hyemoschus* (Tragulidae), the four facets occur on digits II and V, as II and V are free, clearly distinct, and unfused. In all the Giraffidae mentioned previously, we find a combination of four morphologies: (1) the four articular facets; (2) four, and in most cases, five separate medullary cavities internally; (3) a clear, small digit I; and (4) in the two fossil taxa of the

unknown genus, the presence of external elongated grooves where the fusions of II and V have taken place. *Giraffa*, the extant Giraffidae, differs from all the extinct taxa in having more compressed digits. Our findings suggest that: (1) the proximal articular facets are plastic as to where they form, (2) *Giraffa* has a specialized locomotion in some way different from that of many previous Giraffidae, and (3) Giraffidae can be characterized by this new set of four morphological characters. These discoveries provide evidence for new hypotheses as to how bones fuse, and question current hypotheses of digit loss.

**Funding Sources** NSF Postdoctoral Fellowship in Biology.

### Colbert Poster Prize/Evolution & Biology of Non-Avian Theropods

#### BONE HISTOLOGY REVEALS EXTREME GROWTH VARIATION IN THE THEROPOD DINOSAUR *ALLOSAURUS* ACROSS ITS GEOGRAPHIC RANGE

Sombathy, Riley S., D'Emic, Michael  
Biology, Adelphi University, Garden City, New York, U.S.A.

Paleohistological studies are often limited in their power to reconstruct organismal biology by their small sample sizes. The Mesozoic theropod *Allosaurus* provides an opportunity to conduct a large-scale paleohistological study due to its exceptional abundance. Several previous studies have utilized a large paleohistological sample of *Allosaurus*, but all were from a single locality, the Cleveland-Lloyd Dinosaur Quarry of Utah. Based on the Cleveland-Lloyd sample, the existence of two growth strategies has been recognized. To see if these growth strategies characterize other *Allosaurus* populations, we expanded the sample to include seven long bones of five individuals of *Allosaurus* from four localities in Wyoming and Colorado. We test five hypotheses that explain the observed variation in growth strategies: developmental plasticity, sexual dimorphism, hidden taxonomic variation, geographic variation, and stratigraphic variation. We used mass estimates based on the circumferences of lines of arrested growth to calculate the maximum annual growth rate for each individual, and several retrocalculation methods to estimate individual longevities. Three specimens in our sample had reached asymptotic body mass, inferred from the presence of external fundamental systems, with a difference of approximately 1,000 kg between the largest and smallest of these skeletally mature specimens and a three-fold difference in maximum annual growth rates. When including skeletally immature specimens, there is a nearly five-fold difference in

maximum annual growth rate. Retrocalculation estimates suggest a maximum longevity of nearly three decades. Of the two skeletally immature specimens, both were estimated through retrocalculation to have died at 10 years of age, despite a ca. 1,000 kg difference in their body masses. Specimens that reached asymptotic size did so in about two decades, which is consistent with studies of the southwestern populations. These results indicate extreme growth pattern variation in *Allosaurus* across the northern and western extents the Morrison Formation that could be a result of extreme developmental plasticity, sexual dimorphism, hidden taxonomic variation, or a combination of these factors.

**Funding Sources** Jurassic Foundation Research Grant; Paleontological Society Steven M. Stanley Student Research Award.

### Dinosaur Systematics, Diversity & Ecology

#### A JUVENILE *YAMACERATOPS DORNGOBIENSIS* (ORNITHISCHIA, CERATOPSIA) FROM THE UPPER CRETACEOUS JAVKHLANT FORMATION OF MONGOLIA

Son, Minyoung<sup>1</sup>, Lee, Yuong-Nam<sup>1</sup>, Zorigt, Badamkhatan<sup>2</sup>, Park, Jin-Young<sup>1</sup>, Lee, Sungjin<sup>1</sup>, Kim, Su-Hwan<sup>1</sup>, Lee, Kang-Young<sup>3</sup>

<sup>1</sup>School of Earth and Environmental Sciences, Seoul National University, Seoul, Korea (the Republic of), <sup>2</sup>Institute of Paleontology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia, <sup>3</sup>Department of Physics Education, Gyeongsang National University, Jinju, Korea (the Republic of)

A new articulated skeleton of a small individual of *Yamaceratops dorn gobiensis* was recovered from the Javkhant Formation (?Santonian–Campanian) at the Khugenslavkhant locality of Shine Us Khudag, Eastern Gobi of Mongolia in 2014. *Y. dorn gobiensis* was named in 2006 based on the holotype partial skull and some referred cranial and postcranial elements from the same locality. The new specimen is identified as *Y. dorn gobiensis* based on the unkeeled rostral bone and an embayment at the base of the dorsal process of the jugal. The specimen also has a potential autapomorphy of this taxon, which is the rostroventral margin of the fungiform dorsal end of the lacrimal being excluded from the antorbital fossa. Juvenile features of basal neoceratopsians in this specimen include the ventral position of the antorbital fossa relative to the orbit reflecting the inclination of the lacrimal, straight ventral edge of the dentary, long-grained surface texture on the long bones (femur, tibia, fibula, humerus, ulna, and radius), the smooth external surface on the postorbital and predentary, a large orbit relative to the postorbital and jugal, and open neurocentral sutures of all caudal vertebrae,

as are also seen in juvenile *Protoceratops andrewsi*. Furthermore, the new specimen shows some diagnostic characters of some basal neoceratopsians. These include the ventrally hooked rostral bone as in *Aquilops americanus* and very tall middle caudal neural spines about or more than four times as high as the centrum as in *P. andrewsi*, *Koreaceratops hwaseongensis*, and *Montanoceratops cerorhynchus*. The jugal with the subtemporal ramus deeper than the suborbital ramus as in the holotype specimen is also shared with *Liaoceratops yanzigouensis*, *A. americanus*, and juvenile *P. andrewsi*. The phylogenetic relationships of *Y. dorn gobiensis* to other basal neoceratopsians have been variable among different analyses since the initial description. Our phylogenetic analysis, by scoring 35 new characters that were not known from the holotype and referred specimens into the recent comprehensive data matrix of basal Neoceratopsia, recovered *Y. dorn gobiensis* in a polytomy alongside *Helioceratops brachygnathus*, a large clade of all leptoceratopsids except *H. brachygnathus*, and Coronosauria. Therefore, this study adds novel information about the anatomy, provides insights into the ontogenetic variation, and helps to better understand the phylogenetic position of *Y. dorn gobiensis*.

**Funding Sources** National Research Foundation of Korea (grant number 2019R1A2B5B02070240) to Yuong-Nam Lee.

### Permo-Triassic Tetrapods

#### REMARKABLE NICHE PARTITIONING IN THE EXTRAORDINARILY LONG-NECKED TRIASSIC ARCHOSAUIROMORPH *TANYSTROPHEUS*

Spiekman, Stephan  
Paleontological Institute and Museum, University of Zurich, Zurich, Switzerland

*Tanystropheus longobardicus*, mainly known from fossil localities of the UNESCO World Heritage Site of Monte San Giorgio in Switzerland and Italy, represents one of the most remarkable Triassic reptiles. It is characterized by an extraordinarily long and stiffened neck made up of 13 hyper-elongated vertebrae and accompanying ribs to form a structure unique among tetrapods. Due to its unusual morphology, the paleobiology of *Tanystropheus* remains contentious, with both aquatic and terrestrial lifestyles having been discussed extensively. Among the specimens, a small morphotype bearing tricuspid teeth and a large morphotype bearing single-cusped teeth can be recognized, historically considered as juveniles and adults of the same species. Using high resolution synchrotron radiation microtomography, a virtually complete but disarticulated

skull of the large morphotype was three-dimensionally reconstructed, including its endocast and inner ear, to reveal its skull morphology for the first time. The braincase shows the presence of a laterosphenoid, the phylogenetically earliest occurrence of this bone in archosauromorphs. The skull displays a morphology that is specialized towards hunting in an aquatic environment, indicated by the placement of the external nares on the top of the snout and a fish-trap type dentition, similar to that of certain predatory sauropterygians. The findings also corroborate that the large morphotype is morphologically distinct from the small morphotype. A paleohistological study of the femur displays over 20 growth marks including an outer circumferential layer (OCL) in the small morphotype, thus indicating its skeletal maturity and confirming that it is indeed a separate species. The co-occurrence of two species of disparate size ranges and dentitions implies previously unrecognized niche partitioning in *Tanystropheus*. The uniquely constructed neck of *Tanystropheus* was therefore surprisingly versatile and facilitated at least two very distinct lifestyles.

**Funding Sources** This study is funded by the Swiss National Science Foundation (grant no. 2'5321-162775 to Torsten Scheyer).

## Mesozoic Herpetology

### A RHAMPHORHYNCHINE PTEROSAUR MANDIBLE FROM BONE CABIN QUARRY, MORRISON FORMATION, WYOMING

Sprague, Michael<sup>1</sup>, McLain, Matthew<sup>2</sup>

<sup>1</sup>Department of Earth and Biological Sciences, Loma Linda University, Loma Linda, California, U.S.A., <sup>2</sup>Department of Biological and Physical Sciences, The Master's University, Santa Clarita, California, U.S.A.

EDP-SM 2017.02.002 is a mostly complete pterosaur mandible, missing only the posteriormost portion, from Bone Cabin Quarry, Wyoming. The mandible is narrow, with a long symphysis and an edentulous tip, and seven alveoli visible on the left side. The jaw is crushed dorsoventrally as well as compressed laterally, obscuring all but three of the alveoli on the right dentary. This mandible was found less than one meter from the holotype rostrum of the scaphognathine pterosaur *Harpactognathus*. In the paper describing *Harpactognathus*, Carpenter et al. briefly mentioned this mandible, excluding it from this taxon due to the sharp contrast between it and the rostrum. Bennett later tentatively referred the jaw, in addition to a large humerus

also found at the site, to *Harpactognathus* in part because of the close proximity of all three elements. However, it is very unlikely the mandible and the rostrum belong to the same genus. The edentulous tip, narrow shape, shallow profile, and closely-spaced teeth likely place it in a different clade than *Harpactognathus*. Based on these criteria, this jaw probably belongs to a rhamphorhynchine. While many isolated rhamphorhynchine elements are known from the Morrison Formation, there are no named definitive rhamphorhynchines.

Aside from the drastic contrast in morphology between the rostrum and this mandible, scaphognathine mandibles hold five or six widely-spaced teeth. Rhamphorhynchines, conversely, generally have at least seven closely-spaced teeth. The non-rhamphorhynchine rhamphorhynchid *Dorygnathus* also possesses a mandible with an edentulous tip, but the three anterior dentary teeth of *Dorygnathus* are significantly larger than the posterior teeth, a condition not seen in the Bone Cabin specimen where the alveoli are all roughly the same size. The alveolar count and spacing of this jaw most resemble *Rhamphorhynchus*, but is still notably distinct based on these characters. Rhamphorhynchines also have a very well-developed mandibular symphysis that runs over 30% the length of the mandible. The mandibular symphysis of this specimen forms just under 30% the length of the mandible. Most of the symphyses of scaphognathine specimens are obscured, making it difficult to determine the relative length, but in the specimens which we can measure the symphysis, it is well below 30% of the mandibular length. Thus, based on the tooth count and spacing, edentulous tip, and length of the symphysis, we assign this mandible to Rhamphorhynchinae.

**Funding Sources** Department of Earth and Biological Sciences at Loma Linda University.

## Fishes & Chondrichthyan: Evolution & Distribution

### A PERMIAN (ROADIAN) RAY-FINNED FISH (ACTINOPTERYGII) FROM THE MINNEKAHTA LIMESTONE OF SOUTH DAKOTA, U.S.A.

Stack, Jack, Gottfried, Michael D.

Michigan State University, East Lansing, Michigan, U.S.A.

A poor fossil record and understudy has hampered interpretation of the interrelationships of extinct Paleozoic and early Mesozoic ray-finned fishes (Actinopterygii) and their phylogenetic placement relative to modern groups. To help address this issue, we describe a ray-finned fish from the early middle Permian Minnekahta Limestone of South Dakota. This taxon is represented by two specimens, including a partial three-dimensional head and trunk (Field Museum of Natural History PF 3721). PF 3721 preserves

the external anatomy of and some internal elements from the skull, paired fins, and scale cover. We found that this taxon has features of the wastebasket ‘paleoniscoid’ lower actinopterygian group, including a maxilla with a narrow suborbital process and a broad postorbital expansion, a heterocercal caudal fin, and rhombic ganoid scales. We conducted an equally weighted maximum parsimony analysis in PAUP with 93 other taxa and 264 characters that placed this taxon in a large polytomy with other ‘paleoniscoids’ in the strict consensus tree. Although this fish bears superficial resemblance to the well-known Triassic form *Pteronisculus*, it differs from that genus in that its lacrimals do not contribute to the oral margin and in lacking antopercular elements. This well-preserved Permian actinopterygian from South Dakota provides new information on the Late Paleozoic fossil record of ray-finned fishes. Further, incorporating this taxon into broader phylogenetic analyses contributes to a better understanding of ray-finned fish relationships during a critical interval in their history.

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### **Late Cenozoic Mammalian Macroecology & Macroevolution**

#### **THE LAST OF THE OREODONTS: A REVIEW OF THE GENUS *USTATOCHOERUS* (MAMMALIA, ARTIODACTYLA, MERYCOIDODONTIDAE)**

Stevens, Margaret S.<sup>3</sup>, Prothero, Donald R.<sup>1</sup>, Htun, Thein<sup>2</sup>  
<sup>1</sup>Vertebrate Paleontology, Natural History Museum of LA County, La Crescenta, California, U.S.A., <sup>2</sup>Geological Sciences, Cal Poly Pomona, Pomona, California, U.S.A., <sup>3</sup>Earth and Space Sciences, Lamar University, Beaumont, Texas, U.S.A.

Oreodonts were a very abundant and diverse group of sheep-sized ruminant artiodactyls in North America from the late Eocene through the late Miocene. The last surviving clade of oreodonts was the subfamily Ustatochoerinae, consisting of the genera *Ustatochoerus* and *Mediochoerus*, which was the only group of oreodonts to survive after all other groups had vanished about 14.5 Ma. The taxonomy of all oreodonts has been badly confused for over a century with dozens of invalid taxa, largely due to typological oversplitting and the lack of population thinking and statistical concepts in their systematics. We recognize five valid species of *Ustatochoerus*: *U. leptoscelos* new combination from the early Arikareean of Texas; an unnamed new species from the early Hemingfordian of Nebraska; *U. medius* from the

late Barstovian, *U. major* from the Clarendonian, and *U. californicus* from the early Hemphillian, mostly from Nebraska, but also from South Dakota, Kansas, Texas, New Mexico, Montana, Nevada, and California. This lineage shows a dramatic increase in size through time, along with increased hypsodonty of their molars, molarization of premolars, flaring of the occiput, and other distinctive features. *Mediochoerus* was an extremely rare genus, known from *M. johnsoni* (early Hemingfordian) and *M. blicki* (early Barstovian) of Nebraska, and *M. mohavensis* (late Barstovian) of California. The last *Ustatochoerus* vanished about 7 Ma, about the same time as the spread of C4 grasslands, which may have favored obligate grazers with very hypsodont teeth like horses and camels, over oreodonts with their only moderately hypsodont teeth.

### **Fishes & Chondrichthyans: Evolution & Distribution**

#### **THE PECTORAL FIN OF A NEW LATE DEVONIAN ELPISTOSTEGALIAN SPECIMEN FROM ELLESMERE ISLAND**

Stewart, Thomas A.<sup>1</sup>, Lemberg, Justin B.<sup>1</sup>, Daeschler, Edward B.<sup>2</sup>, Shubin, Neil H.<sup>1</sup>

<sup>1</sup>Organismal Biology and Anatomy, The University of Chicago, Chicago, Illinois, U.S.A., <sup>2</sup>Department of Vertebrate Zoology, Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania, U.S.A.

Hypotheses of how fins evolved into limbs hinge upon our understanding of the diversity of tetrapodomorph fishes and the polarity of morphological changes within this group. The elpistostegalian *Tiktaalik roseae* has played a central role in these debates, due to its crownward position among finned tetrapodomorphs and three-dimensionally preserved articulated pectoral fins known from multiple specimens. Here we present pectoral fin materials of a new elpistostegalian specimen, NUFV 137, that was discovered during paleontological prospecting of the Fram Formation on southern Ellesmere Island, Nunavut Territory, Canada in 2004. The locality, NV0401, is slightly older than *T. roseae*, and the specimen is substantially smaller than most *T. roseae* individuals. Pectoral fin materials were discovered in two blocks by microcomputed tomography ( $\mu$ CT) scanning. One block contains a right pectoral fin and part of the pectoral girdle. The humerus is not preserved. The morphologies of the ulna and radius are similar to other non-digited tetrapodomorphs: the radius is blade-like in its geometry, and it is longer and narrower than the ulna. More distal endoskeleton, including at least three mesomeres, are also preserved, however the boundaries of these elements are difficult to demarcate in current  $\mu$ CT scans. Dermal fin rays are preserved in association with the endoskeleton of the fin. Fin rays cover the radius, and the

fin web appears to extend further beyond the endoskeleton than what has been described for *T. roseae*. The fin rays are unsegmented anteriorly and segmented posterior to the radius. The second block contains four pairs of hemitrichia that are not associated with endoskeletal elements. These rays are diagnosed as pectoral fin rays, because they exhibit a characteristic, marked dorsoventral asymmetry that was previously described in the pectoral fins of *T. roseae*. We discuss whether the materials represent a juvenile specimen of *T. roseae* or a new *Tiktaalik*-like taxon, and we explore how these alternative diagnoses impact scenarios for fin development and evolution prior to the fin-to-limb transition.

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### Bird Biology & Evolution

#### PHYLOGENETIC AFFINITIES OF NEW LATE PLIOCENE WATERBIRDS (AVES: AEQUORNITHES) FROM THE SIWALIK HILLS OF INDIA SUPPORT A PLEISTOCENE SHIFT FROM AFRICAN TO ASIAN BIOGEOGRAPHIC AFFINITIES

Stidham, Thomas<sup>1</sup>, Patnaik, Rajeev<sup>2</sup>

<sup>1</sup>Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China, <sup>2</sup>Department of Geology, Panjab University, Chandigarh, India

While fossils of birds from the Neogene deposits in the Siwalik Hills of India and Pakistan have been known for nearly 150 years, little new data on avian diversity has been reported in nearly a century. However, the new fossil discoveries from late Pliocene (~2.6–3 Ma) sites in the Tatrot Formation represent a diverse assemblage of waterbirds including pelicans (Pelecanidae), cormorants (Phalacrocoracidae), darters (Anhingidae), herons (Ardeidae), and storks (Ciconiidae). The pelican taxon uniquely shares a slanted plantar aspect of the hypotarsus with the extant *Pelecanus rufescens* from Africa. Among anhingids, the darter fossils uniquely share with the extant African *Anhinga rufa* phylogenetically derived features including a greatly enlarged medial projection of metatarsal trochlea II and a deep pit on the distal face of metatarsal trochlea IV. The distal tarsometatarsus of a small heron is one of the few Neogene fossil herons known from Asia, and likely is from a species of night heron (*Gorsachius/Nycticorax*). This small heron potentially links with the late Pliocene night heron known from Myanmar. A distal humerus representing an undescribed species of a large Old World stork (*Leptoptilos* sp.) differs from extant and known extinct species in having an autapomorphic condition with the proximal ends of the

dorsal condyle and the dorsal supracondylar ridge subequally positioned proximodistally. The small cormorant represented by a proximal tarsometatarsus with a complete hypotarsus may be the second specimen of the problematic extinct *Valenticarbo praetermissus* (known only from a cast), with their shared size and reportedly similar morphologies. The morphology of the hypotarsus does not match living species and does not clearly indicate phylogenetic affinity among particular extant species.

Prior to the invasion of India by a wave of African derived mammals at the beginning of the Pleistocene, it appears that the Pliocene waterbirds of the Siwalik Hills either had distinct biogeographic links with Africa or are extinct lineages, rather than being connected with the extant species lineages of India today. How did the current biogeographic pattern form? A broader examination, including African fossils, suggests that various individual waterbird species lineages were widespread from Africa to India in the Pliocene, and that sometime during the Pleistocene (perhaps its start), those species were replaced by the (Asian) species lineages occupying India today.

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### Mesozoic Herpetology

#### TWO SMALL CROCODYLIFORMES FROM THE MIDDLE JURASSIC LA BOCA FORMATION OF TAMAULIPAS, MEXICO

Stiegler, Josef<sup>1</sup>, Hernández-Rivera, René<sup>3</sup>, Clark, James M.<sup>2</sup>

<sup>1</sup>Dept. of Anatomical Sciences, Stony Brook University, Stony Brook, New York, U.S.A., <sup>2</sup>Dept. of Biological Sciences, The George Washington University, Washington, District of Columbia, U.S.A., <sup>3</sup>Departamento de Paleontología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Exposures of the Middle Jurassic upper member of the La Boca Formation have yielded a diverse assemblage of terrestrial vertebrates at Huizachal Canyon, Tamaulipas, Mexico, where recovered taxa include tritylodontid and mammaliaform cynodonts, sphenodontians, the burrowing diapsid *Tamaulipasaurus*, a non-pterodactyloid pterosaur, a non-tetanuran neotheropod dinosaur, and an ornithischian dinosaur. Remains of at least three new crocodyliform taxa were preserved within pyroclastic debris flows, and here we report on the anatomy of two taxa represented by small partial skulls. X-ray computed tomography failed to provide sufficient contrast for 3D imaging due to similar density of bone and matrix, so neutron tomography experiments were conducted at the NIST Center for Neutron Research. The skull of Taxon A

is missing the braincase, most of the palate, and the anterior portion of the rostrum. It may represent a juvenile individual, as much of lengths of the maxillary and dentary tooth rows lack interdental septa. The teeth are homodont and are laterally compressed with acuminate apices. The jugal and postorbital portions of the postorbital bar are both strongly inset medially, and the mandible lacks a fenestra. Taxon B is represented by a rostrum that preserves the lacrimals, maxillae and partial mandibles with complete tooth rows in each dentigerous element. The teeth are round in cross-section and have blunt apices, and there is no edentulous portion anteriorly within the mandible. Posteroventral to the small antorbital fenestra, there is a deep fossa on the jugal ramus of the maxilla. The dentaries have a buccal emargination to accommodate the maxillary tooth row. The splenial is notched anteriorly and is not involved in the short mandibular symphysis. Phylogenetic analyses show that Taxon B is the sister taxon of *Platyognathus hsui* from the Lower Jurassic Lufeng Formation of Yunnan, China. The position of Taxon A is more difficult to resolve, but preliminary results suggest it may be a stem metasuchian.

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### Mesozoic Herpetology

#### SKELETALLY IMMATURE PLESIOSAURS FROM A MARINE REPTILE BONEBED FROM THE UPPER CRETACEOUS OF SASKATCHEWAN, CANADA

Street, Hallie P., Bamforth, Emily L.  
T. rex Discovery Centre, Royal Saskatchewan Museum,  
Eastend, Saskatchewan, Canada

An Upper Cretaceous bonebed from the Campanian Dinosaur Park–Bearpaw transition, exposed in western Saskatchewan, is a rare example of a marine reptile dominated assemblage. Among the invertebrate ichnofossils and the micro- to macrovertebrate material, isolated plesiosaur elements are the most common fossils from this site. This assemblage is also significant due to the abundant juvenile plesiosaur fossils that have been recovered. Plesiosaur skeletal elements are identified as coming from juvenile individuals by incomplete ossification (e.g., girdle and limb elements with remaining cartilaginous contributions and undifferentiated joint surfaces) and by incomplete fusion (e.g., developmentally distinct regions of bones remaining separate, such as vertebral centra and neural arches). Numerous examples of vertebral and propodial fossils from this bonebed display these and other markers of skeletal immaturity. The skeletally mature plesiosaur elements from the bonebed are referable to Elasmosauridae and Polycotylidae, and those

juvenile fossils that exhibit diagnostic features are also assignable to these two families. The osteologically immature propodials range in size and degree of ossification, which allows for interpretations of how the area was inhabited by plesiosaurs. If only very young and fully mature elements were recovered from the bonebed, it would suggest that the region served exclusively as a birthing ground. Considering that individuals representing different stages of development lived and died in the region, it is possible the area served as a refuge where the young plesiosaurs could stay as they grew, with or without parental care. Other assemblages of juvenile plesiosaur fossils have been reported from high-latitude sites associated with high marine productivity in both the Northern and Southern Hemispheres. Although this bonebed formed at a slightly lower paleolatitude, its lagoonal depositional setting would also likely have supported high productivity, which could have attracted and supported the plesiosaurs that inhabited the area.

### Evolution & Biology of Non-Avian Theropods

#### CAENAGNATHID (THEROPODA: OVIRAPTOROSAURIA) DINOSAUR SPECIMENS FROM THE UPPER CRETACEOUS WAPITI FORMATION OF NORTHERN ALBERTA

Sullivan, Corwin<sup>1</sup>, Bell, Phil R.<sup>3</sup>, Campione, Nicolás E.<sup>3</sup>, Sissons, Robin<sup>1</sup>, Fanti, Federico<sup>4</sup>, Larson, Derek W.<sup>2</sup>, Vavrek, Matthew J.<sup>6</sup>, Funston, Gregory F.<sup>5</sup>

<sup>1</sup>University of Alberta, Edmonton, Alberta, Canada, <sup>2</sup>Philip J. Currie Dinosaur Museum, Wembley, Alberta, Canada, <sup>3</sup>University of New England, Armidale, New South Wales, Australia, <sup>4</sup>Alma Mater Studiorum – Università di Bologna, Bologna, Italy, <sup>5</sup>University of Edinburgh, Edinburgh, U.K., <sup>6</sup>Royal Ontario Museum, Toronto, Ontario, Canada

Caenagnathid oviraptorosaurs are rare, somewhat enigmatic elements of faunas from the Upper Cretaceous of Asia and North America. In southern Alberta, the upper Campanian Dinosaur Park Formation has yielded three caenagnathids: *Leptorhynchus elegans*, *Chirosstenotes pergracilis*, and *Caenagnathus collinsi*, whereas the Campanian-Maastrichtian Horseshoe Canyon Formation has yielded *Epichirostenotes curriei* and *Apatoraptor pennatus*. The units are separated by the transgressive, marine Bearpaw Formation.

The Wapiti Formation of northern Alberta preserves a continuous terrestrial record roughly time-equivalent to the Dinosaur Park, Bearpaw and Horseshoe Canyon formations. The DC Bonebed is a rich Wapiti Formation locality near Grande Prairie, and is roughly

contemporaneous with the complex transition between the Bearpaw and Horseshoe Canyon formations. This site preserves disarticulated bones and teeth from fish and small to medium-sized dinosaurs, including a caenagnathid pubis, ilium, and fused dentary. The dentary is very small, with a symphyseal length of ~14 mm, whereas the pubis and ilium are proportionally larger. The dentary is potentially the most diagnostic of these specimens. In *Epichirostenotes* and *Apatosauraptor*, the dentary is unknown or poorly known, so informative comparisons are not possible. Among Dinosaur Park Formation taxa, the DC caenagnathid dentary is most similar in size and proportions to the relatively small *Leptorhynchos*, but more closely resembles *Chirostenotes* in lacking well-developed anterior symphyseal ridges and having a distinct facet for articulation with the articular-surangular-coronoid complex. However, the dentary differs from specimens of *Chirostenotes* in having only two lateral occlusal grooves on each side, and in the relative shortness of the symphysis. The identification of the DC caenagnathid material remains unclear, particularly given its geographic and stratigraphic provenance. If the specimens indeed pertain to *Chirostenotes*, the dentary must represent a juvenile, and the length of the symphyseal area and number of lateral occlusal grooves must have increased during growth. The DC material represents the northernmost known occurrence of any caenagnathid, and the presence of three caenagnathid bones among >200 identifiable bones and teeth from the DC Bonebed is sufficient to suggest that the fauna may have been richer in caenagnathids than is typical for Upper Cretaceous North American assemblages.

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## Quantitative Methods

### PALEO-PATHOPHYSIOLOGY: A MULTIDISCIPLINARY-BASED DIG DEEP INTO FOSSIL BONE

Surmik, Dawid<sup>1</sup>, Rothschild, Bruce M.<sup>2</sup>, Szczygielski, Tomasz<sup>3</sup>, Zubko, Maciej<sup>4</sup>, Dulski, Mateusz<sup>5</sup>, Wojtyniak, Marcin<sup>5</sup>, Duda, Piotr<sup>4</sup>

<sup>1</sup>Faculty of Natural Sciences, University of Silesia, Sosnowiec, Silesia, Poland, <sup>2</sup>Carnegie Museum, Pittsburgh, Pennsylvania, U.S.A., <sup>3</sup>Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland, <sup>4</sup>Faculty of Exact and Technical Sciences, University of Silesia, Katowice, Poland, <sup>5</sup>Silesian Centre for Education and Interdisciplinary Research, Chorzów, Poland

Modern-day paleontological research goes beyond the conventional meaning of paleontology, reaching more

distant fields of knowledge including, but not limited to, materials science and nanomechanics. Osteopathologies in the fossil record are one of such themes amenable to multidisciplinary approaches.

One research hypothesis is that the fossilized bone tissue can still contain the original biological signal associated with ongoing pathological processes and that taphonomic processes and diagenesis often have not completely erased genuine features associated with ancient diseases. Our multidisciplinary approach included utilization of atomic force microscopy (AFM), Raman, infrared (FTIR) and X-ray photoelectron (XPS) spectroscopies and selected area electron diffraction (SAED) patterns, as revealed by transmitted electron microscopy (TEM). Heterogeneity of phosphate phases associated with tissue response to pathogenic factors (trauma, infection, tumors) and pathways of cell proliferation was assessed.

TEM studies revealed that mineralized bone is composed of nanometer-size polycrystalline materials. Based on the recorded SEAD patterns, the material was attributed to the apatite crystal phases. However, an apatite of infection-related pathologically-altered bone is characterized by a lower crystallinity rate and an increase of structural distortion with higher hydroxyl moiety incorporation, suggesting a role of the hydroxyl radicals in the infectious process. Increased structural vacancies in calcium phosphate due to the removal of carbonate groups and fluorine ions were inferred. Nanomechanical studies of the cross-section of the neoplasm-affected fossilized bone tissue and calcified cartilage regions reveal that Young's modulus values are within the range typical for bones of modern vertebrates. The lower Young's modulus values of the lamellar bone (12–38 GPa) in contrast with higher values of the calcified cartilage (40–90 GPa) in the thin sections may result from the anisotropic organization of the apatite crystallites in the bone lamellae, in contrast to an unordered, isotropic organization in the cartilage.

Obtained results provide pathophysiological insights into the natural history of diseases and interactions between the pathogens and their hosts. The developmental abnormalities and maladies have the potential of bringing unique data about the normal development of ancient animals, their locomotion, feeding, and how they functioned in their environment.

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## Mesozoic Herpetology

### A TOUGH TURTLE – HEALED DAMAGE ON A MONGOLEMYS SHELL FROM THE LATE CRETACEOUS OF MONGOLIA

Szczygielski, Tomasz<sup>1</sup>, Surmik, Dawid<sup>2</sup>

<sup>1</sup>Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland, <sup>2</sup>Faculty of Natural Sciences, University of Silesia, Sosnowiec, Poland

ZPAL MgCh/77, an undescribed specimen of *Mongolemys elegans* from Tsagaan Khushuu (Upper Cretaceous of Mongolia), exhibits a unique pattern of damage on its shell. On the carapace the bone surface in the region to the left of the second and third vertebral scute as well as a small patch to the right of the third vertebral scute loses its normal fine-scale texture and instead shows some small pitting and wrinkling, most notably around the interscutal sulci. The sulci themselves lose clarity in the affected region and their layout seems to be slightly deformed, compared to the unaffected side of the specimen. The areas of the first and the last left pleural scute show probable bite marks located outside of the malformed area. While localized malformation of the sulci alone could result from a predator attack damaging the cornifying layer of the skin, the modification of the bone surface is too extensive to be explained solely by that. The possible origin of the scars may thus include epibionts, skin diseases, or mild burn damage caused by wildfires. The bone shows signs of healing proving that the event was not lethal. On the plastron some probable bite marks and minor shell rot damage is identifiable, but no surface modification is involved and the bone retains its normal microsculpture. The specimen preserves the skull, right hindlimb (including the articulated metatarsal region), and articulated base of the tail. The skull and limb are relocated outside of the carapacial rim, but the articulated state of most of the bones in the limb and the tail indicates that the post-mortem transport was very limited and the burial happened soon after death. This also suggests that the predation was not the cause of death of the individual and apparently it was not scavenged. This is the only occurrence of such a morphology in over a hundred specimens of the Cretaceous-Neogene Mongolian turtles housed in the collection of the Institute of Paleobiology, Polish Academy of Sciences (ZPAL).

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### Macroecology & Macroevolution

#### RAPTOR EVOLUTION IN RESPONSE TO MEGAFUNAL EXTINCTION

Takano, Oona M.  
Biology, University of New Mexico, Albuquerque, New Mexico, U.S.A.

The Quaternary extinctions in North America 50,000–11,700 years ago marked the decline of the Pleistocene

megafauna. Compared to mammals, the effects of these extinctions have been poorly studied in birds. These mammal extinctions likely caused changes in raptor diets because of reduced competition with other carnivores, leading to modern raptors becoming apex predators. I investigated raptor evolution since the Pleistocene and how morphological changes relate to shifts in dietary niche. For raptors, toe size and shape are important traits determining the type of prey captured. The La Brea Tar Pits in California have yielded thousands of raptor fossils, spanning Pleistocene glacial periods to the warmer Holocene. I compared foot morphology of two raptor species from La Brea, Golden Eagles (*Aquila chrysaetos*) and Bald Eagles (*Haliaeetus leucocephalus*), which have persisted from the Pleistocene to the present. Four toe elements of both species were measured from ~500 Pleistocene fossils and modern skeletons using digital calipers. Geometric morphometric analyses of talon shape were conducted using *geomorph* in R. Changes in Golden Eagle toe morphology indicate an increase in size in modern birds, while Bald Eagle toes have remained the same size and shape since the Pleistocene. Examining changes in raptor niches provides insights on individual species' evolutionary responses when dominant predators are removed.

**Funding Sources** American Ornithological Society, UCMP Welles Fund, Los Angeles County NHM, UNM Biology Department, UNM Biology Graduate Student Association.

### Romer Prize

#### EVOLUTIONARY HISTORY OF ARCHOSAUR GASTROLITH USES

Takasaki, Ryuji  
Hokkaido University, Sapporo, Hokkaido, Japan

Gastroliths are commonly present within archosaurs (crocodylans and dinosaurs), but an evolutionary appreciation of these stones is poorly understood. Goals of this study are; to provide anatomical comparisons of archosaur stomachs, to examine how diet affects the shape of chicken gastroliths, to examine the relationship between diet and gastrolith shape in extant archosaurs, and to apply these results to extinct archosaurs to understand the evolution of gastrolith use in archosaurs.

Stomach comparisons of 117 extant archosaur taxa reveal five stomach morphotypes. Histological comparisons further demonstrate that 'gizzards' in birds and crocodylans are not homologous. However, correlations between body mass and gastrolith mass and between gastrolith occurrence frequency and diet type suggest gastroliths in archosaurs support gastric mechanical digestion.

An experiment using 68 domestic chickens shows that chickens actively ingest sharp stones regardless of diet. With time and use gastrolith shapes reflect diet types (less sharp in herbivorous diet) due to gastric abrasion in the gizzard. This is pattern was consistent with changes in diet from herbivory to carnivory, or vice versa, during the experiment, suggesting gastrolith shapes even reflect short-term diets.

Discriminant analyses on quantitative and qualitative data on gastrolith shapes of 46 extant archosaur taxa show differentiation in the respective diets of these taxa (invertebrates, vertebrates, omnivore, and plant+seed) in a maximum of 78% accuracy. Application of this discriminant analysis to 17 extinct dinosaur taxa demonstrates (1) that basal ornithischians, a sauropod, a tyrannosaurid, and semi-aquatic Mesozoic birds have gastroliths similar to carnivorous extant archosaurs, (2) that ornithomimosaur, an oviraptorosaur, and seed-eating Mesozoic birds have gastroliths similar to plant+seed eating extant archosaurs, and (3) that a ceratosaur has gastroliths similar to carnivorous and omnivorous extant archosaurs. The inferred diets from this analysis are consistent with osteological features in all taxa except non-theropod dinosaurs (basal ornithischians and a sauropod). These results suggest that gastrolith shapes can be used as a proxy for theropod diets but not for other dinosaurs, which may have other digestive attributes that play significant roles such as oral mastication and bacterial gastric fermentation, and that bird-like gastrolith use evolved in the lineage of Theropoda.

**Funding Sources** Grant-in-Aid for JSPS Research Fellow (Grant Number 17J06410).

## Evolution & Biology of Non-Avian Theropods

### A LARGE NEOVENATORID (DINOSAURIA: THEROPODA) FROM THE UPPER CRETACEOUS BISSEKTY FORMATION (TURONIAN), UZBEKISTAN

Tanaka, Kohei<sup>1</sup>, Anvarov, Otabek U.<sup>1</sup>, Ahmedshaev, Akhmadjon<sup>2</sup>, Kobayashi, Yoshitsugu<sup>3</sup>

<sup>1</sup>Life and Environmental Sciences, University of Tsukuba, Tsukuba, Ibaraki, Japan, <sup>2</sup>State Geological Museum of the State Committee of the Republic of Uzbekistan on Geology and Mineral Resources, Tashkent, Uzbekistan, <sup>3</sup>Hokkaido University Museum, Hokkaido University, Sapporo, Hokkaido, Japan

Neovenatoridae is a group of medium to large-sized predatory theropods, distributed worldwide during the Cretaceous. Previous studies suggested that neovenatorids and other large-bodied theropods (Ceratosauridae, Carcharodontosauridae, and Spinosauridae) were apex predators in Laurasia until tyrannosauroids occupied top

predatory niches in the last 20 million years of the Late Cretaceous, implying that the evolution of gigantism of tyrannosauroids is likely influenced by the presence of these large theropods. Nevertheless, co-occurrences of small tyrannosauroids and large neovenatorids are scarcely known, with only two cases in the Early Cretaceous (Barremian) of the U.K. and the mid-Cretaceous (Cenomanian) of the U.S.A. Here we report on a new specimen of a large neovenatorid, represented by an isolated maxilla, from the Upper Cretaceous (Turonian) Bissekty Formation of the Kyzylkum Desert, the Republic of Uzbekistan, where the small tyrannosauroid *Timurlengia* has been previously reported.

This new specimen preserves a main body of the left maxilla (24.2 x 13.1 cm), missing the ascending ramus and posterior half of the jugal ramus. Our phylogenetic analysis places it within Neovenatoridae, although the interrelationships within the family shows a polytomy. The size and general morphology of the maxilla are similar to those of *Neovenator*, but it shows some unique features (e.g., a series of shallow depressions, which become larger posteriorly, near the ventral edge; prominences on the ridged rim of the antorbital fossa; vertically-oriented ridges on the lateral surface; and large foramina at a dorsal edge of dental plates), indicative of a new taxon.

The size of the maxilla is two folds of that of sympatric *Timurlengia*, suggesting this Uzbekistan neovenatorid is so far the largest predatory theropod in the Bissekty Formation. This study provides rare evidence of a large Neovenatoridae coexisting with a small tyrannosauroid in the Central Asia as seen in other areas (Europe and North America) in Laurasia and supports the hypothesis that tyrannosauroids were marginal predators until they achieved large body size.

**Funding Sources** Short-Term Overseas Travel Grant Program FY2019 at the University of Tsukuba, Japan.

## Mammalian Skeletal Morphology

### THE COEVOLUTION (OR LACK THEREOF) OF BODY MASS AND LOCOMOTION IN RODENTS

Tantash, Anas M., Calede, Jonathan  
The Ohio State University, Westerville, Ohio, U.S.A.

Forty percent of living mammal species in the world are rodents. In addition to this incredible species diversity, rodents also exhibit immense morphological variation. The smallest rodents are only a few grams while the largest rodent on the planet, the capybara, weighs over 60 kilograms. Fossil rodents expand the range of body sizes to extremes not observed today; for example, the giant beaver of North America, *Castoroides*. Rodents also display great diversity in the way they move around the landscape. Some rodents are burrowers, some live in trees, some can jump

incredible distances, others can swim, glide, or run. Although the nature of physics and physiology suggest that there are constraints on the size of rodents associated with their locomotion, this hypothesis remains largely untested. We investigated the relationship between body mass and locomotion in rodents and quantified their possible co-evolution.

We used species means reported in the literature to investigate differences in body mass across locomotory categories (including arboreal, semi-aquatic, ricochetal, fossorial, terrestrial, semi-fossorial, gliding, and cursorial species). Our dataset ranges in body mass from 6.43 grams to 47,500 grams and contains 842 species of rodents including 38 fossil species from North America. The results of our analyses show that cursorial rodents have the highest mean body mass of any locomotory category (over 4,600 g) and ricochetal rodents have the lowest mean body mass (~250 g). The latter are not significantly different from terrestrial rodents; both groups are significantly smaller than all other locomotory categories. The comparison of variance shows that arboreal rodents have a significantly higher variance than cursorial, fossorial, ricochetal, and terrestrial rodents. Cursorial rodents occupy a significantly narrower range of body size compared to other locomotory modes. A phylogenetic ANOVA run on 755 of the extant species in the dataset suggests that there are no significant differences in mean body size among locomotory modes when considering phylogenetic relationships. Instead, our current results suggest an important role of phylogenetic conservatism.

### Symposium: Dietary Reconstruction

#### MAGNESIUM STABLE ISOTOPE RATIOS OF EAST AFRICAN LARGE MAMMALS

Tarng, Cheng<sup>1</sup>, Hu, Lihai<sup>2</sup>, Mwebi, Ogeto<sup>3</sup>, Cerling, Thure E.<sup>1</sup>, Fernandez, Diego<sup>1</sup>

<sup>1</sup>Geology and Geophysics, University of Utah, Salt Lake City, Utah, U.S.A., <sup>2</sup>Earth Sciences, University of Ottawa, Ottawa, Ontario, Canada, <sup>3</sup>Zoology, National Museums of Kenya, Nairobi, Kenya

Over the past several decades, stable isotopes of various elements preserved in fossil enamel have provided quantitative insights into past terrestrial ecological structures. Recent developments in metal isotope geochemistry called for exploration of non-traditional isotopic systems for paleoecological applications, among which a multi-proxy approach was proposed. Following earlier research performed by Jeremy Martin and colleagues, we report on a modern calibration of magnesium isotopic systematics with large mammalian faunas of two East African savanna ecosystems. The results of our survey show distinctive isotopic signals between carnivores and non-ruminant herbivores but are

independent of parent bedrock lithology. However, ruminant grazers are found to have significantly higher magnesium isotopic ratios than ruminant browsers and non-ruminant herbivores. In sum, these findings highlight the capability and limitations of magnesium isotopes in enamel hydroxyapatite; they offer promising insights for multi-proxy interpretations of past ecological systems.

### Mammalian Skeletal Morphology

#### THE EVOLUTION OF LOCOMOTOR ECOLOGY IN BASAL ODOBENIDS (MAMMALIA, CARNIVORA)

Tate-Jones, Kellum

University of Oregon, Eugene, Oregon, U.S.A.

Each of the three modern pinniped families displays a different mode of swimming. True seals and eared seals employ hindlimb and forelimb propulsion, respectively. Conversely, the modern walrus *Odobenus rosmarus* (the sole living member of family Odobenidae) swims with a combination of both hind and front flippers. As *O. rosmarus* displays a highly derived morphology in comparison to many fossil walruses, the ancestral swimming mode of Odobenidae remains unclear. Basal odobenids such as *Proneotherium repenningi*, *Pelagiarctos* sp., *Prototaria planicephala*, and *Imagotaria downsi* are especially enigmatic. Known primarily from skulls, these early walruses appear more superficially similar to their sister taxon the Otariidae, or eared seals, than to the highly adapted odobenine walruses like *O. rosmarus*. This resemblance has led previous workers to speculate that these early odobenids occupied a similar ecological niche to modern otariids. Lack of investigation into basal odobenid locomotor ecology has, however, precluded the testing of this hypothesis. To remedy this knowledge gap, I first collected 13 landmarks corresponding to cranial attachment sites for locomotor muscles from 22 species of modern marine carnivorans and six species of fossil pinnipeds, including the basal odobenids *Proneotherium repenningi* and *Imagotaria downsi*. These data were then used to construct a canonical variates analysis (CVA) distinguishing between the three swimming modes: hindlimb-propelled (cross-validated classification rate 94.3% correct), forelimb-propelled (100%), and intermediate (90%). Surprisingly, both *P. repenningi* and *I. downsi* were returned as intermediate swimmers despite their superficial resemblance to otariids. Such results support the apomorphy of this intermediate swimming mode in Odobenidae while illustrating that ecological equivalence cannot be assumed from comparative morphology alone.

**Funding Sources** University of Oregon Department of Earth Science, Geological Society of America Graduate Student Research Grant.

### **Anatomical & Developmental Explorations of the Mammalian Skull**

#### **PETROSAL MORPHOLOGY OF THE BASAL PROTOCERATID *LEPTOREODON***

Theodor, Jessica<sup>1</sup>, Robson, Selina V.<sup>1</sup>, Ludtke, Joshua A.<sup>2</sup>  
<sup>1</sup>Biological Sciences, University of Calgary, Calgary, Alberta, Canada, <sup>2</sup>Biological Sciences, MiraCosta College, Oceanside, California, U.S.A.

The record of the Protoceratidae, a family of North American artiodactyls, spans from the middle Eocene to the early Pliocene. The family has been placed within both the Tylopoda and the Ruminantia by varying authors. The petrosal morphology of protoceratids has been described from broken skulls of the basal form *Leptotragulus*, and from computed tomography (CT) data for *Protoceras* and the highly derived *Syndyoceras*. The petrosal morphology of these taxa is more similar to that of ruminants than to that of camelids.

CT scans of another basal protoceratid, *Leptoreodon*, reveal a petrosal morphology that is somewhat intermediate. While many morphological features are shared with other protoceratids, *Leptoreodon* shows a mosaic of derived and ancestral features, such as a deep subarcuate fossa. On the endocranial surface, as in other protoceratids, the subarcuate fossa has a raised caudal border that creates a ridge separating the cerebral and cerebellar space, though this ridge is not as pronounced as in *Leptotragulus*. The internal acoustic meatus (IAM) and subarcuate fossa are subequal in size, and the crista transversa is located within the IAM. On the tympanic face, the promontorium is poorly preserved; the fenestra cochleae is round and caudally oriented, and the smaller, ovate fenestra vestibuli faces laterally. The petrosal lacks a rostral tympanic process, which differs from *Leptotragulus*. The tegmen tympani is triangular in outline. The basicapsular groove is ventrally oriented and entirely on the petrosal. The cochlear aqueduct is visible on the caudal side, oriented ventrally. The mastoid region is small and wedge-shaped.

**Funding Sources** NSERC Discovery Grant to JMT.

### **Permo-Triassic Tetrapods**

#### **SEGMENTED MICRO-CT SCANS OF 3D, ARTICULATED DREPANOSAURID FORELIMBS FROM THE SAINTS AND SINNERS (SS) QUARRY (UPPER TRIASSIC, NUGGET SANDSTONE, NORTHEASTERN UTAH) PROVIDE**

#### **INFORMATION ON THE UNUSUALLY CONSTRUCTED ARM AND HAND**

Theurer, Brandon C.<sup>1</sup>, Britt, Brooks B.<sup>1</sup>, Chure, Dan<sup>2</sup>, Engelmann, George F.<sup>3</sup>, Scheetz, Rod D.<sup>1</sup>, Jackson, Alexa<sup>1</sup>  
<sup>1</sup>Geology, Brigham Young University, Provo, Utah, U.S.A., <sup>2</sup>Retired, Jensen, Utah, U.S.A., <sup>3</sup>Geology, University of Nebraska, Omaha, Omaha, Nebraska, U.S.A.

Six 3D, uncrushed, articulated forelimbs provide valuable insights into the nature of the drepanosaurid forelimb and allow a detailed description of the bizarre manus of this clade. As with other derived drepanosaurids, the pectoral girdle is co-ossified and the forearm consists of four elements. In the SS taxon, the distal end of the scapula articulates with a cotyle on the elongated and expanded neural spine of an anterior dorsal vertebra. Medial carpals, along with metacarpal 1, are fused into an L-shaped complex, locking proximal motion of digit I with the wrist. Dorsolaterally, a proximal condyle of the 'L' articulates with a deep cotyle of the radius while the medial extension of the L (carpal 2) articulates with a laterally wide, proximal phalanx of digit II, which is perforated distally by a large dorsoventral canal. The phalangeal formula is 2-2-2-2-2. The articulated arms and digits on one individual are extended straight, slightly supinated, and the forelimbs closely appressed from the elbows through the hands, with the blade-like ulnae extended backward at 45 degrees to the body's transverse plane. In other specimens, the metacarpophalangeal joints are extended and interphalangeal joints hyperflexed, with the most extreme extension/flexion on hypertrophied digit II and to a lesser extent digit I, indicating a wide range of motion by these elements. Digit I is reduced, with its needle-like ungual moderately recurved and an elongate, ventromedially-facing flexor fossa occupying half the ungual's length. This fossa indicates the element pulled medioventrally and the needle-like shape suggests a piercing or perhaps grooming function.

Ungual II morphology changes substantially with ontogeny. In lateral view, in juveniles (determined by size), it is large but relatively straight. It becomes increasingly recurved and ultimately semicircular with age. One small individual shows substantial size disparity between left and right unguis II. Thus morphology is unreliable as a diagnostic trait for this element, except in adults.

While the manus of most drepanosaurs are interpreted as adapted to grasping, the manus of the SS taxon, like other advanced drepanosaurids, is better adapted to scratch digging, an interpretation supported by the high bracing of the scapula against the vertebral column. The small, specialized digit I, however, is ill-adapted to digging and likely served a specialized function.

### **Quantitative Methods**

## CROSS-POLARIZATION AND SECOND HARMONIC GENERATION IMAGING REVEAL BONE COLLAGEN DECAY PATTERNS IN FOUR FOSSILS

Thomas, Brian<sup>1</sup>, Taylor, Stephen<sup>1</sup>, Solliday, James<sup>2</sup>

<sup>1</sup>Electrical Engineering and Electronics, University of Liverpool, Glenn Heights, Texas, U.S.A., <sup>2</sup>Microscopical Society of Southern California, Los Angeles, California, U.S.A.

Experimentally measured protein decay kinetics imply a much shorter shelf-life than standard fossil ages permit. In spite of this, there is a steady stream of publications showing morphological and molecular evidence of protein remnants in fossils across geologic time and geographic space. This incongruity in timing remains unresolved. New approaches are needed to reveal biochemical decay patterns relevant to this research question.

A polarizing microscope equipped with a first order red retardation plate (XPOL) reveals birefringent regions such as collagenous structure within bone. Second harmonic generation imaging (SHG) uses a laser scanning confocal microscope to target structural proteins including collagen. Our previous research demonstrated that SHG visualises in situ collagen within archaeological bone. It offers an independent verification of collagen remnants suggested by XPOL micrographs.

We present new spongy bone thin section images from four different taxa of extinct reptile from three different geologic Systems. XPOL images were collected from a Cretaceous *Edmontosaurus annectens*, a Jurassic plesiosaur, a Permian *Diadectes* sp., and a Permian *Eryops megacephalus*. Images of modern bone (*H. sapiens*) were obtained as controls.

Images revealed permineralization mixed with highly fragmented bone. Some regions morphologically resembled intact bone but showed no optical evidence of bone collagen. However, rarely encountered microscopic patches inside morphological bone contained apparently collagenous remnants. XPOL images showed apparent bone collagen patches in *Edmontosaurus*, *Plesiosaurus*, *Diadectes*, and *Eryops*. Both XPOL and SHG images showed apparent bone collagen patches in *Eryops*. Results showed no stratigraphic or taxonomic preservational biases in these few specimens. The patchy shapes, often surrounded by rotting and permineralized bone, suggest a diagenesis whereby collagen retreats into ever-shrinking microscopic patches until it vanishes.

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### Quantitative Methods

## A NEW METHODOLOGICAL FRAMEWORK FOR ACCURATELY INFERRING AMNIOTE CLAW FUNCTION USING MULTIPLE MORPHOLOGICAL METRICS AND FUNCTIONALLY BASED CATEGORIES

Thomson, Tracy J.

Earth and Physical Sciences, University of California, Davis, Davis, California, U.S.A.

Claws are important for understanding animal ecology because they function at direct points of contact between the animal and its environment. But the link between claw form and function has been historically difficult to quantify, analyze and interpret. Previous studies have been hampered by various confounding factors. Focus is placed on claw curvature, while other aspects of morphology are mostly ignored. Either the unguis or sheath is considered but both structures are rarely analyzed together. Finally, specimens are assigned to categories based on ecology/life habit rather than mechanical function. Is there a method that would allow claw function to be inferred from morphology with high accuracy? If so, the ecology of fossil amniotes could be understood more clearly.

I investigated relationships between claw form and function through a detailed inspection of 80 modern bird and mammal claw specimens. These were assigned to one of 8 new, functionally based categories after an extensive review of direct observations recorded in the literature. 20 morphological metrics of the whole claw (9 from the sheath, 11 from the unguis) with biomechanical relevance were measured and analyzed using principle component (PCA) and linear discriminant (LDA) analyses. PCA shows that the sheath is morphologically more disparate than the unguis. However, a small portion of the morphospace covered by the unguis is not overlapped by the sheath, indicating that the unguis contains morphological information not captured by the sheath. Sheath measurements do a slightly better job at correctly predicting claw function than unguis measurements in LDA. However, using both structures decreases the misclassification rate by more than half, allowing claw function to be correctly predicted from morphology with a success rate around 90%.

I applied this approach to 10 claws (six pes, four manus) from three *Archaeopteryx* specimens. Whether this genus was primarily arboreal or terrestrial is a controversial subject. None of the claws overlap in morphospace with claws used by modern animals for running; they overlap with claws used for grasping, climbing, and generalist functions. LDA classifies the claws as either climbing, generalist, or grasping. This suggests *Archaeopteryx* was not a runner but a tree climber/generalist. This methodological framework can be applied to other fossil organisms as well, opening a new way to better understand

the paleoecologic and evolutionary contexts of claw function.

### Fishes & Chondrichthyans: Evolution & Distribution

#### A NEW CLADOSELACHID CHONDRICHTHYAN FROM THE FAMENNIAN OF MOROCCO

Torres Ladeira, Marta S.<sup>1</sup>, Frey, Linda<sup>1</sup>, Coates, Michael I.<sup>2</sup>, Ginter, Michal<sup>3</sup>, Klug, Christian<sup>1</sup>

<sup>1</sup>Paläontologisches Institut und Museum, University of Zurich, Zurich, Switzerland, <sup>2</sup>Department of Organismal Biology and Anatomy, University of Chicago, Chicago, Illinois, U.S.A., <sup>3</sup>University of Warsaw, Warsaw, Poland

*Cladoselache* is probably the best studied genus of Devonian chondrichthyans, sometimes displaying exceptional preservation both in the Cleveland Shale of Ohio and in the Famennian shales of Morocco. From the desert of the Moroccan Anti-Atlas (southern part of Maïder Basin), we present new materials of a similar chondrichthyan. This locality is world-renowned for its excellent outcrops and large numbers of well-preserved fossils, especially in the eastern Anti-Atlas. The new chondrichthyan material presented here belongs to a new taxon of Devonian symmoriid chondrichthyans, which were found in the early middle Famennian Thylacocephalan Layer. They co-occur with other chondrichthyans such as *Phoebodus* and cladodonts as well as placoderms and rare osteichthyans. The most abundant macrofossils, however, are carapaces of the eponymic thylacocephalans. The red coloration of the sediment derives from altered pyrite and is interpreted as reflecting poorly oxygenated conditions of the bottom waters in the Maïder Basin. Chondrichthyans originated in the Silurian, but the divergence of elasmobranchs and holocephalans happened during the Devonian. Since *Cladoselache* is among the oldest known symmoriid chondrichthyan (stem holocephalans), the Moroccan material represents an important discovery. Also from the Late Devonian, they bear striking similarities to this well-studied genus particularly in the swimming apparatus, the general shape of the skull, and relative body size. However, particular characters suggest a new group of symmoriid (Paleozoic stem holocephalans). The chondrichthyans considered here measure between 1 and 2 m in length and are exceptionally preserved including cartilage, muscles, liver remains, skin denticles, and stomach contents. The caudal part is more rarely preserved and all specimens are dorsoventrally or laterally compacted. The body proportions resemble those of other symmoriids, such as *Cobelodus* and *Symmorium*; the dentition is cladodont and the overall morphology of the body is close to that of *Cladoselache*. Amongst other particular characters, the presence of a single, posterior dorsal fin, absence of an extension of the anterior dorsal

fin, the 'Y'-shaped pelvic plate, and the large size of the scapulocoracoid makes these specimens worthy of their own taxon.

### Mesozoic & Early Cenozoic Mammalian Evolution

#### SEARCH FOR THE LAST EOCENE HYPERTHERMAL IN THE UINTA BASIN, UTAH, U.S.A.

Higgins, Penny<sup>2</sup>, Townsend, Kathryn E. B.<sup>1</sup>

<sup>1</sup>Anatomy, Midwestern University, Glendale, Arizona, U.S.A., <sup>2</sup>EPOCH Isotopes, Williamson, New York, U.S.A.

The Middle Eocene Climatic Optimum (MECO) was a global warming event the onset of which fell between 41.5 and 40 Ma. Marked by an increase of global sea surface temperatures by ~4°C and North American continental temperatures by ~9°C, it is considered one of the more significant global warming events of the Cenozoic due to its abruptness and magnitude of temperature increase. The MECO was first observed in the Southern Ocean and more recently discovered in a terrestrial sequence in Montana bracketing the boundary between the Uintan and Duchesnean North American Land Mammal 'Ages' (NALMAs).

The Uintan–Duchesnean boundary is broadly exposed in the Uinta Basin of Utah, where the type faunas for both the Uintan and Duchesnean NALMAs are also found. Based upon the known timing of the onset of the MECO, and the distribution of fossil mammals in the Uinta Basin, the MECO is expected to begin within the Duchesne River Formation (DRF), which ranges in age from ~42–38 Ma. Unpublished radiometric dates indicate the 41.5–40 Ma interval would lie somewhere between the Brennan Basin (Tdb) and Dry Gulch Creek (Tdd) members of the DRF.

During the summer of 2019, carbonate-bearing rocks were sampled bracketing the boundaries between all three members of the DRF, Tdb, Tdd, and the Lapoint member (Tdl) and were analyzed for isotopes of carbon and oxygen. Results show an increase in values of  $\delta^{18}\text{O}$  within the Tdd member compared to those from the Tdb and Tdl. Our data suggests that the MECO is preserved within the DRF and begins at or near the boundary between the Brennan Basin and Dry Gulch Creek members as predicted. We consider these results as preliminary evidence of the MECO event recorded in the Uinta Basin that warrant further research, both in terms of geochemical analysis and detailed study of effects of the MECO on vertebrate faunas.

At the Uintan–Duchesnean boundary there is a documented loss of 25% of mammalian genera, mainly small mammals, representing the most significant extinction since the end-Cretaceous. This is in direct opposition to the diversity patterns of the earlier Paleocene–Eocene Thermal Maximum (PETM) and early Eocene climatic optimum (EECO), wherein mammalian diversity increased in

association with (and likely in response to) hyperthermal events. As we confirm the presence of the MECO in the Uinta Basin, we will also evaluate faunal response to the last Eocene hyperthermal.

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### Biomechanics & Functional Morphology

#### THE CARTILAGINOUS HIPS OF DIPLODOCOIDEA: FUNCTIONAL IMPLICATIONS FOR HIGHLY SPECIALIZED LOCOMOTOR BEHAVIORS AMONG SAUROPODS

Tsai, Henry P.<sup>1</sup>, Griffin, Christopher<sup>2</sup>

<sup>1</sup>Biomedical Sciences, Missouri State University, Springfield, Missouri, U.S.A., <sup>2</sup>Department of Geosciences, Virginia Tech, Blacksburg, Virginia, U.S.A.

Sauropods are characterized by exceptionally massive body size and highly derived appendicular morphologies. However, the rarity of cartilage preservation in the fossil record has hampered inferences of their locomotor biology, such as loading, range of motion, and muscular attachments, because cartilage forms a large portion of appendicular modules. We investigated the evolutionary and functional significance of pelvic and femoral cartilages in Diplodocoidea, a diverse and well-represented clade of sauropods. We digitized femora, pelves, and caudal vertebrae of 35 sauropod and outgroup taxa before estimating key evolutionary transitions in cartilage morphology using maximum likelihood ancestral state reconstruction of osteological correlates. Like other sauropods, the rugose femoral head growth plate indicates thickening of hyaline cartilage in the capital region. However, diplodocoids uniquely possess terminally flattened capital growth plates, which indicate a greater contribution of hyaline cartilage in forming the convex, functional femoral head. Moreover, the expanded metaphyseal shelves of diplodocoid femora suggest extensive contribution of fibrocartilage in constructing the ventral femoral head. Finally, rugosities on the postacetabular ilial rim, as well as dorsoventrally expanded transverse processes on the anterior caudal vertebrae, suggest that diplodocoids possessed massive cartilaginous shelves that expanded the ilial blade caudally, buttressed by the anterior caudal transverse processes. The anterior caudal vertebrae are therefore incorporated into the functional sacrum as ‘cryptic sacra’. This novel interpretation of the pelvic skeleton challenges traditional anatomical reconstruction of the diplodocoid hindlimb, and suggest that the hips and tail are functionally integrated to

allow diplodocoids to adopt a greater range of locomotor postures, potentially even tail-assisted bipedalism.

**Funding Sources** Missouri State University Faculty Research Grant (to HPT).

### Late Cenozoic Mammalian Macroecology & Macroevolution

#### FIRST DETERMINATION OF THE DIETARY ECOLOGY OF TWO OLIGO-MIOCENE-AGED SHREWS, *DOMNINA* AND *PSEUDOTRIMYLUS*, USING GEOMETRIC MORPHOMETRICS

Tse, Yuen Ting (Athena), Calede, Jonathan  
Evolution, Ecology and Organismal Biology, The Ohio State University, Columbus, Ohio, U.S.A.

The family Soricidae (shrews) is the fourth most species-rich mammalian family. Much attention has been given to studying its taxonomic diversity, both among extant and extinct shrews. However, little work has been undertaken on the ecomorphology of shrews, particularly in the fossil record. This is in part a consequence of a fossil record dominated by isolated teeth and partial jaws. Two extremely well-preserved crania enable such study to be undertaken: one belongs to *Domnina* from the Arikareean of Montana, the other to *Pseudotrimylus* from the Barstovian of Nevada.

Although shrews are sometimes considered uniformly invertivorous, there are in fact variations in the size and hardness of the food consumed across species. There is also variation in skull morphology within the family. We explored the association between craniodental morphology and dietary ecology in a training set of 136 specimens from 42 extant species spanning all three sub-families of Soricidae. Each species was assigned to one of three diet hardness categories (soft, intermediate, hard) based on published literature. We used geometric morphometrics to capture variations in the size and shape of muscle attachment sites, teeth, and the in-levers/out-levers for the lateral and ventral sides of the skull and the lateral side of the dentary. The results of our principal component analyses (PCA) and canonical variate analyses (CVA) confirm that the dietary ecology of shrews can be inferred from morphology. Thus, for example, a dorsoventrally tall snout and mediolaterally wide palatine are associated with processing harder food.

We applied this approach to the two extinct species. Both PCA and CVA results reveal that the morphologies of the fossil species are distinct from all extant shrews studied; they occupy a very different part of the morphospace. The two fossil species have much wider palatines and less elongated basicrania. They also have more robust dentaries with broader coronoid processes than those observed in extant species. *Pseudotrimylus* differs from *Domnina* in having a buccolingually broader P4 and a relatively longer

tooththrow. The results suggest that *Domnina* and *Pseudotrimylus* had a different diet than extant shrew species. Specifically, their shortened skulls with broad palatines may have enabled them to produce greater bite forces than extant shrews and, thus, use hard food sources like the abundant mollusks recovered in the same deposits.

## Biomechanics & Functional Morphology

### A CONSTRUCTIONAL CONSTRAINT HYPOTHESIS FOR VERTEBRATE JAW EVOLUTION

Tseng, Z. Jack, Garcia Lara, Sergio  
Integrative Biology, University of California, Berkeley, California, U.S.A.

The jaw is a major morphological and biomechanical innovation in the macroevolutionary record of vertebrates. Despite the impressively broad array of shapes and functions across the clades of jawed vertebrates (gnathostomes), all jaws share a common developmental origin from the embryonic first pharyngeal (mandibular) arch. In this study, we ask whether this shared developmental origin for the jaw in gnathostomes is correlated with a common constructional constraint in lower jaw structure-mechanics mapping. We synthesized 2D lateral mandible outlines from datasets across the evolutionary record of jawed vertebrates, spanning more than 400 million years of geologic time and taxonomic breadth ranging from acanthodians to living tetrapod clades. We applied elliptical Fourier and principal component analyses to generate a pan-gnathostome mandible morphospace, and employed finite element modeling to contextualize the biomechanical landscape over which gnathostome jaw shapes are distributed. Statistical evaluation of the gnathostome morphospace occupation pattern against a null distribution pattern, random with regard to jaw stiffness, indicates that gnathostomes occupy a morphospace that is bound by extreme evolved morphotypes in a non-random manner. Evolved jaw shape distributions are consistent with substantial over-representation of jaw shapes with high bending stiffness within a broader theoretical morphological framework. In addition, there is extensive overlap among all analyzed gnathostome clades near the origin of the morphospace. These findings suggest that the general morphofunctional body plan of the lower jaw in gnathostomes exhibits substantial overlap in a region of the morphospace corresponding to moderate jaw stiffness, and divergences or specializations in gnathostome jaw shape

may be governed by constructional stiffness regardless of ecology or clade. Future expansion of the dataset to increase taxonomic coverage, capture 3D jaw morphology, and account for biomaterial variability would allow further rigorous testing of this hypothesis.

**Funding Sources** University at Buffalo, University of California at Berkeley.

## Mesozoic & Early Cenozoic Mammalian Evolution

### THE UPDATED VERTEBRATE FAUNA OF THE UPPER EOCENE ERGILIN DZO FORMATION OF MONGOLIA

Tsubamoto, Takehisa<sup>1</sup>, Tsogtbaatar, Khishigjav<sup>4</sup>, Chinzorig, Tsogtbaatar<sup>2</sup>, Iijima, Masaya<sup>3</sup>, Egi, Naoko<sup>5</sup>  
<sup>1</sup>Faculty of Science, Ehime University, Matsuyama, Ehime Pref., Japan, <sup>2</sup>North Carolina Museum of Natural Sciences, Raleigh, North Carolina, U.S.A., <sup>3</sup>Department of Biological Sciences, Clemson University, Clemson, South Carolina, U.S.A., <sup>4</sup>Institute of Paleontology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia, <sup>5</sup>National Museum of Nature and Science, Tsukuba, Ibaraki Pref., Japan

The upper Eocene Ergilin Dzo Formation of southeastern Mongolia has been known for yielding many terrestrial vertebrate fossils. The mammals from this formation are important in Cenozoic mammalian paleontology because they define the type fauna of the Ergilian Asian Land Mammal Age. Since 2004, we have been working on the sediments and vertebrate fossils of the formation.

Here, we review the vertebrate fauna of the Ergilin Dzo Formation with a focus on the mammals, on the basis of recent findings and systematic revisions. The vertebrate fauna of the formation currently consists of 110 species of five classes: two species of Osteichthyes, one species of Amphibia, nine species of Reptilia, 11 species of Aves, and 87 species of Mammalia. A recent discovery has revealed that the fauna includes a crocodyliform, implying that southeastern Mongolia probably fulfilled thermal requirements of crocodyliforms during the late Eocene. The mammalian fauna of the formation currently consists of 11 orders: six species of Eulipotyphla, one species of Anagalida, two species of Mesonychia, one species of Cimolesta, two species of Leptictida, five species of Rodentia, four species of Lagomorpha, five species of Carnivora, eight species of Hyaenodontida, 13 species of Artiodactyla (or Cetartiodactyla), and 40 species of Perissodactyla. In the mammalian fauna, perissodactyls are dominant in terms of the number of described species. In terms of the collected specimens, brontotheriid and

rhinocerotid perissodactyls and ruminant artiodactyls are dominant. Compared with the early Oligocene faunas of northern Asia, taxonomic diversity and specimen occurrences of rodents, lagomorphs, and carnivorans are low in the Ergilin Dzo fauna. In contrast, the perissodactyls are more common in terms of the relative abundance of the collected specimens as well as the taxonomic abundance than those of the former faunas. The taxonomic diversity of the Hyaenodontida in the formation is as high as that of the former faunas, but the relative number of the collected hyaenodontid specimens in the formation is higher than that in the former faunas.

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### **Symposium: Paleoneurology**

#### **ECOMORPHOLOGICAL AND ALLOMETRIC SIGNATURES IN ENDOCRANIAL SHAPE IN CROCODYLIFORMS**

Turner, Alan H.<sup>1</sup>, Beyl, Alexander R.<sup>1</sup>, Brusatte, Stephen<sup>2</sup>, Gignac, Paul<sup>4</sup>, Pol, Diego<sup>3</sup>, Schwab, Julia A.<sup>2</sup>, Smaers, Jeroen B.<sup>1</sup>, Watanabe, Akinobu<sup>5</sup>, Wilberg, Eric<sup>1</sup>, Young, Mark T.<sup>2</sup>

<sup>1</sup>Stony Brook University, Stony Brook, New York, U.S.A., <sup>2</sup>University of Edinburgh, Edinburgh, U.K., <sup>3</sup>Museo Paleontológico Egidio Feruglio, Trelew, Argentina, <sup>4</sup>Oklahoma State University Center for Health Sciences, Tulsa, Oklahoma, U.S.A., <sup>5</sup>New York Institute of Technology, Old Westbury, New York, U.S.A.

Many ecological transitions are associated with morphological transformations as organisms adapt to new environments. Extinct crocodylomorphs evolved an impressive range of ecologies (e.g., rivaling those of mammals) that contrast the semiaquatic lifestyle of modern crocodylians. The earliest diverging crocodylomorphs were predominantly small terrestrial predators. However, by the Jurassic marine thalattosuchians had evolved towards their eventual conquest of pelagic domains. Notosuchians, on the other hand, included terrestrial forms ranging from small herbivores and omnivores to large predators, the latter group surviving well into the Cenozoic. The extent to which the neuroanatomy of these taxa tracked their ecological specialization and associated skeletal adaptations is not well established. Preliminary data, based largely on extant sampling, have suggested that brain morphology in extant crocodylians retains ecomorphological signal.

To explore how ecological preferences among fossil crocodylomorphs is reflected in brain morphology, we used a high-density 3D morphometric approach on cranial endocasts, broadly sampling extant and extinct crocodylomorphs. We analyzed whole endocasts as well as

focused on the cerebrum, optic lobe, cerebellum, and medulla, individually. We found that overall endocranial shape exhibits phylogenetic clustering with major clades occupying different, but in some cases overlapping, regions of morphospace. Especially distinct are the basalmost crocodylomorphs and the notosuchians. To interrogate these patterns further, we used a time-calibrated phylogeny of Crocodylomorpha to perform a suite of comparative phylogenetic analyses. Results indicate that allometry accounts for nearly 10% of total endocranial shape variation after correcting for phylogenetic structure. Surprisingly, habitat preference and overall shape variation for each brain region shows little association. Our current data suggest that neuroanatomical evolution in crocodylomorphs is more complex than might typically be expected for saurians, with convergence of brain morphology among distantly related and ecologically distinct taxa. Significant brain regions such as the olfactory tract and bulb as well as the pituitary/infundibulum, which remain to be explored, may add needed clarity. The findings of the present study contrast strongly with other aspects of neurosensory anatomy in crocodylomorphs, namely that inner ear morphology tracks aquatic habitat evolution.

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### **Biomechanics & Functional Morphology**

#### **INTERMETATARSAL MOBILITY AND GRADES OF FOOT CONTACT IN THE AMERICAN ALLIGATOR: BUILDING A NEW PERSPECTIVE ON ARCHOSAURIAN FOOT EVOLUTION**

Turner, Morgan L., Gatesy, Stephen M.  
Ecology and Evolutionary Biology, Brown University, Providence, Rhode Island, U.S.A.

An animal's foot must effectively mediate animal-substrate interactions across the entire range of limb poses used in life. Despite its importance, the foot is typically either ignored or treated as a 'black box' – an anatomically complex set of visually obscured components that are difficult to measure or simulate. Metatarsals, the 'bones of the sole,' are the dominant skeletal elements. In plantigrade animals, intermetatarsal mobility offers the potential for active and passive reconfiguration within the foot itself. Using marker-based X-ray Reconstruction of Moving Morphology (XROMM), we measured metatarsal kinematics in three American alligators (*Alligator mississippiensis*) across their locomotor and maneuvering repertoire. Alligators are capable of postural extreme, from a belly sprawl to a high walk to sharp turns, how does the foot accommodate these diverse demands?

We found that regardless of limb placement, the metatarsals conform to the ground to maintain fully plantigrade contact throughout most of the stance phase. The outermost weight-bearing metatarsals (I and IV) are spread up to 170% relative to their most compressed configuration during swing. Intermetatarsal adduction precedes the stance-swing transition as the foot passes through 'digitigrade' and 'unguligrade' contact. Across the wide range of plantigrade foot placements sampled from postural extremes, alligators predominantly inverted and abducted the pes. Notably, a positive relationship was found between inversion and distance from the midline. Intermetatarsal skewing contributed significantly to inversion-eversion of the foot (up to 63 degrees excursion). This work reveals a close relationship between intermetatarsal mobility, foot function, and limb posture. As many of the major archosaurian shifts in posture and locomotion are predicted from shifts in pedal morphology, the foot is crucial to inferring function from the fossil record. Intermetatarsal mobility likely plays a significant role in maintaining ground contact in plantigrade species with complex ankles and greater postural extremes. In lineages with transitions toward simplified ankles and stabilized metatarsals, the animal interfaces with the substrate entirely through the digits, likely restricting the range of limb poses. Patterns of intermetatarsal adduction with reduced foot contact found here in *Alligator* offer a new functional perspective on these transitions towards digitigrady and more erect hind limb posture.

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## Marine Mammals

### FIRST CONFIRMED BASILOSOURID ARCHAEOCETES FROM THE NORTH PACIFIC

Uhen, Mark D.

Atmospheric, Oceanic, and Earth Sciences, George Mason University, Fairfax, Virginia, U.S.A.

Basilosaurid archaeocetes are known from the late Eocene of virtually all coastlines bearing coeval marine rocks except the North Pacific Basin, until now. Here we report on three consecutive posterior thoracic vertebrae of a large, basilosaurid archaeocete from a late Eocene horizon in the Keasey Formation, northwest Oregon. These vertebrae were morphologically and morphometrically compared to other cetacean vertebrae of similar age from around the world using a 3D plot of vertebral centra shapes. This analysis reveals that this specimen is similar in shape to *Dorudon* and *Cynthiacetus* but represents a significantly larger species. The specimens were determined to be different from all currently named species of fossil

cetacean, but most similar to those of basilosaurid archaeocetes found in the Gulf Coast region of North America. These vertebrae thus represent the first confirmed specimen of a late Eocene basilosaurid from the North Pacific. These and other basilosaurids known only from vertebrae are reviewed here in the context of late Eocene paleoceanography and cetacean evolution. Archaeocetes are likely rare due to the prevalence of deeper water marine deposits in along North Pacific coastlines, compared to the shallow water deposits of the former Tethys Sea and the East and Gulf Coasts of North America where archaeocetes are fairly common.

## Symposium: Dietary Reconstruction

### COMBINING FOSSIL ENAMEL STABLE ISOTOPES AND DENTAL MICROWEAR TEXTURE ANALYSIS TO ASSESS DIETARY NICHE-PARTITIONING AMONG PRIMATES (CERCOPITHECIDAE AND HOMINIDAE) FROM THE LOWER OMO VALLEY, ETHIOPIA

Uno, Kevin T.<sup>1</sup>, Merceron, Gildas<sup>3</sup>, Brown, Morgan<sup>6</sup>, Guy, Franck<sup>3</sup>, Hlusko, Leslea<sup>4</sup>, Martin, Jérémy<sup>2</sup>, Balter, Vincent<sup>2</sup>, Souron, Antoine<sup>5</sup>, Boissierie, Jean-Renaud<sup>7</sup>

<sup>1</sup>Biology and Paleo Environment, Lamont-Doherty Earth Observatory, Palisades, New York, U.S.A., <sup>2</sup>ENSL, Univ Lyon 1, CNRS, LGL-TPE, University of Lyon, Lyon, France, <sup>3</sup>PALEVOPRIM, CNRS, University of Poitiers, Poitiers, France, <sup>4</sup>Department of Integrative Biology, University of California, Berkeley, Berkeley, California, U.S.A., <sup>5</sup>PACEA, CNRS, University of Bordeaux, Bordeaux, Nouvelle-Aquitaine, France, <sup>6</sup>Department of Ecology, Evolution, and Environmental Biology, Columbia University, New York, New York, U.S.A., <sup>7</sup>PALEVOPRIM, CNRS, and Ministry of Europe and Foreign Affairs, Ethiopia, University of Poitiers, CFEE, Poitiers, Nouvelle-Aquitaine, France

As the sole surviving hominin lineage, the evolution and reasons for the persistence of the genus *Homo* are of great scientific interest. Diet is an important aspect of hominin ecology that may help explain key ways in which *Homo* differed from other hominins and primates. Tooth enamel geochemistry and tooth wear are two methods for investigating diet, which are widely applied on their own and increasingly in tandem. Here, we combine stable isotope analysis and dental microwear texture analysis (DMTA) of hominin and cercopithecoid molars from the Shungura Formation in the Lower Omo Valley, Ethiopia, to study diet type and dietary niche partitioning of these taxa. We focus on the period from ~ 2.3–2.0 Ma because of the high taxonomic diversity of cercopithecids and hominins, the former represented in this study by *Theropithecus*, *Papio*, and the colobines *Paracolobus* and

*Rhinocolobus*, and the latter by *Australopithecus*, *Paranthropus*, and *Homo*.

We developed a DMTA-based dietary morphospace using PCA of 20 textural characteristics on a data set of four extant primate species (n = 104) with different dietary preferences. In the DMTA morphospace, fossil *Theropithecus* (n = 44) falls near its extant congener, the gelada, whereas fossil *Papio* (n = 32) lies closer to modern vervets than their extant counterparts. Smaller sample sizes of the colobines (n = 9) show the extinct *Rhinocolobus* had a diet most similar to the arboreal *Colobus guereza* whereas the terrestrial *Paracolobus* had a highly variable diet, including hard objects. For the hominins, DMTA data show no evidence of durophagy. The diet of *Paranthropus* (n = 10) falls closest to that of extinct and extant *Theropithecus*. Smaller data sets for *Homo* (n = 4) and *Australopithecus* (n = 2) suggest variable diets that fall farther outside of the extant primate morphospace compared to *Paranthropus*.

Carbon isotope ( $\delta^{13}\text{C}$ ) data from cercopithecids and hominins show *Paranthropus* (n = 18) and *Theropithecus* (n = 19) had  $\text{C}_4$ -dominated diets, thus overlapping in  $\delta^{13}\text{C}$  and DMTA space. *Papio* (n = 11) shows a high range of  $\delta^{13}\text{C}$  values, mirroring the high diversity in the DMTA PC1 dimension. The diet of *Homo* (n = 10) spans  $\text{C}_3$ - to nearly  $\text{C}_4$ -dominated values and overlaps considerably with *Paranthropus*. *Australopithecus* (n = 4) has a wide  $\delta^{13}\text{C}$  range; colobines (n = 9) have  $\text{C}_3$  diets, but based on DMTA results, sourced different foods. The combined isotope and DMTA data reveal complex dietary niche partitioning among hominins and primates.

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## Mesozoic Herpetology

### IDENTITY, HOMOLOGUE, AND COMPOSITION OF FIBER-LIKE STRUCTURES ASSOCIATED WITH THE PTEROSAUR INTEGUMENT

Unwin, David M.<sup>1</sup>, Martill, David<sup>2</sup>

<sup>1</sup>School of Museum Studies, University of Leicester, Leicester, U.K., <sup>2</sup>School of the Environment, Geography and Geological Sciences, University of Portsmouth, Portsmouth, U.K.

Fiber-like structures are frequently preserved in association with fossilized remains of the pterosaur integument. Several fiber types have been recognized. Among the commonest are aktinofibrils, typically 40–100+  $\mu\text{m}$  in breadth and present throughout the flight patagia, exhibiting the same patterns of alignment across Pterosauria. Occasionally partially mineralized in distal

regions of the patagia, aktinofibrils were composite, helically-wound structures composed of much finer filaments a few microns in diameter. Comparable in size to aktinofibrils, but less common, are single-stranded, hair-like pycnofibers, seemingly branched in two specimens of the anurognathid *Jeholopterus*, that supposedly adorned parts of the cranium, neck, and body. Fiber-like structures have also been reported in cranial crests, foot webs, and tail flaps. The identity, homology, composition, and function of integumentary fibers is fiercely disputed. This study aimed to resolve these issues through analysis of 150+ specimens where the integument is preserved, representing >25% of known pterosaur species, 15 of the 20 principal lineages, and almost the entire temporal range of the clade. Details of the macro- and microstructure of fibers was obtained using light, UV and laser-UV photography, and binocular and scanning electron microscopy. Results of this study provide broad support for a new model in which pterosaur integumentary fibers of all types had a single common origin: dermal collagen. This idea is consistent with: (1) exceptionally preserved examples of cranial crests, wing membranes, and integument associated with the neck and body, which demonstrate that fibers were embedded within the integument, and formed part of the dermis; (2) calcification of fibers in the cranial crest and, occasionally, in distal parts of the flight patagia; (3) the composite construction of fibers, which were composed of much finer, helically-wound fibrils. Multiple specimens with soft tissues preserved in four different preservational modes, show that the integument had a glabrous, fine granular, or even polygonal external texture. Aktinofibrils and other collagenous dermal fibres (e.g., in cranial crests and skin associated with the neck and body) exposed by decay of the remarkably thin epidermis have frequently been misinterpreted as pycnofibers. External fibers fringing the jaws of anurognathids may be an exception, although branching, reported in one specimen, is likely an artifact of preservation.

## Holocene & Pleistocene Mammalian Macroecology & Faunal Studies

### METHODS OF DETERMINING THE GENDER, SIZE, AND AGE OF 'COLA', A PLEISTOCENE MAMMOTH DISCOVERED IN SOUTHEASTERN IDAHO

Usachenko, Natalya S.

Geology, University of Idaho, Moscow, Idaho, U.S.A.

North America's recent geologic history has been shaped by several periods of sudden, rapid environmental and climatic changes coinciding with the emergence and extinction of a diverse array of species. Much of this history is reflected in the distribution and diversity of the

remains of ancient life, which are studied to further the understanding of how the evolution of species has occurred in response to an ever-changing natural world. This project focuses on the reconstruction and anatomical analysis of a nearly complete skeleton of a 11,700 +/- 40-year-old mammoth specimen originally excavated from a site at the El Paso Products phosphate plant northeast of Soda Springs, Idaho in 1966. The specimen is currently being studied at the University of Idaho in Moscow, Idaho. In reference to the locality of its discovery near Soda Springs, the mammoth was nicknamed 'Cola'. Aims of this study are to: (1) Discern whether the remains belong to a male or female mammoth, and (2) Interpret the specimen's approximate size and age at the time of its death. Analytical methods have included taking measurements of Cola's tusks, molars, and frontal limb bones, both fragmented and complete, as well as determining the extent of dental and skeletal maturation through the assessment of epiphyseal fusion in the limbs and the number of dentin layers and lamellar frequencies on the molars. Calculations made based on humerus measurements indicate that this mammoth was approximately 8.7 feet tall at the shoulder. Tusks were measured to be approximately 8.6 feet long and dental analysis suggests that it had likely been on its fourth set of molars. Assessments of the limb bones have revealed that none of its epiphyses had yet fused. Based on these observations, Cola is currently hypothesized to have been a juvenile or young adult male between 10–18 years old. In contrast, adult mammoths were 13 feet tall at the shoulder with tusks of males reaching 13–16 feet long, while the tusks of females were only 5–6 feet long. This mammoth was living not long before the extinction of its species, thus, broader objectives of this research include making inferences as to what caused their extinction, how they responded to climatic and environmental changes, and their relationship to extant proboscideans.

### **Paleozoic Tetrapods & Lissamphibians**

#### **THE UNEXPECTED PRESENCE OF A CARIBBEAN FROG IN THE LATE OLIGOCENE OF FLORIDA**

Vallejo-Pareja, Maria C.<sup>1</sup>, Bloch, Jonathan I.<sup>2</sup>, Blackburn, David C.<sup>2</sup>

<sup>1</sup>Department of Biology and Florida Museum of Natural History, University of Florida, Gainesville, Florida, U.S.A., <sup>2</sup>Florida Museum of Natural History, University of Florida, Gainesville, Florida, U.S.A.

Biogeographic analyses of phylogenomic data suggest that the extant native anuran faunas of North America have three different geographic origins. Components of the current faunas originated in North America during the Mesozoic whereas others were established during the Cenozoic from Asia or South America. Yet, direct

evidence to evaluate these geographic origin scenarios is scarce due in part to a poorly documented fossil record of late Mesozoic and early Cenozoic anurans. During the past few decades, several studies on extinct faunas have suggested similarities between mid-Cenozoic anurans and extant Caribbean taxa, suggesting that more extensive systematic studies of the anuran fossil record could provide new insights into the North American faunas during the Cenozoic. Here we document the anuran faunas of three fossil localities from the Oligocene of Florida: I-75 (early Oligocene, Whitneyan North American Land Mammal Age [NALMA]), Live Oak (SB 1A), and Brooksville 2 (late Oligocene, Arikarean NALMA). Fossils were identified using comparative specimens that included previously identified fossils, dry skeletal preparations of extant anurans, and digital three-dimensional models of alcohol-preserved specimens based on data derived from X-ray computed microtomography (microCT scans). We identified and cataloged 351 anuran fossils representing seven families and ten genera that are similar to those present today in Florida, with the exceptions of two genera, *Spea* (Scaphiropodidae) and *Rhinophrynus* (Rhinophrynidae). Unexpectedly, the most abundant fossil morphotypes can be clearly classified in the genus *Eleutherodactylus* (Eleutherodactylidae), a highly diverse clade of Caribbean origin that was established in the Antilles by the early Oligocene. These 150 fossils include ilia, sacral vertebrae, urostyles, humeri, and radioulnae that are morphologically distinctive from other taxa in the Oligocene of Florida and represent individuals of small body sizes. These newly described fossils represent the earliest records of *Eleutherodactylus* in North America and the second oldest for the genus, which raises questions about the early geographic distribution of this species-rich clade. Together, these results point to the possibility that *Eleutherodactylus* dispersed to North America much earlier than previously thought and provides further evidence suggesting dispersal from the Great Antilles into peninsular Florida during the Oligocene.

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### **Biomechanics & Functional Morphology**

#### **INTRODUCING THE NATURAL FREQUENCY METHOD: TAIL BIOMECHANICS PREDICT ENERGETICALLY OPTIMAL WALKING SPEED OF TYRANNOSAURUS REX**

van Bijlert, Pasha A.<sup>1</sup>, van Soest, A.J. ("Knoek")<sup>1</sup>, Schulp, Anne S.<sup>2</sup>

<sup>1</sup>Human Movement Sciences, Vrije Universiteit Amsterdam, Amsterdam, Netherlands, <sup>2</sup>Naturalis Biodiversity Center, Leiden, Netherlands

Animals minimize locomotor energy expenditure by selecting gaits tuned to the natural frequencies of relevant body parts. We demonstrate that this allows estimation of the optimal step frequency and walking speed of *Tyrannosaurus rex*, using an approach we introduce as the Natural Frequency Method. *T. rex* is reconstructed with a predominantly horizontal spinal posture. Its largest muscle, *M. caudofemoralis longus* (CFL), retracted the femur to produce forward propulsion during locomotion. The tail was constantly subject to flexion torque due to gravity and CFL contractions, and the caudal interspinous ligaments counteracted this torque at zero metabolic cost. Tail heaving with each step caused cyclical peaks in the strain of the caudal ligaments. Therefore, these ligaments were an important site for elastic energy storage, greatly improving metabolic efficiency of this mode of locomotion. The well-preserved adult *T. rex* specimen RGM.792000 allowed high fidelity 3D scans of the caudal vertebrae. Subsequently, we employed a biomechanical reconstruction of the ligament-suspended tail to determine its natural frequency ( $0.72 \text{ s}^{-1}$ ,  $0.62\text{--}0.87$ ), and combined it with step lengths from trackway data to find an optimal walking speed ( $1.39 \text{ m s}^{-1}$ ,  $1.21\text{--}1.70$ ) for *T. rex*.

This is the first time the energetically optimal walking speed of a dinosaur has been estimated, and our method can be applied to any specimen with a well-preserved tail. As such, it opens up a new research avenue within paleobiomechanics. Reconstructing locomotor ability of extinct dinosaurs is difficult, and various methods have led to conflicting results. Due to the uncertainties involved in any method of dinosaur speed estimation, it is important to explore independent lines of evidence. Our results suggest that trackway calculations may overestimate walking speed, owing to the high spread in the original data used for the regression equation. A major advantage of our approach is that predicted speed is independent of the muscularity of the reconstruction. Steady-state locomotion has a large effect on an animal's ecological niche. Therefore, the Natural Frequency Method can provide us with new insights into possible gait patterns, habits and locomotor ability of dinosaurs.

### Mesozoic & Early Cenozoic Mammalian Evolution

#### THE CRETACEOUS–PALEOGENE FOSSIL MAMMAL PROJECT: DIGITIZING AND SHARING WYOMING'S RARE FOSSIL MAMMAL COLLECTION FOR UNDERSTANDING MAMMAL EXTINCTION AND RECOVERY THROUGH ECOSYSTEM COLLAPSE

Vietti, Laura A.<sup>1</sup>, Wright, Susannah<sup>2</sup>, McKim, Shadow<sup>1</sup>, Clementz, Mark<sup>2</sup>, Hutchen, Chad<sup>3</sup>

<sup>1</sup>Geological Museum, University of Wyoming, Laramie, Wyoming, U.S.A., <sup>2</sup>Geology & Geophysics, University of

Wyoming, Laramie, Wyoming, U.S.A., <sup>3</sup>Coe Libraries, University of Wyoming, Laramie, Wyoming, U.S.A.

The University of Wyoming's (UW) Fossil Vertebrate Collection houses a rich and rare fossil mammal collection originating from before and after the Cretaceous–Paleogene (K–Pg) mass extinction ( $n = 26,277$  specimens). The UW K–Pg Fossil Mammal Collection is understudied and underutilized due to our geographical remoteness, the physical size and fragility of our specimens, and the invisibility of our collection. Furthermore, imaging small mammal teeth is challenging due to their small size and high vertical relief. In an effort to promote the use of the UW K–Pg Fossil Mammal Collection, we partnered with the UW Libraries for a two-year project to digitize and make globally accessible a significant portion of the UW K–Pg Fossil Mammal Collection. Here we present the results of this major digitization project including our solution to imaging small mammal teeth specimens at the collections scale, our final digitization workflow, and examples of images from the final digitization project.

In summary, we captured 15,000 research-quality images of 5,000 tooth elements representing ~500 mammal species spanning the K–Pg interval (Cretaceous, Paleocene, Eocene, and Oligocene). Specimen selection was challenging, and we ultimately chose specimens that were complete and unworn dental elements representing all tooth positions for each identified species in the collection. We also imaged multiple teeth of the same species and tooth position but from different localities to enable paleogeographic studies. For imaging, we used a Keyence VHX-5000 imaging station that is capable of automated focal stacking and image tiling at high magnifications (20–200x) as well as in-program annotation and scale-bar insertion. We took three images per specimen at orientations best suited for research purposes including the occlusal (chewing surface), the medial (towards the tongue), and lateral (towards the cheek) orientations. Original K–Pg specimen images in TIFF format were then archived on UW's petaLibrary, and derivative jpegs were published on our online Specify Database as well as shared with the large data aggregator and web-portal iDigBio.

Generating and mobilizing research-quality images of the UW K–Pg fossil mammal material will make globally available for the first time, a comprehensive record of mammal collapse and recovery associated with the K–Pg extinction event, which will promote its use for broad applications in research, museums, education, and the general public.

**Funding Sources** Institute of Museum and Library Services: Museums for America Grant.

### Permo-Triassic Tetrapods

## A MULTI-INDEX CHARACTERIZATION OF FAUNAL DYNAMICS REVEALS THE NATURE OF SOUTH AFRICA'S LATEST PERMIAN MASS EXTINCTION

Viglietti, Pia A.<sup>1</sup>, Benson, Roger B.<sup>2</sup>, Smith, Roger M.<sup>3</sup>, Botha, Jennifer<sup>4</sup>, Kammerer, Christian F.<sup>5</sup>, Skosan, Zaituna<sup>6</sup>, Mtalana, Nolusindiso<sup>6</sup>, Mtungata, Sibusiso<sup>6</sup>, October, Paul<sup>6</sup>, Wolvaardt, Derik<sup>3</sup>, Strong, Mike<sup>6</sup>, Skinner, Georgina<sup>6</sup>, Angielczyk, Ken<sup>1</sup>

<sup>1</sup>Negaunee Integrative Research Center, Field Museum of Natural History, Chicago, Illinois, U.S.A., <sup>2</sup>Earth Sciences, University of Oxford, Oxford, U.K., <sup>3</sup>Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, Gauteng, South Africa, <sup>4</sup>Palaeontology, National Museum, Bloemfontein, Free State, South Africa, <sup>5</sup>Paleontology, North Carolina Museum of Natural Sciences, Raleigh, North Carolina, U.S.A., <sup>6</sup>Karoo Palaeontology, Iziko South African Museum, Cape Town, Western Cape, South Africa

The mass extinction at the end of the Permian Period was the largest biotic crisis in Earth's history. On land, this event witnessed a transition from therapsid- to archosauriform-dominated tetrapod assemblages and a general restructuring of terrestrial ecosystems. Study of this event has yielded key insights into mass extinctions, but at most terrestrial sections detailed understanding has been limited by a lack of high-precision fossil occurrence data that could resolve the sequence of events on sub-million-year timespans. We analyzed a unique database of Karoo Basin fossil tetrapods spanning 4.5 million years through the *Daptocephalus* and *Lystrosaurus* assemblage zones, comprising 926 specimens belonging to 130 species and placed into 15 stratigraphic intervals (~300,000 kya each). Using sample-standardised methods, we characterized South African faunal assemblage dynamics across the end-Permian mass extinction.

We found evidence for high extinction rates through a protracted interval estimated as ~1 Ma. Early phases of extinction co-occur with suppressed origination rates, which continue up to the acme of extinction (<300,000 kya) around the *Daptocephalus*-*Lystrosaurus* Assemblage Zone boundary. After this, high origination rates co-occur with high extinction, resulting in high turnover and positive net diversification rates. This pattern of rapid turnover at the onset of the *Lystrosaurus* Assemblage Zone resulted in an assemblage of short-lived taxa including archosauriforms (*Proterosuchus fergusi*), amphibians (*Lydekkerina bothriceps*), cynodonts (*Thrinaxodon liorhinus*), diapsids (*Paliguana whitei*), dicynodonts (*Lystrosaurus* spp.), parareptiles (*Owenetta kitchingorum*), and therocephalians (*Regisaurus jacobi*). The unusual composition of this assemblage resulted in ecosystem instability in an earliest post extinction 'recovery fauna'. The 'disaster taxon' *Lystrosaurus*, comprising four closely-related species (*L. curvatus*, *L. declivis*, *L.*

*maccaigi*, *L. murrayi*), comprises 50% of all specimens by the onset of the latest extinction phase and culminates in a 75% share in the extinction aftermath. This pattern of early increases in *Lystrosaurus* abundance suggests an opportunistic response to changing environments rather than ecological expansion facilitated by the extinction of other species. Our findings suggest a decoupling of key ecosystem parameters such as evenness, stability, and possibly richness during biotic crises of the deep past.

**Funding Sources** PAV would like to thank the Field Museum's Women in Science Board for their generous support.

## Colbert Poster Prize/Cenozoic Herpetology

### ANALYSIS OF TERRESTRIAL VERTEBRATE BIOGEOGRAPHICAL HISTORY OF THE GREATER ANTILLES

Vinola, Lazaro W.

Florida Museum of Natural History, Gainesville, Florida, U.S.A.

The Greater Antilles are a group of islands with a very complex geological and biogeographical history that spans over 90 million years. The origin of its modern and recently extinct biota has been a hotly debated topic among researchers with radically different points of views for over a century. Numerous mechanisms involving land bridges, overwater dispersal, and island hopping are often invoked to explain the faunal assemblages, but little consensus has been reached with many questions regarding their feasibility. Each of these scenarios is associated with specific geologic events across the history of the Caribbean and thus patterns timing of first occurrences in the Greater Antilles can be used to test these competing hypotheses. Here we present the results of an extensive revision of the Pre-Quaternary fossil record of non-volant terrestrial mammals, amphibians, and reptiles within the region. Also, we created a database with updated ages of origin of lineages of amphibian, reptiles and mammals obtained from molecular studies on extant or recently extinct taxa. Our results show that a combination of multiple biogeographical models best explains the current faunal assemblage within the region. The origin of most lineages can be traced back into South America while a few derive from North American and African ancestors, as it would be expected from wind and current patterns and possible land connection. Although scarce, the Paleogene-Neogene fossils also suggest that multiple groups that arrived at the Proto-Caribbean did not survive into the Quaternary, indicating that non-anthropogenic extinction played an important role in shaping faunal assemblage on the islands. Both molecular and fossil evidence supports that most lineages colonized the Proto-Caribbean after the middle

Eocene when the islands became permanently exposed, while a few groups like Solenodonta, *Anolis* and *Cricosaura* lizards may have arrived in the Late Cretaceous or Early Paleogene. We also found a cluster of dates of origin of several lineages near the Eocene-Oligocene transition that may correlate with the GAARlandia hypothesis, although overwater dispersal, primarily from South America, seems to have played an important role during the rest of the Neogene.

## Holocene & Pleistocene Mammalian Macroecology & Faunal Studies

### PHYLOGENY OF FOSSIL AND EXTANT NEW WORLD PORCUPINES: RE-EVALUATION OF AN EARLY PLEISTOCENE PORCUPINE SKELETON FROM FLORIDA WITH TROPICAL, ARBOREAL MORPHOLOGY

Vitek, Natasha S.<sup>1</sup>, Hoeflich, Jennifer C.<sup>2</sup>, Magallanes, Isaac<sup>2</sup>, Moran, Sean M.<sup>2</sup>, Narducci, Rachel E.<sup>2</sup>, Ocon, Samantha B.<sup>2</sup>, Perez, Victor J.<sup>2</sup>, Pirlo, Jeanette<sup>2</sup>, Riegler, Mitchell S.<sup>2</sup>, Rodgers, Michael<sup>2</sup>, Selba, Molly C.<sup>2</sup>, Vallejo-Pareja, Maria C.<sup>2</sup>, Ziegler, Michael J.<sup>2</sup>, Granatosky, Michael C.<sup>2</sup>, Bloch, Jonathan I.<sup>2</sup>

<sup>1</sup>Ecology & Evolution, Stony Brook University, Stony Brook, New York, U.S.A., <sup>2</sup>Florida Museum of Natural History, University of Florida, Gainesville, Florida, U.S.A.

At least two species of New World porcupines (Erethizontinae) must have crossed the Panamanian Isthmus to North America during the Great American Biotic Interchange (GABI) based on modern species distributions. One was related to the large, short-tailed, cold-adapted *Erethizon dorsatum* and the other related to the smaller, mostly prehensile-tailed, tropical *Coendou* spp. However, the oldest potential fossils of either clade from the southeastern U.S.A. remain controversial because they preserve a mix of features characteristic of *Erethizon* and *Coendou*.

A lack of phylogenetic context for extinct erethizontines precludes polarization of these features and a determination of which characters are informative about relationships. In addition, the vast majority of these fossils are gnathic, limiting the number of characters that can be used to assess affinities. To help resolve the question about the generic affinity of one of these species, we described and analyzed one of the most complete early Pleistocene fossils of a New World porcupine from North America. The specimen represents most of the skeleton of an individual of *Erethizon poyeri* from the late Blancan Haile 7G site in Florida. It includes a complete dentition, crushed skull, mandible, limbs including the pectoral and pelvic girdles, podials, and axial elements including vertebrae and sternebrae. From these elements we were able to recognize

149 morphological characters and score them for 12 extinct and extant species of Erethizontidae in a character-taxon matrix.

Results from separate analyses using parsimony and Bayesian criteria unambiguously support the hypothesis that *Erethizon poyeri* is in a clade exclusively comprised of all other *Erethizon* species and can be identified by at least 15 apomorphies across the skeleton. Incorporation of molecular data do not change this hypothesized relationship. In the recovered cladograms many of the *Coendou*-like characters of *Erethizon poyeri* are plesiomorphies, including features previously considered diagnostic such as a parallel or subparallel orientation of the mandibular tooth rows and the presence of a prehensile tail. These characters provide critical information for understanding the evolutionary history of *Erethizon*, particularly about the timing of its morphological modernization, but they should not alone be the basis of generic classification of erethizontine fossils.

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## Collections

### NEW MEXICO MUSEUM OF NATURAL HISTORY AND SCIENCE PALEONTOLOGY COLLECTIONS DATA MADE PUBLICLY AVAILABLE THROUGH ARCTOS

Volden, Nicole, Mayfield-Meyer, Teresa, Cantrell, Hannah

New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, U.S.A.

In 2017, the New Mexico Museum of Natural History and Science (NMMNHS) completed an Institute of Museum and Library Services Museum Assessment Program. One of the critical needs identified from this assessment was an up to date, publicly accessible collections database. This database will facilitate research and outreach of our paleontology collections, whose strengths include New Mexican fossils, particularly Permian trackways, Triassic amphibians and reptiles, Paleocene mammals, and Neogene mammals. These fossils are studied by researchers across the globe and the new online database will allow these researchers to browse our collections remotely. In 2018 we choose Arctos as our new database based on several criteria, particularly that Arctos is entirely online and allows us to connect our collections to partnering institutions already using Arctos. Approximately 79,000 specimen records and 12,300 locality records from our old database were cleaned and standardized. New agents, parts, geology, and geography

were added to Arctos data tables that are shared between institutions. The data were then bulk uploaded to Arctos. One challenge of moving into Arctos was that it had not been used by many other paleontology collections. Thus, several new data types and data structures had to be created in Arctos. For example, we worked with the Arctos programmer to expand and refine locality encumbrances in Arctos. Formerly it was only possible to encumber locality coordinates. The new model allows us to create two localities, one public and one private. Both localities include lithostratigraphy, chronostratigraphy, higher geography, and other details such as names and dates. However, the private locality includes exact coordinates and any specific locality information that would allow a person to re-find the site, while the public locality only includes county level information and obscured coordinates.

The new database makes our collection both more accessible and more connected. Staff, the public, researchers, and land managers can access our data from anywhere. The database will be a platform for our nascent digitization program, allowing us to add media, publications, and detailed trait information to specimen records. One of the most powerful aspects of the database is the ability to connect with external resources, allowing us to create extended specimens linked to research, people, and other resources.

### Symposium: Dietary Reconstruction

#### HIGH-PRECISION STABLE ISOTOPE ANALYSIS OF STRUCTURAL CARBONATE IN <100 MG TOOTH ENAMEL SAMPLES BY CONTINUOUS-FLOW MASS SPECTROMETRY

Vonhof, Hubert<sup>1</sup>, Tütken, Thomas<sup>2</sup>, Leichliter, Jennifer N.<sup>2</sup>, Luedecke, Tina<sup>1</sup>, Haug, Gerald<sup>1</sup>

<sup>1</sup>Climate Geochemistry, Max Planck Institute for Chemistry, Mainz, Germany, <sup>2</sup>Institute of Geosciences, Johannes Gutenberg-Universität Mainz, Mainz, Germany

For decades,  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  analysis of structural  $\text{CaCO}_3$  in tooth enamel has been a key technique for paleodietary and paleoenvironmental studies. In principle, the analysis is straightforward, because tooth enamel can be processed in the same manner as  $\text{CaCO}_3$  samples, by dissolution in phosphoric acid, followed by isotope analysis of the liberated  $\text{CO}_2$  gas. Because tooth enamel's structural  $\text{CaCO}_3$  content is on the order of 5%, the necessary sample size is commonly 20 times that of standard  $\text{CaCO}_3$  samples. In most labs, this means that tooth enamel samples of ~1 mg (the equivalent of 50  $\mu\text{g}$  structural  $\text{CaCO}_3$ ) are required for precise  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  analysis.

Here we present experiments on a Thermo Scientific GASBENCH system, equipped with a cold trap and

interfaced with a Delta-V mass spectrometer. The experiments consist of replicate analyses of the tooth enamel standard AG-Lox, and several more fossil and modern tooth enamel samples <100  $\mu\text{g}$  in weight.

A number of hardware modifications were required to improve system stability and to remove the observed effects of the contribution of blank  $\text{CO}_2$  when analysing samples of <100  $\mu\text{g}$  tooth enamel. With these modifications, external reproducibility of the set-up for tooth enamel aliquots between 25 and 80  $\mu\text{g}$  (structural  $\text{CaCO}_3$  equivalent of 2-7  $\mu\text{g}$ ) reaches a precision of <0.10‰ (1 $\sigma$ ) for both  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$ . This is comparable to precisions typically attained for routine analysis of much larger samples in standard operation on the same equipment, and demonstrates that automated stable isotope analysis of <100  $\mu\text{g}$  amounts of tooth enamel is achievable with Continuous Flow mass spectrometry.

This novel method opens new research avenues for high spatial resolution intra-tooth sampling of very small or thin enamelled teeth to reconstruct past seasonality and climate conditions. It also enables minimally-invasive sampling of precious fossil teeth such as hominins.

**Funding Sources** The project was funded by the Max Planck Society.

### Evolution & Biology of Non-Avian Theropods

#### ONTOGENETIC VARIATION BETWEEN *GORGOSAURUS LIBRATUS* AND *DASPLETOSAURUS TOROSUS* (THEROPODA: TYRANNOSAURIDAE) AND TAXONOMIC IDENTIFICATION OF JUVENILE TYRANNOSAURIDS

Voris, Jared T.<sup>1</sup>, Zelenitsky, Darla K.<sup>1</sup>, Therrien, François<sup>2</sup>  
<sup>1</sup>Department of Geoscience, University of Calgary, Calgary, Alberta, Canada, <sup>2</sup>Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada

Tyrannosaurids underwent well-known changes in cranial morphology through ontogeny, where the skull became deeper and more robust, cranial ornamentation enlarged, and cranial sinuses inflated. However, less is known about the differences in cranial ontogeny among tyrannosaurid species and what features can be useful for the taxonomic identification of immature individuals. Here we examine previously known and recently discovered juvenile material of *Daspletosaurus torosus* (Tyrannosaurinae) and *Gorgosaurus libratus* (Albertosaurinae), two contemporaneous tyrannosaurids from the Upper Cretaceous (upper Campanian) Dinosaur Park Formation of Alberta (Canada), in order to compare the cranial morphology of these taxa. Examination of the only juvenile '*Daspletosaurus*' skull known, TMP 1994.143.1 curated at the Royal Tyrrell Museum of Palaeontology, leads to its

reassignment as *Gorgosaurus* based on several characteristics (e.g., presence of a small postorbital horn adjacent to the orbit, lacrimal horns situated anterior to the ventral ramus, and the presence of 13 maxillary teeth). Our results reveal differences in juvenile characters and cranial ontogeny between the two tyrannosaurid taxa. All known ontogenetic stages of *Daspletosaurus* possess a postorbital process of the squamosal that terminates posterior to the anterior margin of laterotemporal fenestra, a dorsoventrally constricted jugal ramus of the maxilla, and 15–17 maxillary teeth. In *Gorgosaurus*, all known ontogenetic stages have a squamosal process of the postorbital that terminates anterior to the posterodorsal corner of the laterotemporal fenestra and long medial premaxillary processes of the nasal. Additionally, some characters are found to develop earlier (e.g., postorbital horn) or change more dramatically through ontogeny (e.g., maxillary fenestra becomes elongate and encroaches on the anterior margin of the antorbital fossa, increasing interdigitation of the maxilla and nasal) in *Daspletosaurus* than in *Gorgosaurus*. Contrary to previous studies that suggested juvenile individuals of different tyrannosaurid species were hard to differentiate, we find that although *Daspletosaurus* and *Gorgosaurus* undergo distinct ontogenetic changes, many genus-diagnostic features develop early in each taxon. Our study demonstrates that the taxonomic identification of juvenile tyrannosaurids may be easier than previously thought.

**Funding Sources** Roger Soderstrom Scholarship, Royal Tyrrell Museum Cooperating Society Student Research Grant, DRI Student Project Grant to J.T.V.; NSERC Discovery Grant to D.K.Z.

## Biomechanics & Functional Morphology

### TORSO MORPHOLOGY IN EXTANT QUADRUPED AMNIOTES TO INFER THE BODY MORPHOLOGY OF FOSSIL TAXA

Walsh, Myles<sup>1</sup>, Shimada, Kenshu<sup>2</sup>

<sup>1</sup>Biological Sciences, DePaul University, Chicago, Illinois, U.S.A., <sup>2</sup>Biology & Environmental Science, DePaul University, Chicago, Illinois, U.S.A.

Body size and form are fundamentally important properties when considering the biology of each organism. Reconstructions of extinct vertebrates are often determined using quantitative relationships between the size of certain skeletal elements and the body mass or size of extant taxa, whereas variations of their torso morphology have been poorly investigated to date. This study examined torso shapes of 114 extant quadrupedal amniote taxa comprising small to large, terrestrial and semi-aquatic reptiles and mammals. Complex torso morphology from the ribcage to the pelvic girdle was conceptually simplified to represent

two combined ‘elliptic conical frustum’ shapes defined by nine basic variables: total torso length, anterior and posterior torso length, maximum torso width and height, anterior torso width and height, and posterior torso width and height. Preliminary analyses indicate that these two combined frusta provide a reasonable approximation of the amniote torso morphology, where calculated volumes ( $M = 2245.6$ ,  $SD = 3320.5$ ) using these frusta demonstrated no significant difference ( $p = 0.370$ ) from torso volume data of the same taxa attained by the use of a more sophisticated (digital convex hull) method in a previously published study ( $M = 2503.25$ ,  $SD = 3629.5$ ). In addition to torso morphology, this study also examined two additional variables, the maximum humerus and femur lengths, in order to elucidate potential relationships and predictive values within the quadrupedal body plan. Correlation analyses yielded several significant relationships between maximum femur and/or humerus lengths and certain aspects of the amniote torso. For example, there exists a significant relationship between maximum humerus length and maximum torso height ( $p < 0.001$ ) as well as, to a certain extent, between maximum humerus length and maximum torso width ( $p = 0.049$ ). In addition, there is a relationship between maximum femur length and maximum torso height ( $p < 0.001$ ). These relationships suggest that the limb lengths of terrestrial amniotes may be able to predict at least some portions of the quadrupedal body plan that can be useful for inferring the body forms of extinct quadruped amniotes, including non-bipedal dinosaur taxa, even from incomplete specimens, as long as a reasonably complete humerus or femur is preserved.

## Anatomical & Developmental Explorations of the Mammalian Skull

### DIET AND JAW DISPARITY IN THE ARTIODACTYL IN RELATION TO CLIMATE AND TOPOGRAPHY

Wang, Bian<sup>1</sup>, Badgley, Catherine<sup>2</sup>, Zelditch, Miriam<sup>3</sup>, VanValkenburg, Ethan<sup>2</sup>

<sup>1</sup>Earth and Environmental Sciences, University of Michigan, Ann Arbor, Michigan, U.S.A., <sup>2</sup>Ecology and Evolutionary Biology, University of Michigan, ANN ARBOR, Michigan, U.S.A., <sup>3</sup>Museum of Paleontology, University of Michigan, ANN ARBOR, Michigan, U.S.A. The order Artiodactyla is a taxonomically and ecologically diverse group of mammals that has been widely studied in ecomorphological research, with important applications for paleoecological and paleoenvironmental reconstructions. Here we investigate the relationships within the artiodactyls between: (1) mandibular morphology and dietary habit, (2) species richness among dietary categories and climatic and physiographic variables, and (3) jaw disparity and climatic and physiographic variables. We quantify mandibular shape

with landmark-based geometric morphometric methods. We documented 153 extant artiodactyl species, with an average of four specimens per species, covering all families within the order that are fully terrestrial and herbivorous as well as all tribes within the Bovidae, the largest extant family. Ten landmarks were chosen to capture the overall morphology of the mandible, and semi-landmarks were used to document the curvature between landmarks. Species were divided among six feeding categories based on a dataset of detailed forage selectivity and documented preferences compiled from the literature: obligate grazers, variable grazers, intermediate feeders, browsers, frugivores, and generalists. Multivariate analyses show significant differences ( $p < 0.05$ ) in the jaw morphology of most feeding categories. Significant variables include the depth of the mandibular body, the length of the cheek-tooth row, and the shape of the angular and coronoid processes. Dietary extremes (e.g., obligate grazers vs. frugivores) occupy distinct regions of morphospace, whereas generalist and intermediate feeding categories overlap with other categories in morphospace. We aim to establish a dietary model using the quantitative relationship between mandibular shape and diet of living artiodactyls. Our morphospace model provides a new tool for paleoecological inference for fossil ungulates, which constitute a widely distributed and diverse component of the Cenozoic fossil record of several continents. In addition, we incorporate mandibular morphology into a large dataset of artiodactyl occurrences, climatic variables, and physiographic variables of 353 faunal localities across the world. Seasonal extremes of temperature and precipitation are the best predictors of the number and proportion of species in dietary categories.

#### **Colbert Poster Prize/Dinosaur Systematics, Diversity & Ecology**

#### **ANATOMICAL AND HISTOLOGICAL DATA INDICATE UNCINATE PROCESSES TO BE HOMOLOGOUS ACROSS ARCHOSAURIA**

Wang, Yan-Yin, Sullivan, Corwin, LeBlanc, Aaron R.  
Biological Sciences, University of Alberta, Edmonton, Alberta, Canada

Uncinate processes are ossified or cartilaginous structures extending posteriorly from the corresponding dorsal ribs, and they are present in *Sphenodon* and nearly all extant archosaurs. The uncinates of birds and many other pennaraptoran theropods are ossified barbs, and well documented in the literature. By contrast, cartilaginous, tab-like uncinates are present in modern crocodylians, and rarely found in fossil archosaurs. Additionally, uncinates in modern birds are functionally linked to respiration, as shown by in vivo experiments on the associated muscles. The presence of uncinates in multiple archosaur groups suggests they may be homologous throughout Archosauria,

and hints at the possibility that they may have been a part of the respiratory system in many archosaurs. However, cartilaginous features are rarely preserved in fossils, which makes the distribution of uncinates in fossil archosaurs difficult to determine.

We used surface osteological correlates,  $\mu$ CT scans, and histology to identify anatomical proxies for uncinata attachment in extant *Caiman crocodilus* and *Meleagris gallopavo*. Three proxies were found in both extant archosaurs. Removing an uncinata from the corresponding dorsal rib revealed a rugose, concave scar (uncinate scar) on the rib's posterior surface, a feature also evident in other extant taxa. The  $\mu$ CT scans showed that the cortical bone was perforated near the uncinata scar. Histological sections at the level of the uncinata scar suggest that the uncinata is connected to the dorsal rib by fibrous connective tissues, and that Sharpey's fibers are abundant at the uncinata scar. We sampled fossil ribs to test for the presence of uncinates, using these proxies. Uncinate scars were identified in 42 taxa, in three basic forms: oval concavities in most archosaurs, narrow grooves in ceratopsians, and oval concavities each with one accompanying proximal ridge in tyrannosaurids. Cortical perforations are present in tyrannosaurids, but absent in ceratopsians. Fibrous connective tissues with potential Sharpey's fibers are present at the uncinata scar in tyrannosaurids. By contrast, fibrous connective tissue is absent, and abundant Sharpey's fibers are present, in ceratopsians. Preliminary ancestral state reconstructions using parsimony and likelihood methods suggest that the presence of cartilaginous uncinates is the plesiomorphic condition for Archosauria. Uncinates may have had a respiratory role ever since the dawn of archosaur evolution.

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#### **Fishes & Chondrichthyans: Evolution & Distribution**

#### **ARE SPIRAL BROMALITES ENTEROSPIRAE OR COPROLITES? A BRIEF REVIEW WITH SOME ADDITIONAL EVIDENCE**

Ward, David J., Duffin, Christopher J., Ward, Alison  
Earth Sciences, Natural History Museum, London, U.K.

An academic fascination with bromalites, often referred to as coprolites (fossil fecal material) goes back almost two centuries. In the draft of Henry de la Beche's cartoon *Duria Antiquior*, translated as 'A more ancient Dorset' all the

marine reptiles were immortalized in the process of defecation. In the finished work, an editorial paintbrush had reduced the number of putative coprolites heading for the sea floor. At the time, it was assumed that spiral coprolites, common at Lyme Regis, were produced by marine reptiles, namely ichthyosaurs and plesiosaurs. It was William Buckland in the 1830's who, by filling the intestine of a dogfish with Roman cement, demonstrated that spiral coprolites could have been produced by sharks. He suggested that they were formed by a plastic ribbon of faeces leaving the spiral valve and coiling up within the confines of the colon. However, in 1907 Anton Fritsch introduced the concept of 'enterospirae' - that some coprolites were not excrement but fossilized spiral valves of fish. This idea was explored by Michael Williams in 1972 who produced histological evidence of mucosal folds preserved in an early Permian spiral bromalite. He did accept that some bromalites were true coprolites. This view was re-evaluated by James McAllister in 1985, who regarded Williams's mucosal folds as dubious and noted that the number of coils seen in some bromalites exceeded the number of coils in the spiral valve of a Recent dogfish. McAllister did not, however, rule out the possibility that some coprolites are true enterospirae.

Bromalites from the early Carboniferous of Leith, Scotland demonstrate a clear separation between the individual whorls of sectioned specimens. A similar separation, between 300 and 500  $\mu\text{m}$  wide can be seen in those from the Lower Lias, Lower Jurassic of Dorset, England. In both cases fish scales within the fecal matrix do not penetrate from one whorl to another. This is consistent with the individual whorls being separated by a thin mucosal membrane and is difficult to explain if these were fecal ejecta.

In contrast two spiral coprolites from the latest Cretaceous of Khouribga, Morocco have the spiral axis at  $90^\circ$  and  $45^\circ$  to the polar axis respectively. These demonstrate that the partially flexible fecal ribbon having left the spiral valve was deviated from the long axis of the colon and reformed as a fusiform coprolite.

Conclusions: most spiral bromalites are coprolites but true enterospirae probably exist.

### **Symposium: Paleoneurology**

#### **GETTING IT INSIDE YOUR HEAD: A UNIFIED ANALYSIS OF BRAIN AND SKULL EVOLUTION**

Watanabe, Akinobu<sup>1</sup>, Bedell, Mariel<sup>1</sup>, Felice, Ryan<sup>2</sup>, Balanoff, Amy<sup>3</sup>

<sup>1</sup>New York Institute of Technology, Old Westbury, New York, U.S.A., <sup>2</sup>University College London, London, U.K.,

<sup>3</sup>Johns Hopkins University, Baltimore, Maryland, U.S.A.

The brain is a profoundly complex structure shaped by myriad processes, both intrinsic and extrinsic to the

organism. Combined with modern comparative methods, advances in imaging and morphometric modalities have accelerated our search for drivers of brain evolution through deep time. However, these analyses typically neglect that the brain is encased by the skull and that they share important developmental pathways. It is therefore crucial to assess how the brain and the skull, along with other cranial structures, evolved in a highly coordinated way. To examine this interplay, we bring together high-density geometric morphometric data of endocranial and cranial shapes across crown birds, a clade exemplified by its disparate skull and brain anatomy. Comparative analyses clearly demonstrate that skull and endocranial shapes are highly correlated. As expected, endocranial shape is closely associated with braincase morphology and skull depth, but interestingly, it is also strongly linked to beak length variation, a hallmark of cranial innovation in birds compared to non-avian archosaurs. Of the four major brain regions that we analyzed (cerebrum, optic lobe, cerebellum, medulla), the cerebrum exhibited the strongest correlation with overall skull shape which agrees with the current molecular understanding of brain and skull development. Furthermore, we find that songbirds and species with elaborate cranial ornamentations deviate from the large-scale integration pattern, implying reduced coupling of brain and skull evolution in these taxa. Taken together, these results imply that there is substantial interplay between brain and skull shape that should not be ignored in macroevolutionary studies. By placing the brain in the broader context of cranial evolution, we present a more holistic approach to understanding how these complex structures have evolved.

**Funding Sources** National Science Foundation, European Research Council.

### **Colbert Poster Prize/Taphonomy & Stratigraphy**

#### **REVISED STRATIGRAPHIC RELATIONSHIPS OF THE MIDDLE PART OF THE TULLOCK MEMBER OF THE FORT UNION FORMATION (GARFIELD COUNTY, MONTANA, U.S.A.) ELUCIDATES POST K-PG MAMMALIAN RECOVERY DYNAMICS**

Weaver, Lucas N.<sup>1</sup>, Tobin, Thomas S.<sup>2</sup>, Claytor, Jordan R.<sup>1</sup>, Clemens, William A.<sup>3</sup>, Wilson, Gregory P.<sup>1</sup>

<sup>1</sup>University of Washington, Seattle, Washington, U.S.A.,

<sup>2</sup>University of Alabama, Tuscaloosa, Alabama, U.S.A.,

<sup>3</sup>University of California, Berkeley, California, U.S.A.

The Hell Creek region of northeastern Montana is an excellent study system to explore ecological recovery from the Cretaceous–Paleogene (K–Pg) mass extinction. The Tullock Member of the Fort Union Formation (Tullock, hereafter) was deposited during the first 1.2 million years after the mass extinction. Mammalian local faunas from the

lowermost Tullock are ‘disaster’ faunas, dominated by a few abundant, mostly insectivorous survivors. Mammalian faunas from the middle Tullock are ‘recovered’ faunas: they exceed pre-K–Pg levels of both taxonomic and ecological richness, largely driven by abundant archaic ungulates and plesiadapiform primates. Middle Tullock fossil assemblages, however, have been interpreted as deposited in a single, large channel complex, the Garbani Channel, that is coarsely constrained stratigraphically. Ashes bracketing the Garbani Channel constrain deposition to an interval of ~623 thousand years, but the stratigraphic relationships of localities within this interval are largely unknown. Thus, our view of the local recovery is temporally aggregated, and the record of biotic recovery in the interval between ‘disaster’ and ‘recovered’ faunas is unclear. Here, we present a new stratigraphic model for the middle Tullock resulting from a combination of field mapping, stratigraphic logging, and petrography.

We find that middle Tullock fossil localities are not derived from one channel complex but rather two temporally and lithologically distinct sedimentary units: the Biscuit Springs Beds (BSB) and the Garbani Channel (GC). The BSB are ~10 m thick and laterally continuous, cropping out across much of the study area; whereas the GC is ~20–30 m thick and has a limited lateral extent (~100 m across). The top of the GC is stratigraphically ~10–15 m above the top of the BSB, and in some places the GC cuts through the entirety of the BSB, a relationship that previously complicated interpretations of their relative age. This cross-cutting relationship reveals that the BSB, and the mammalian fossils they host, are likely older than the GC. Thus, the BSB represent a potential intermediate fauna between the older, post-K–Pg ‘disaster fauna’ and younger GC local fauna. Further, the BSB local fauna can now be temporally constrained by two ashes dated to 65.741 and 65.540 Ma. Studying the succession of Tullock local faunas in light of these new findings may help clarify the tempo and mode of mammalian recovery in the aftermath of the K–Pg mass extinction.

#### **Symposium: Dietary Reconstruction**

### **PERMIAN TERRESTRIAL VERTEBRATE FOOD WEBS: A COMBINED DENTAL WEAR AND ISOTOPE APPROACH**

Weber, Katrin<sup>1</sup>, Winkler, Daniela E.<sup>1</sup>, Weber, Michael<sup>1</sup>, Fröbisch, Jörg<sup>2</sup>, Kaiser, Thomas M.<sup>3</sup>, Tütken, Thomas<sup>1</sup>

<sup>1</sup>Institute of Geosciences, Johannes Gutenberg-University, Mainz, Germany, <sup>2</sup>Leibniz Institute for Evolution and Biodiversity Research, Museum of Natural History, Berlin, Germany, <sup>3</sup>Department of Mammalogy and Paleoanthropology, University of Hamburg, CeNaK, Hamburg, Germany

Food is the major link between animals and their environment. The evolution of distinct dietary adaptations

and subdivision of niches are fundamental aspects of vertebrate ecology. Herbivory in non-mammalian tetrapods was a key innovation that allowed (mostly) amniotes to access the vast resources provided by biomass rich in cellulose. The fossil record suggests that a trophic web structure similar to modern terrestrial ecosystems, in which many herbivores support only a few carnivores, first evolved during the Permian.

Teeth are most resistant against early diagenetic alteration and therefore often represent the only remains available for inferring the dietary and food processing behavior of extinct vertebrates. Non-mammalian tetrapods typically have homodont dentitions and thus the morphology of their teeth does not allow for unequivocal determination of their feeding adaptation. Recently, applications of non-traditional stable isotope systems (e.g., Ca, Mg, Zn) have become promising proxies for distinguishing faunivorous from herbivorous taxa and determining trophic position in food webs. In addition, dental microwear texture analysis (DMTA) serves as a non-destructive dietary proxy for mechanical food properties of the last meals and enables us to distinguish soft- from hard-object feeders. So far, DMTA has mainly been performed on extant and fossil mammalian species and has only recently been transferred to non-mammalian taxa. This is challenging because non-mammalian tetrapods do often not necessarily chew and thus their dentition is proposed to have received reduced attritional and abrasional wear as compared to a modern mammal of equal ecology and body mass.

Here we present preliminary data using a novel approach which combines non-traditional stable isotopes and DMTA to assess the diets of Permian non-mammalian tetrapods.  $\delta^{44/42}\text{Ca}$  and DMT of tetrapod teeth (and bone) were analyzed from different presumed herbivores and faunivores from lower and upper Permian sites. Our preliminary DMTA results show that diet-related wear is preserved and may separate insectivorous taxa from those with other feeding strategies. This has great potential for diet reconstruction in taxa such as Caseidae, in which an ontogenetic diet shift from insectivory to herbivory has been hypothesized. First  $\delta^{44/42}\text{Ca}$  results indicate that Ca isotopes (enamel and bone) are a reliable deep time trophic level proxy to separate faunivores from herbivores, even in Permian ecosystems.

**Funding Sources** This project received funding from the European Research Council (ERC) under the European Union’s Horizon 2020 research & innovation programme, grant agreement No 681450.

#### **Symposium: Dietary Reconstruction**

### **ASSESSING THE VARIABILITY OF CA AND SR ISOTOPES IN VERTEBRATE SOFT- AND HARD-TISSUES: IMPLICATIONS FOR RECONSTRUCTING DIET AND PROVENANCE**

Weber, Michael<sup>1</sup>, Tacail, Theo<sup>2</sup>, Lugli, Federico<sup>3</sup>, Clauss, Marcus<sup>4</sup>, Tütken, Thomas<sup>1</sup>

<sup>1</sup>Johannes Gutenberg University Mainz, Mainz, Germany, <sup>2</sup>University of Bristol, Bristol, U.K., <sup>3</sup>University of Bologna, Bologna, Italy, <sup>4</sup>University Zürich, Zürich, Switzerland

The addition of new geochemical proxies to the paleontology toolbox enables us to improve the understanding of past ecosystems and animal behavior. Vertebrate soft- and hard-tissues (bones and teeth) provide geochemical information about the animal's dietary and physiological traits. Tooth enamel as incrementally growing and diagenetically robust highly mineralized tissue records isotope time series of ingested diet and water.

Strontium (Sr) is a non-essential trace element mainly ingested with the diet substituting for Ca in enamel and bone bioapatite. Radiogenic Sr isotopes (<sup>87</sup>Sr/<sup>86</sup>Sr) are a well-established provenance proxy to reconstruct past and present animal migration behavior and habitat use. Stable Sr isotopes ( $\delta^{88/86}\text{Sr}$ ) vary in mass-dependent manner in the environment and decrease along the food chain, similar to Ca isotopes ( $\delta^{44/42}\text{Ca}$ ), both being proxies for diet and trophic level. Combined  $\delta^{88/86}\text{Sr}$  and <sup>87</sup>Sr/<sup>86</sup>Sr analyses enable us to determine the animal's diet and habitat bedrock, respectively. However, Sr in bioapatite (< 0.1 wt%) is prone to diagenesis while Ca (38 wt%) is not. Thus,  $\delta^{44/42}\text{Ca}$  is more robust than  $\delta^{88/86}\text{Sr}$  for diet and trophic level reconstructions of fossil vertebrates.

Knowledge of intra- and inter-individual Sr and Ca isotope variability at population level is paramount for reliable diet and provenance reconstructions. Here we present Sr and Ca isotope data of soft- and hard-tissues with different turnover rates from controlled feeding experiments of rats and guinea pigs, fed for up to 59 days with pelleted and natural plant-, insect- and meat-based diets. To assess the influence of water vs. food, one group received Ca- and Sr-rich water instead of tap water. Dietary changes in ever growing rodent incisors (~0.5 mm/day) were monitored with high temporal resolution by in-situ LA-MC-ICP-MS Sr isotope analysis.

Fast growing incisor enamel shows a higher variability in its Sr isotopic composition in comparison to slower growing bone. Stable Sr isotope values for rodents feeding on different diets display a diet-to-enamel depletion of up to -0.4 ‰, in agreement with literature values. Despite controlled diet and water, intra- and inter-individual Sr isotope variability was high within the experimental rodent populations. Implications of this isotope variability for the reconstruction of diet, trophic level, and locally bioavailable <sup>87</sup>Sr/<sup>86</sup>Sr ranges in fossil food webs will be discussed.

**Funding Sources** This project received funding from the European Research Council (ERC) under the European

Union's Horizon 2020 research & innovation programme, grant agreement No 681450.

## Late Cenozoic Mammalian Macroecology & Macroevolution

### A LATE BLACAN LOCAL FAUNA FROM NORTHERN IDAHO

Welch, Jonathan, Blua, Marlana, Magone, Neville, Case, Judd A.

Biology, Eastern Washington University, Cheney, Washington, U.S.A.

A newly discovered site (JW) near Priest River, Idaho yields early Pleistocene-age fossil mammals. Numerous teeth and bone fragments have been recovered from an oxbow paleohabitat cropping out along the Pend Oreille River.

Specimens of nine different taxa have been found including muskrat, beaver, porcupine, deer, horse, pronghorn antelope, canid, lynx, and bear. A right mandible containing i1 and m1–m2 is of an *Ondatra* sp. of muskrat. The m1 is significantly shorter, narrower, and the L/W ratio smaller than that of *O. zibethicus*. Yet the m1 length and width are both larger than either *O. idahoensis* and *O. annectens*. The beaver is represented by an isolated incisor, two lower molars, and one upper molar. All three molars share the S enamel occlusal pattern seen in *Castor*, contrasting with the occlusal pattern of *Dipoides*. The one external striid and three internal striids on the lower molars that are unequal in length indicate *Castor californicus* rather than *C. canadensis*. A p4 and m1 of a species of *Erethizon* porcupine are significantly larger than the p4 and m1 of either *E. bathygnathum* or *E. dorsatum*. The deer specimens include a complete right M2 and a near complete m3. The M2 has four distinct main cusps, a prominent paracone, a paracone rib, a metastyle, and a very small entostyle, suggesting that this is a species of *Bretzia*, albeit smaller than *B. pseudalces*. A P2, dP3, and dp3 of *Plesippus idahoensis* are also present. Finally, an m1 of *Capromeryx*, a right P3 of a *Lynx* sp., a left p3 of an *Ursus* sp., and a right m1 of a *Canis* sp. are also present.

The Priest River local fauna (l.f.) cannot be older than 2.58 Ma or the beginning of Blancan V (= early Pleistocene) because of the FAD for *Erethizon* from South America at GABI1. The Priest River l.f. cannot be younger than 1.72 Ma (end of Blancan V) as *Plesippus* has its LAD in Froman Ferry l.f. at the end of Blancan V. *Capromeryx tauntonensis* was previously restricted to Blancan IV and the Taunton l.f. from central Washington and *C. tauntonensis* would be a time range extension into the Blancan V NALMA sub-age, which argues against the Priest River l.f. being younger than Blancan V.

This is the first mammalian fauna known from northern Idaho as previously known Cenozoic faunas from the region are the early to late Blancan faunas, from the Glenn's Ferry Fm., SW Idaho, some 570 miles to the south and the early to mid-Blancan faunas from the Ringold Fm., central Washington, 225 miles away.

### Mesozoic & Early Cenozoic Mammalian Evolution

#### CAINOTHERIIDAE FROM QUERCY (SW OF FRANCE): DIVERSITY DYNAMICS AND BIOTIC/ABIOTIC INTERACTIONS AROUND THE EOCENE–OLIGOCENE TRANSITION (34–33.5 MA)

Weppe, Romain<sup>1</sup>, Condamine, Fabien<sup>1</sup>, Blondel, Cécile<sup>2</sup>, Guinot, Guillaume<sup>1</sup>, Orliac, Maëva J.<sup>1</sup>

<sup>1</sup>Institut des sciences de l'évolution (ISE-M), Montpellier, Occitanie, France, <sup>2</sup>PALEVOPRIM, Poitiers, Nouvelle Aquitaine, France

Understanding the diversity dynamics of species is a central topic in evolutionary biology and paleontology. After the massive extinction of the Cretaceous–Tertiary crisis, the Eocene–Oligocene transition (34–33.5 Ma) coincided with one of the major extinction events of the Cenozoic. It is indeed associated with major climatic, geographical, and ocean circulation changes. At the same time, a major faunal turnover occurred in Europe, known as the 'Grande Coupure'. This event is associated with the extinction of numerous endemic European placental mammals, which had evolved in the 'island Europe' context from the middle to the upper Eocene. European artiodactyls are particularly impacted by these changes, and many endemic families died out around this transition. However, a family of small artiodactyls, the Cainotheriidae, crossed the Eocene–Oligocene boundary and diversified during the Oligocene. Here we applied, for the first time, a well-known biological model of diversity analysis to a group of extinct artiodactyls, the Cainotheriidae. Using the cainotheriid fossil record from the karstic infillings of the Quercy Phosphorites (south-western France), we observe that this family experienced a major radiation phase during the early Oligocene, followed by a decline phase until the end of the Oligocene. The exceptional fossil record of the Quercy phosphorites provides us with an extremely precise vision of the evolution of Cainotheriidae diversity over 10 million years, on both sides of the Grande Coupure, with incomparable preservation indices. Our results also highlight the absence of direct correlation between the speciation and extinction phases and the important environmental changes of the Eocene–Oligocene transition and the end of the Oligocene. These results thus suggest the potentially important role of biotic interactions in the evolutionary success and then decline of the Cainotheriidae from Quercy.

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### Mesozoic & Early Cenozoic Mammalian Evolution

#### A NEW SPECIES OF *PLEUROSTYLODON* (MAMMALIA, NOTOUNGULATA) FROM THE LATE EOCENE LOS QUEÑES LOCALITY, ANDEAN MAIN RANGE, CENTRAL CHILE

Wheat, Theodore C.<sup>1</sup>, McGrath, Andrew J.<sup>1</sup>, Croft, Darin A.<sup>2</sup>, Wyss, André<sup>1</sup>, Flynn, John J.<sup>3</sup>

<sup>1</sup>Department of Earth Science, University of California, Santa Barbara, Santa Barbara, California, U.S.A., <sup>2</sup>Department of Anatomy, Case Western Reserve University, Cleveland, Ohio, U.S.A., <sup>3</sup>Division of Paleontology and Richard Gilder Graduate School, American Museum of Natural History, New York, New York, U.S.A.

Notoungulata, the most diverse group of ungulates present during South America's Cenozoic isolation, is classically subdivided into Toxodontia and Typotheria. Here we describe a new species of *Pleurostylodon* (a toxodontian) based on a left hemimandible bearing a complete dentition. 'Isotemnidae,' to which *Pleurostylodon* has long been assigned, is currently considered a non-monophyletic assemblage of basal toxodontians. *Pleurostylodon* was first identified from the Casamayoran South American Land Mammal Age (SALMA) of Argentine Patagonia (now including both Vacan and Barrancan 'subages'); other isotemnids became known subsequently from the Casamayoran and Mustersan SALMAs of Patagonia and the Casamayoran of northwest Argentina. This discovery likely extends the range of *Pleurostylodon* into the Mustersan SALMA of central Chile.

The type and only specimen of this new taxon, SGOPV 5529, includes a complete left lower tooth row, including i1–i3, the lower canine, p1–p4, and m1–m3. SGOPV 5529 bears, at mid-crown height, a small projection on the posterior face of the metaconids of m1–m3 that, with wear, merges with the metaconid forming the 'curved' metalophid seen in some species of *Pleurostylodon* and differing from other isotemnids. SGOPV 5529 is distinct from other species of *Pleurostylodon* in being more hypsodont and lacking cingulids on p3–m3. Incorporating the new taxon from Chile into a previously published genus-level phylogenetic analysis pairs SGOPV 5529 with *Pleurostylodon*.

SGOPV 5529 was recovered from the Abanico Formation near the town of Los Queñes in the Andean Main Range of central Chile. This area records at least two stratigraphically superposed SALMAs. The strata from which SGOPV 5529 was recovered are likely late Eocene in age and assignable to the Mustersan SALMA. This

discovery thus extends the biochron of *Pleurostylyodon*, which was previously restricted to the Casamayoran SALMA. In addition to *Pleurostylyodon* n. sp., the late Eocene strata at Los Queñes host a diverse, as yet undescribed mammalian fauna. Future reports on other elements of this fauna promise to shed light on the biogeographical relationships between Patagonia and northwest Argentina for the middle to late Eocene.

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### **Colbert Poster Prize/Cenozoic Herpetology**

#### **LIZARD BYTES: THREE-DIMENSIONAL DENTAL TOPOGRAPHY ANALYSIS OF EXTANT PLEURODONT SQUAMATES, WITH IMPLICATIONS FOR RECONSTRUCTING THE DIETS OF EXTINCT FOSSIL SQUAMATES**

Whiting, Evan, Fox, David L.  
Earth & Environmental Sciences, University of Minnesota,  
Minneapolis, Minnesota, U.S.A.

Dental topography analysis has emerged as a powerful quantitative tool for dietary reconstructions of fossil vertebrates, with multiple, homology-free metrics capable of distinguishing among different dietary categories. So far, these methods have almost entirely been applied to mammals, but more recent applications to non-mammalian vertebrates have shown great promise. Further application of these techniques to non-mammalian vertebrates could provide novel or enhanced insights into the quantitative associations between tooth morphology and diet throughout vertebrate evolution.

Squamate reptiles (lizards and snakes) constitute one of the most taxonomically and ecologically diverse clades of terrestrial vertebrates. Squamate diets fall along a continuum from carnivory to herbivory, often with overlapping intermediate dietary categories. Previous dental topography work on extant squamates has relied on geographic information systems (GIS) methods, in which tooth surfaces are converted into digital elevation models instead of being treated as three-dimensional surface meshes. For our study, we used computed microtomography ( $\mu$ CT) to generate high-resolution, three-dimensional dentary tooth row surface meshes for 66 extant, pleurodont species of lizards and snakes. We assigned each species to one of four dietary categories (herbivore, omnivore, invertivore, carnivore) based on data from the literature. Then, using molarR and CloudCompare, we obtained values for each of our surface meshes for the following dental topography metrics: Orientation Patch Count Rotated (OPCR), Dirichlet Normal Energy (DNE), and Ambient Occlusion (PCV).

All three metrics are capable of differentiating between dietary categories, although their efficacy varies. OPCR

and DNE values for entire tooth rows are moderately to highly successful at distinguishing among all four dietary categories; herbivores and omnivores have the highest values. However, this pattern becomes somewhat muddled when those values are averaged along tooth rows. PCV seems to be independent of OPCR and DNE, exhibiting an inverse pattern, but there is more overlap between categories. The number of teeth also appears to have a greater impact on PCV results; specimens with more teeth have lower PCV values. This is the first time that any of these three-dimensional dental topography metrics have ever been applied to squamates, paving the way for future work, including dietary reconstructions of extinct fossil squamates.

**Funding Sources** Thesis Travel Grant, University of Minnesota; Joyce Davenport Fellowship, Bell Museum; Richard Estes Memorial Grant, Society of Vertebrate Paleontology.

### **Dinosaur Systematics, Diversity & Ecology**

#### **A JUVENILE DIPLODOCID SAUROPOD FROM THE MORRISON FORMATION (LATE JURASSIC) PRESERVING A SKIN IMPRESSION**

Whitlock, John A.<sup>1</sup>, Smith, Kathlyn<sup>2</sup>, Winters, Samuel<sup>2</sup>  
<sup>1</sup>Biology, Mount Aloysius College, Cresson, Pennsylvania, U.S.A., <sup>2</sup>Geology and Geography, Georgia Southern University, Statesboro, Georgia, U.S.A.

Carnegie Museum of Natural History (CM) specimen 41682 consists of a fragment of a dorsal rib, five incomplete dorsal neural arches, and a small (12 x 5 cm), subtriangular skin impression. Originally collected by Earl Douglass in 1910 from Dinosaur National Monument (Tithonian; Morrison Formation; Utah, U.S.A.), the skin impression was discovered much later during subsequent preparation. CM 41682 is a diplodocoid sauropod based upon the lack of flaring triangular processes on the dorsal neural spine; it is furthermore assignable to the successively less inclusive clades Flagellicaudata (based upon the presence of ventrally conjoined centropostzygapophyseal and posterior centriapophyseal laminae) and Diplodocidae (based upon the presence of a posterior centroparapophyseal lamina). The early loss of bifurcation (here incipient by, at latest, the sixth dorsal) and the early migration of the parapophysis to a position level with the zygapophyseal table both suggest affinities with either *Apatosaurus* or *Barosaurus*; the lack of an accessory lamina on the spinodiapophyseal lamina differentiates CM 41682 from *Barosaurus* and makes a referral to *Apatosaurus* the most likely conclusion.

The skin impression preserves approximately 32 distinct, non-overlapping scale impressions, ranging from

approximately 1.0–1.5cm in diameter. Most of the scales are hexagonal in shape, although the larger scales grade into what has been termed a ‘pebble’ morphology in hadrosaurs. There is no evidence for any of the varied tubercle patterns seen in the embryonic skin impressions from Auca Mahuevo; there only appears to be the ‘ground’ arrangement of densely arranged, roughly uniformly distributed tubercles. This ‘ground’ pattern appears to be the standard arrangement for post-hatching diplodocids, based upon comparisons with other sauropod skin impressions, including those attributable to both *Diplodocus* and *Apatosaurus* as well as more distantly related taxa such as *Tehuelchesaurus*.

CM 41682 represents a small individual, only slightly larger than CM 3390 (‘Ajax’), one of the osteologically youngest specimens of *Apatosaurus* (approximately 5–7 on the Histologic Ontogenetic Stage scale). Histological analysis of the dorsal rib of CM 41682 is ongoing but confirms the juvenile status of the individual.

### Romer Prize

#### HISTOLOGICAL INSIGHTS INTO MAMMALIAN DENTAL EVOLUTION FROM THE DENTITIONS OF NON-MAMMALIAN SYNAPSIDS

Whitney, Megan  
Museum of Comparative Zoology, Harvard University,  
Cambridge, Massachusetts, U.S.A.

The acquisition of derived dental features such as prismatic enamel, diphodonty, and multiple tooth cusps are considered to be hallmarks of mammalian evolution. Further, fossils belonging to the synapsid stem lineage document the stepwise acquisition of such key innovations. Homoplasy, however, is common when traits are examined within the non-mammalian synapsid subclades, leading to some discordance between the evolutionary patterns observed along the stem and those observed within evolutionary ‘side-branches’. For example, the periodontal ligament and prismatic enamel were once considered uniquely mammal-like traits that have, in fact, repeatedly been acquired in well-studied groups of non-mammalian synapsids. Such findings offer an alternative hypothesis for mammalian trait acquisition: ‘mammalness’ evolved in parallel multiple times rather than through a series of key innovations. Here, using histological and morphological data from the dentition, I quantify patterns of trait acquisition at coarse and fine taxonomic scales throughout the synapsid stem lineage to test existing and emerging paradigms about synapsid dental evolution.

Histological analyses of 17 taxa were incorporated with gross morphological data on 457 jaws of 25 synapsid families to sample a wide range of non-mammalian

synapsid taxa. Histological traits included mode of tooth attachment, enamel microstructure, and measurements of enamel thickness while gross morphological data included proxies for frequency of tooth replacement and periodontal ligament width. For each synapsid taxon, the dentition as a unit was scored combining the phenotypic similarity of these traits to mammalian dentitions. Across major synapsid clades, the dentition follows the classic stepwise pattern. By contrast, at a finer scale, variation with major groups does not ascribe to a single pattern. This suggests a more nuanced interpretation of the traditional stepwise pattern in which the overall trend is underlain by high phenotypic plasticity and frequent homoplasy. Furthermore, the number of unique combinations of dental features was reduced throughout synapsid history suggesting that phenotypes became increasingly fixed over synapsid evolution. This reduction in phenotypic diversity, combined with the observed parallel evolution across clades, suggest that integration of dental traits earlier in synapsid evolution may characterize the origin of the mammalian dentition.

**Funding Sources** NSF DEB-1701383; EAR-1337569; PLR-1441498; SVP Dawson Predoctoral Fellowship Grant.

### Holocene & Pleistocene Mammalian Macroecology & Faunal Studies

#### ATTRIBUTION OF GENERA ACCORDING TO THE INDONESIAN PROBOSCIDEAN MORPHOLOGY OF THE HIND LIMB

Wibowo, Unggul P.<sup>1</sup>, van den Bergh, Gerrit<sup>2</sup>, Hayes, Susan<sup>2</sup>

<sup>1</sup>Geological Museum, Geological Agency of Indonesia, Bandung, West Java, Indonesia, <sup>2</sup>University of Wollongong, Wollongong, New South Wales, Australia

Analysis of homologue skeletal elements pertaining to distinct members of closely related vertebrate taxa can reveal qualitative diagnostic distinctive characteristics. This study applied biometric analysis combined with 3D Geometric Morphometric (GM) analysis of fossil and recent skeletal parts of Indonesian proboscideans. The study aimed at characterizing the morphological differences between proboscidean taxonomic groups using two skeletal elements, the femur and the tibia. The studied sample comprises a recently excavated femur and tibia of a single adult individual of the very small-sized *Stegodon sondaari* from Flores.

First, a surface morphology assessment and Principal Component Analysis (PCA) of biometric variables taken from the literature were performed on femora and tibiae of known species belonging to the genera *Stegodon*, *Elephas*, and *Sinomastodon*. Next, 3D GM analysis was performed on all specimens and a set of meaningful 3D landmarks was

defined. This revealed a set of additional distinctive morphological features. *Stegodon* and *Sinomastodon* both have a more robust femur and tibia than *Elephas*. The third trochanter of the femur is longer and flares outward more in *Stegodon* and *Sinomastodon* than in *Elephas*, which has a weakly developed third trochanter and as a result a more columnar femur. The angle of femur rotation in *Elephas* shows greater values than in most *Stegodon* and *Sinomastodon*, with the exception of *Stegodon sondaari*, which has a rotational angle even greater than in *Elephas*. Regarding the tibia, all *Stegodon* specimens have a markedly deeper and longer medial collateral ligament (MCL) attachment scar than *Elephas* (no *Sinomastodon* tibia was available for study).

The differences between *Stegodon* and *Elephas* suggest that the *Elephas* hindlimb is designed to restrict movement and reduce energy consumption, while the *Stegodon* hind limb is more flexible in movement during locomotion and has a higher strength and robustness. The more slender and columnar hind limb of *Elephas* is shared with *Mammuthus* and supports a shared close common ancestry for these genera, while the more robust hind limb bones of *Stegodon* and *Sinomastodon* is the primitive character state shared with *Mammut*. These results support classification of *Elephas* and *Stegodon* into distinct subfamilies. The *Stegodon sondaari* hind limb is morphologically different from all other *Stegodon* species examined, in showing a mixture of advanced and primitive morphologies.

**Funding Sources** This study financed by University of Wollongong and an Australian Research Council (ARC) Discovery grant to Mike Morwood/Gert van den Bergh (DP1093342).

## Late Cenozoic Mammalian Macroecology & Macroevolution

### RECENT RESEARCH INTO NORTH AMERICAN MIO-PLIOCENE MAMMUTIDAE

Widga, Chris<sup>1</sup>, Von Koenigswald, Wighart<sup>3</sup>, Göhlich, Ursula<sup>2</sup>, Inabinett, C. Matthew<sup>1</sup>

<sup>1</sup>Center of Excellence in Paleontology, East Tennessee State University, Johnson City, Tennessee, U.S.A., <sup>2</sup>Natural History Museum, Vienna, Austria, <sup>3</sup>Institut für Geowissenschaften (Paläontologie), University of Bonn, Bonn, Germany

The Mammutidae are present in North America from the late Hemingfordian to their extinction at the end of the Pleistocene. During this time, they are important large herbivores in terrestrial vertebrate communities. Despite their high visibility and potentially important role in regional ecosystems, the systematics of this group have been under-researched; the last specimen-based, continent-scale review was almost 90 years ago. We present ongoing

efforts to: (1) update the status of Mio-Pliocene mammutid type materials, (2) describe extant specimens, and (3) assess the accuracy of various scenarios of North American mammutid evolutionary history.

We assembled a dataset of 19 mammutid localities dating to the Barstovian, Clarendonian, Hemphillian, and Blancan land mammal ages, including previously undescribed mammutid materials from Oregon. Updated chronological information, the status of extant specimens, and morphological descriptions were collected through on-site visits as well as shared 3D models and photographs. These data were used to review evolutionary trends in dentition and skull morphology.

*Zygodon* is present in eight localities from the mid-Barstovian through Clarendonian. This genus had short, downward-directed upper tusks with an enamel band and an extended symphysis with mandibular tusks. *Mammut* appears as *M. furlongi* during the Clarendonian, in the form of a shortened, tuskless mandible. During the Hemphillian and Blancan (nine localities), this genus continues to develop large, upward-curving upper tusks with a short mandibular symphysis that includes mandibular tusks that are reduced in size or absent. Although molar characteristics are highly conserved within mammutids, molar size, shape, and loph(id) frequency is variable in both groups, suggesting dental characteristics may be of limited use for distinguishing between genera in phylogenetic studies.

Despite limitations imposed by small sample sizes and poor preservation, this dataset tentatively demonstrates the synchronous presence of *Zygodon* and *Mammut* during the Clarendonian. It also suggests that recently-recognized morphological variability that is present in late Pleistocene mammutids may extend into the Mio-Pliocene as well.

**Funding Sources** Deutsche Forschungsgemeinschaft (Bonn), ETSU Center of Excellence in Paleontology.

## Colbert Poster Prize/Biomechanics & Functional Morphology

### THREE-DIMENSIONAL ATLAS OF PECTORAL MUSCULOSKELETAL ANATOMY IN THE EXTANT TINAMOU *NOTHOPROCTA PENTLANDII* (PALAEOGNATHAE: TINAMIDAE)

Widrig, Klara E.<sup>1</sup>, Watanabe, Junya<sup>1</sup>, Bhullar, Bhart-Anjan S.<sup>2</sup>, Field, Daniel J.<sup>1</sup>

<sup>1</sup>Earth Sciences, University of Cambridge, Cambridge, U.K., <sup>2</sup>Geology and Geophysics, Yale University, New Haven, Connecticut, U.S.A.

Palaeognaths (ratites and tinamous) are the sister group of all other living birds, with recent phylogenetic and developmental work supporting the hypothesis that

tinamous are phylogenetically nested within ratites. Tinamous are notable among extant palaeognaths for being the only group that has retained the ability to fly, and may therefore provide key insight into the nature of ancestral crown palaeognaths, and, in turn, crown birds. To reveal new information about the musculoskeletal anatomy of tinamous, we imaged an Andean Tinamou (*Nothoprocta pentlandii*) using diffusible iodine-based contrast-enhanced computed tomography (diceCT). Visible components of the musculoskeletal system in the resultant high-resolution scans were segmented in order to create a three-dimensional anatomical atlas of tinamou forelimb musculature. Origins and insertions of the pectoral flight musculature are generally consistent with those in other volant birds specialized for burst flight, casting doubt on the already dubious notion that tinamous may be secondarily flighted. The pectoralis thoracica and supracoracoideus are robust, similar to the condition in other extant clades of burst-fliers such as Galliformes. Contrary to the condition in most extant neognaths, the pronator superficialis is larger than the pronator profundus, although most other anatomical observations are broadly consistent with the condition in Neognathae. This work will form an important basis for future comparative studies of the avian musculoskeletal system in light of ongoing advances in soft tissue imaging.

**Funding Sources** University Future Leaders Fellowship MR/S032177/1, Royal Society Research Grant RGS/R2/192390.

### Romer Prize

### FOSSIL BIOMOLECULES REVEAL THE PHYSIOLOGY AND PALEOBIOLOGY OF EXTINCT AMNIOTES

Wiemann, Jasmina

Earth and Planetary Sciences, Yale University, New Haven, Connecticut, U.S.A.

Birds and mammals independently evolved the highest metabolic rates among modern animals. They generate heat as a by-product of differently modified enzymes in the mitochondrial respiratory chain. Resulting metabolic thermoregulation, or endothermy, shapes the ecological niches of birds and mammals, and is considered a key advantage in their survival of the K/Pg mass extinction and subsequent radiation.

Due to the lack of a direct metabolic proxy applicable to fossils, it is not known how avian and mammalian endothermy evolved. However, physiology leaves molecular signatures: can fossil biomolecules, when analyzed in a phylogenetic framework, reveal the evolution of metabolic rates and resulting thermal strategies in extinct amniotes?

To explore molecular metabolic markers in commonly fossilizing skeletal tissues, I developed a novel *in situ* Raman spectroscopy protocol that allows molecular characterization of both modern and fossil samples. Non-destructive analysis (500–3000 cm<sup>-1</sup>, 10s, 10 replicates) of >60 extant amniote long bones demonstrated that the quantity of skeletal lipoxidation markers, byproducts of oxygen respiration, correlates ( $r = 0.87$ ) directly to the basal metabolic rate. I assessed diagenetic alteration of this biomarker during fossilization by analyzing >40 corresponding Phanerozoic amniote bones, and showed that the signal is preserved in deep time. All fossil metabolic data were calibrated and corrected for allometry. An ancestral state reconstruction reveals that high metabolic rates consistent with (facultative) endothermy evolved independently in therapsids, plesiosaurs, varanids, turtles, and the ancestral archosaur with an increase along the avian lineage. Avian-level metabolic rates were acquired independently on the major branches of ornithodirans. Crocodylomorphs and representatives of major ornithischian lineages reduced their metabolic rates towards secondary ectothermy. Physiological activities of such ectotherms were strongly dependent on environmental heat and thermoregulatory behaviors, in contrast to highly active lifestyles in endothermic amniotes. Notably, widespread endothermy in many Late Cretaceous non-mammalian and non-avian amniotes suggests that features other than metabolism determined their fate during the terminal Cretaceous mass extinction. Insights from the biomolecular fossil record have the potential to fundamentally advance our understanding of the physiology and paleobiology of long extinct amniotes.

**Funding Sources** PhD Stipend from Yale University; Research grants by the Geological Society of America and the Yale Institute for Biospheric Studies.

### Taphonomy & Stratigraphy

### ORGANIC PHASE PRESERVATION IN FOSSIL DINOSAUR AND OTHER TETRAPOD BONE FROM DEEP TIME: OSTEOCYTE-LIKE STRUCTURES LIBERATED FROM TETRAPOD BONES FROM THE LOWER PERMIAN OF TEXAS

Wiersma-Weyand, Kayleigh, Läbe, Sashima, Sander, P. Martin

Institute for Geosciences, Paleontology Department, University of Bonn, Bonn, Germany

Since the 1960s, soft tissues and bone proteins have been detected in fossil dinosaur bone, eroding the dogma that the organic phase in bone is completely destroyed during fossilization. Indeed, fossil bone from the Mesozoic Age frequently appears to retain soft tissues such as cells, blood vessels, and extracellular matrix, which can be liberated by

dissolution in weak organic acids. However, these putative tissue remnants (osteocytes, blood vessels, extracellular matrix) found in the residue have led to a controversy over whether these organic remains represent original soft tissue preservation or if they are instead biofilms produced by bone-degrading bacteria, either during fossilization or in the shallow subsurface. Although the weight of the evidence tips in favor of the interpretation of the remains as original tissue or its degradation products, the intense discussion on this controversy has led to the realization that the material nature of pre-Quaternary fossil bone remains poorly characterized and that the mode of preservation of the organic phase is not well understood. Using the rationale that oxidizing, in particular fluvial, environments appear to maximize preservation potential, we demineralized amphibian and reptile bones from one of the oldest land vertebrate faunas from fluvial deposits, the classical lower Permian redbeds of North Texas. The fossils are from the Sakmarian to early Artinskian upper Archer City ('Nocona') Formation. Given that the Sakmarian/Artinskian boundary is dated to 290.1 my, our observation of osteocyte-like structures liberated from the tetrapod bones extend the previous oldest record of such remains by at least 40 million years. The previously oldest record derives from the late Olenekian (ca. 247 my, late Early Triassic) of Poland. We propose that these structures are preserved organic phase and not taphonomic artifacts and that the Texas lower Permian record is far from the actual maximum age for organic phase preservation, despite extending the record from the Mesozoic into the Paleozoic.

## Late Cenozoic Mammalian Macroecology & Macroevolution

### PALEOECOLOGICAL ANALYSIS OF CARNIVORANS FROM THE OPTIMA LOCAL FAUNA OF OKLAHOMA (MIOCENE; LATE HEMPHILLIAN)

Wilbert, Greg<sup>1</sup>, Cohen, Joshua<sup>5</sup>, Frederickson, Joseph A.<sup>2</sup>, Hunt, Tyler C.<sup>3</sup>, Czaplewski, Nicholas<sup>4</sup>, Engel, Michael<sup>6</sup>  
<sup>1</sup>Biology, University of Oklahoma, OMNH, Norman, Oklahoma, U.S.A., <sup>2</sup>Weis Earth Science Museum, Menasha, Wisconsin, U.S.A., <sup>3</sup>Biology, Florida State University, Tallahassee, Florida, U.S.A., <sup>4</sup>Vertebrate Paleontology, OMNH, Norman, Oklahoma, U.S.A., <sup>5</sup>Loyola Marymount University, Los Angeles, California, U.S.A., <sup>6</sup>Geosciences, University of Oklahoma, Norman, Oklahoma, U.S.A.

The Optima (Guymon) Local Fauna represents a well-studied, diverse assemblage of late Miocene (Hemphillian, Hh3) mammals from the panhandle of Oklahoma. This site, and other contemporaneous faunas from the western strip,

represents an important transition in North American ecosystems from savannah to grassland environments. Research into this ecological change has understandably focused largely on grazing herbivores. In this study, we used carbon isotopes and tooth breakage to investigate how expanded representation of C4-feeding prey species affected niche partitioning among presumed carnivores from locality V52 (Optima), a large fossil assemblage housed at the Sam Noble Oklahoma Museum of Natural History. Carbon isotope analysis was performed on enamel taken from five taxa: a large bear (*Agriotherium schneideri*, n = 7), a saber-toothed cat (*Amphimachairodus coloradensis*, n = 16), two canids (*Eucyon davisi*, n = 5; *Borophagus secundus*, n = 15), and a badger (*Pliotaxidea nevadensis*, n = 4). Isotopic results show a significant difference in  $\delta^{13}\text{C}$  between *A. schneideri* (average =  $-10.90 \pm 0.66$ ) and all other taxa, with *A. coloradensis* (average =  $-8.96 \pm 0.79$ ) being the most enriched. Tooth breakage analysis was performed on two taxa: *A. coloradensis* (n = 27) and *B. secundus* (n = 888). Tooth breakage was higher in *B. secundus* (5.4% of teeth broken) than *A. coloradensis* (3.7% of teeth broken). The breakage rate in *B. secundus* is higher than most modern carnivorans, most similar to modern hyaenids and the proposed Pleistocene bone crusher, *Canis dirus*. *A. coloradensis* tooth breakage rates are higher than modern felids, but lower than most modern canids and hyaenids. These data indicate that there was niche partitioning between the large carnivorans in the Optima ecosystem. *A. coloradensis* was almost certainly a hypercarnivore with a diet consisting of more  $\delta^{13}\text{C}$ -enriched herbivores (such as horses), and lower tooth breakage rates. The isotopically-depleted result for *A. schneideri* is consistent with a more omnivorous or herbivorous diet similar to that of many modern ursids. Tooth breakage and isotope data indicate the canids had an intermediate and varied lifestyle, likely consisting of captive predation, a level of scavenging, and, in the case of *B. secundus*, osteophagy consistent with published anatomical and taphonomic data.

## Biomechanics & Functional Morphology

### A DETAILED ANATOMICAL STUDY OF THE M. CAUDOFEMORALIS LONGUS IN ALLIGATOR MISSISSIPPIENSIS WITH IMPLICATIONS FOR RECONSTRUCTIONS OF TAIL MUSCULATURE IN EXTINCT ARCHOSAURS

Wilhite, Ray  
Anatomy Physiology and Pharmacology, Auburn University, Auburn, Alabama, U.S.A.

*M. caudofemoralis longus* in crocodylians has been referenced by multiple authors as a guide for reconstruction of *m. caudofemoralis longus* in extinct archosaurs.

However, a comprehensive anatomical study of this important muscle using multiple imaging modalities has never been published. A detailed anatomical study of *m. caudofemoralis longus* in *Alligator mississippiensis* based on osteological data, anatomical dissections, cross-sectional anatomy, and 3D reconstructions from CT data was undertaken to better understand the anatomy of this important muscle. While many aspects of *m. caudofemoralis longus* anatomy were found to agree in parts with previous authors' works, a number of significant differences were found between the current study and the most often cited studies of *m. caudofemoralis longus* anatomy. These differences were mostly related to the origin of *m. caudofemoralis longus*, which the most cited references list as the bodies of the caudal vertebrae and the caudal transverse processes. However, the chevrons and the membranous spaces between the chevrons were found to constitute the overwhelming majority of the origin of *m. caudofemoralis longus* in *Alligator*, contra to the most often cited studies. Also, new distal components of *m. caudofemoralis longus* via the insertion of *m. gastrocnemius* show that *m. caudofemoralis longus* has direct effect to the level of the metatarsophalangeal joint. A fat and fascia layer separating *m. caudofemoralis longus* from *m. ilio-ischio-caudalis* which allows *m. caudofemoralis longus* to contract at least somewhat independent of the surrounding hypaxial and epaxial tail muscles was also noted. Finally, the most important finding of this study is that chevron morphology, not caudal vertebral morphology, is the most important anatomical feature to consider when reconstructing *m. caudofemoralis longus* anatomy in extinct archosaurs.

### Biomechanics & Functional Morphology

#### COMPARATIVE BIOMECHANICS OF THE OTIC JOINT AND SUSPENSORIUM IN SAUROPSIDS

Wilken, Alec<sup>1</sup>, Sellers, Kaleb<sup>1</sup>, Cost, Ian<sup>2</sup>, Rozin, Rachel<sup>1</sup>, Middleton, Kevin<sup>1</sup>, Holliday, Casey<sup>1</sup>

<sup>1</sup>Integrative Anatomy, University of Missouri-Columbia, Sedalia, Missouri, U.S.A., <sup>2</sup>Biology, Albright College, Reading, Pennsylvania, U.S.A.

Gnathostomes all share the common challenge of assembling the first pharyngeal arch cartilages of the suspensorium with the cartilaginous neurocranium into a functioning linkage system. In many tetrapods, the otic and palatobasal articulations between suspensorium and neurocranial elements form the joints integral for cranial kinesis. Among sauropsids, the otic (quadratosquamosal) joint is a key feature in this linkage system and shows considerable variability in shape, tissue-level construction, and mobility among lineages of reptiles. Here we explore the biomechanics of the suspensorium and the otic joint in

five disparate species of sauropsids of different kinetic capacity (two squamates, one non-avian theropod dinosaur, two avian species). Using 3D muscle modeling, cross-sectional geometries, and finite element analysis, we characterize biomechanical differences in the resultants of protractor, loading of otic joints, and bending properties of pterygoid bones. We found that avian species oriented palatal muscles more rostrocaudally and have relatively smaller quadrate otic articular surfaces than squamates. Lineages with tubular pterygoids evolved from lineages with mediolaterally thin, plate-like pterygoids. These pterygoid transformations likely accompany new biomechanical loading regimes and feeding specializations. Our new approaches and findings elucidate on our understanding of evolution and diversity of the suspensorium in tetrapods.

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### Taphonomy & Stratigraphy

#### PALEONTOLOGY AND SEDIMENTOLOGY OF A MULTI-TAXIC BONEBED IN THE HELL CREEK FORMATION OF MONTANA, U.S.A.

Wilkinson, Ryan D.<sup>1</sup>, Cullen, Thomas M.<sup>3</sup>, Evans, David<sup>2</sup>  
<sup>1</sup>Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario, Canada, <sup>2</sup>Natural History, Royal Ontario Museum, Toronto, Ontario, Canada, <sup>3</sup>Paleontology, North Carolina Museum of Natural Sciences, Raleigh, North Carolina, U.S.A.

The holotype locality of the dromaeosaurid dinosaur *Acheroraptor temertyorum* is a multi-taxic bonebed of vertebrate microfossils along with small, well preserved macrofossils in the Late Cretaceous Hell Creek Formation of Montana, U.S.A. These 'mesofossil' assemblages provide exceptionally preserved bones of rare, small bodied dinosaurs and thereby contribute new data on the anatomy of these poorly known taxa and their paleoecology. The *Acheroraptor temertyorum* holotype locality (AHL) has produced several significant published specimens, including the ontogenetically youngest cranial material of *Pachycephalosaurus* and the holotype and referred jaws of *A. temertyorum*, but the locality has never been documented in detail. Here we described the sedimentology of the site, refine its stratigraphic position within the Hell Creek Formation, describe new macrofossil material, and document its diverse microfossil assemblage. The large bonebed occurs as a lag deposit in a stacked channel sequence characterized by mature, moderately

well sorted fine-grained sandstone. Due to limited outcrop in the area, palynological samples were taken from a mudstone unit directly underlying the bonebed to determine its age. The presence of *Striaticorpus pyriformis* and the absence of *Pseudoaquilapollenites bertillonites* suggests that the sample occurs in the lower to middle part of the Hell Creek Formation, but not in the lowest ~20 m of the unit. New macrofossil material includes three dromaeosaurid manual phalanges and one manus claw that we refer to *A. temertyorum*. The pachycephalosaurid *Sphaerolithus buchholtzae* is represented by two frontoparietals and three squamosals, the caenagnathid *Anzu wyliei* is represented by a dentary, and the crocodylian *Borealosuchus sternbergii* is represented by the posterior portion of the skull. A surface collected microfossil assemblage of the AHL contains at least 17 species representing a broad range of aquatic and terrestrial vertebrates. The relative abundance of salinity-intolerant lissamphibians and the absence of sharks among the preserved microvertebrates suggest that the AHL assemblage was deposited with little or no marine influence. The AHL is a rare occurrence of a diverse mesofossil assemblage in the middle to lower Hell Creek Formation, which has been comparatively undersampled historically, and provides valuable information for understanding dinosaur diversity dynamics leading up to the end Cretaceous extinction event.

**Funding Sources** Ontario Graduate Scholarship to RDW; NSERC Discovery Grant to DCE (RGPIN-2018-06788).

### Mesozoic & Early Cenozoic Mammalian Evolution

#### PRELIMINARY REPORT OF AN ARTICULATED MAMMALIAN HAND FROM THE HELL CREEK FORMATION IN NORTHEASTERN MONTANA

Williams, Daniel<sup>2</sup>, Burnham, David A.<sup>1</sup>, Gurche, Loren<sup>1</sup>  
<sup>1</sup>Biodiversity Institute, University of Kansas, Lawrence, Kansas, U.S.A., <sup>2</sup>Dept. of Biology, University of St. Mary, Leavenworth, Kansas, U.S.A.

Late Cretaceous mammals are almost entirely known from disarticulated fragmentary remains, with nearly all taxa being known from teeth alone. Paleocological data recovered from mammals is usually therefore relegated to diet-correlated variables. While this is valuable data, species' postcranial characteristics can add to current hypotheses on Late Cretaceous ecology. Here we describe the locomotor characters and geometric morphometrics of an articulated partial mammalian manus from the Hell Creek Formation of Garfield County, Montana. The ungual phalanges were characterized using outline analysis of the lateral and dorsal views with landmarks included for registration. We concluded from the morphology and morphometrics of the phalanges that the Hell Creek

specimen was not likely to be fully arboreal but was more likely scansorial or semi-fossorial. The ungual phalanges have strong flexor tubercles and a narrow blade. We noted in the lateral view that the claws were similar to the arboreal Southern Tamandua (*Tamandua tetradactyla*), which uses its claws to rip open ant nests. We observed from the dorsal view that the stout proximal end of the claw combined with its gradual taper most resembled the scansorial Virginia Opossum (*Didelphis virginiana*). When combined with the more scansorial or semi-fossorial proportions of the phalanges, we conclude that the manus most likely belonged to a terrestrial taxon, likely a scansorial species somewhat larger than the modern Virginia Opossum.

### Fishes & Chondrichthyans: Evolution & Distribution

#### INITIAL DESCRIPTION AND IDENTIFICATION OF LARGEST KNOWN LONGNOSE GAR, *LEPISOSTEUS BEMISI* (HOLOSTEI: LEPISOSTEIFORMES), FROM THE EARLY EOCENE FOSSIL BUTTE MEMBER OF THE GREEN RIVER FORMATION, WYOMING, U.S.A.

Willson, Mary B., Matzen, Benjamin L.  
Science Department, Oxbridge Academy, West Palm Beach, Florida, U.S.A.

The lower Eocene Green River Formation (48.5-53.5ma) of Fossil Lake in southwest Wyoming was a tropical/subtropical freshwater paleoenvironment in a volcanically active area. Within the Green River Formation, the Fossil Butte Member (52 Ma) is a layer of rock famous for an abundance and variety of exceptionally preserved fossils. Among the largest organisms found in the Green River are gar (*Lepisosteiformes*). Four species of gar have been described from the Fossil Butte Member sediments of the Green River Formation: *Masillosteus janei*, *Atractosteus atrox*, *Atractosteus simplex*, and *Lepisosteus bemisi*. The specimen we examined is currently housed at the Wyoming Dinosaur Center (Specimen ID JJSF-2012-001) and is an example of the excellent preservation common to the Split Fish layer of the Fossil Butte Member in which it was discovered. Based on the locality of the specimen and numerous diagnostic features; the size, elongated jaw, number of caudal rays, the pointed build of the teeth, and lack of a supraoccipital bone, we identify specimen JJSF-2012-001 as a specimen of *Lepisosteus bemisi*, commonly referred to as the Green River longnose gar. The quality of preservation and the detail of preparation of this specimen will allow for considerable future research that will enrich our understanding of *L. bemisi* and related gar. Specimen JJSF-2012-001 is also the largest *L. bemisi* specimen described to date, with a total length (TL) of 1655 mm, 45 mm longer than the largest previously known specimen.

## Colbert Poster Prize/Fishes & Chondrichthyans: Evolution & Distribution

### NEW ACTINOPTERYGIANS FROM THE TOURNAISIAN OF BLUE BEACH, NOVA SCOTIA

Wilson, Conrad D.<sup>1</sup>, Mansky, Chris<sup>3</sup>, Anderson, Jason<sup>2</sup>

<sup>1</sup>Biological Sciences, University of Calgary, Calgary, Alberta, Canada, <sup>2</sup>Comparative Biology and Experimental Medicine, University of Calgary, Calgary, Alberta, Canada, <sup>3</sup>Blue Beach Fossil Museum, Hantsport, Nova Scotia, Canada

Devonian and Carboniferous gnathostome faunas appear distinct and disparate. Faunal turnover between clades occurs abruptly at the Devonian-Carboniferous boundary, supporting the hypothesis that the Hangenberg mass extinction significantly affected gnathostomes. Under the mass extinction hypothesis, the earliest Carboniferous vertebrate fauna is interpreted as a homogeneous and restricted recovery fauna, and actinopterygian diversification is interpreted as a post-extinction adaptive radiation. However, testing of this hypothesis has been impeded by the fragmentary fossil record in the Early Carboniferous leading to a poor understanding of actinopterygian interrelationships. When limited windows into Early Carboniferous fauna occur, they appear to show a gnathostome fauna that comprises both Devonian and Carboniferous representatives. One Tournaisian locality, Blue Beach, Nova Scotia, has previously revealed a blended tetrapod fauna, as well as a Devonian-Carboniferous boundary crossing actinopterygian, *Avonichthys*. We examined several new actinopterygian specimens from this locality using  $\mu$ CT. Two incomplete posterior braincases could not be assigned to genus or species, but one is most similar to Devonian taxa and the other to actinopterygians deeply nested in a broad post-Devonian radiation. Another actinopterygian, recovered as a Devonian-Carboniferous boundary crosser in phylogenetic analysis, combines a plesiomorphic pectoral girdle, pectoral fin, and opercular-gular series with a relatively derived suspensorium. Another specimen represents the earliest occurrence of a deep-bodied actinopterygian in the fossil record and is similar to some Euamerican '*Platysomus*' specimens from the Viséan and Serpukhovian. These specimens increase the number of Devonian-Carboniferous boundary crossing actinopterygians at Blue Beach, with *Avonichthys*, to three. The diversity and disparity of these actinopterygians weakens interpretations of a homogeneous earliest Tournaisian actinopterygian fauna and overlap between relatively plesiomorphic and derived actinopterygians at Blue Beach suggests overlap between Devonian and Carboniferous actinopterygian faunas. Devonian-

Carboniferous actinopterygian faunal turnover may be more gradual than expected.

**Funding Sources** Research was supported by an NSERC CGS M award to Conrad Wilson and an NSERC Discovery Grant to Jason Anderson.

### Symposium: Paleoneurology

### NEW INSIGHTS INTO THE NEUROCRANIUM AND INNER EAR OF THE EARLY STEM ARCHOSAUR *TRILOPHOSAURUS BUETTNERI*

Wilson, Jacob D.<sup>1</sup>, Wisniewski, Anna<sup>2</sup>, Bever, Gabriel S.<sup>1</sup>

<sup>1</sup>Center for Functional Anatomy and Evolution, Johns Hopkins School of Medicine, Baltimore, Maryland, U.S.A., <sup>2</sup>Department of the Geophysical Sciences, University of Chicago, Chicago, Illinois, U.S.A.

Establishing patterns of amniote sensory evolution has traditionally been hindered by the long phylogenetic stem lineages that mark the major crown radiations. Digital imaging techniques in paleontology have done much to diminish this problem by providing detailed neurocranial and endocast data directly from the fossils that populate these stems. Crown Archosauria, and theropod dinosaurs in particular, have received considerable research attention, with much less being paid to stem archosaurs. The few studies that do exist tend to concentrate on the crown-ward portion of this history, rendering the base of the radiation as an important empirical gap.

*Trilophosaurus* is a North American Triassic stem archosaur, generally recovered near the base of the radiation just crownward of proterosaurids. We segmented and studied the details of its neurocranium using HRCT scans of an adult specimen of *T. buettneri*. Our study builds on previous works, which were limited to external examinations, and is the first to detail the inner ear. Results help to clarify several problematic character scorings including the confirmed absence of a semilunar depression, the unfused nature of the exoccipitals, and a club-shaped ventral ramus of the opisthotic. Similar to more crown-ward stem archosaurs, the individual neurocranial elements of *T. buettneri* are riddled with small, internal air cavities, thus pulling this feature nearer to the base of the archosaur stem. A complex of features also suggest *T. buettneri* was capable of apomorphically powerful head flexion, including an additional ossified element posterior to the basitubera, a strongly overhanging occipital condyle, and a ventral recess in the braincase formed by lateral expansions of the basioccipital that could brace the basitubera against posteriorly directed muscular forces. Perhaps the most interesting discoveries are from the inner ear, whose morphology is unusual in that the anterior semicircular canal is two times the diameter and length of the other canals. This single canal enlargement appears to be unique among stem archosaurs and therefore represents a marked

convergence on a common theropod condition. These observations re-raise the question of whether *T. buettneri* might have had a highly specialized behavioral ecology. Our description of *Trilophosaurus* adds to an increasing bounty of braincase data of stem archosaurs that can be crucial to understanding the relationships of animals in Sauria.

**Funding Sources** NSF-DEB-1457181, 1947025.

## **Evolution & Biology of Non-Avian Theropods**

### **NEW MANUAL UNGUALS OF THE ALVAREZSAURID THEROPOD DINOSAUR FROM THE HELL CREEK FORMATION, MONTANA, AND THE ONTOGENETIC DEVELOPMENT OF THE FUNCTIONAL ALVAREZSAURID HAND CLAW**

Wilson, John P., Freimuth, William J.

Department of Earth Sciences, Montana State University, Bozeman, Montana, U.S.A.

Alvarezsauridae is a clade of highly-specialized, small-bodied theropod dinosaurs known predominantly from Asia and South America, with a comparatively sparse record from North America. Alvarezsaurids express proportionally reduced yet highly robust forelimbs, with hypertrophied deltopectoral crests of the humeri and olecranon processes of the ulnae, fused carpometacarpus, and a single functional manual digit. This digit bears a distinctive ungual with a strongly ginglymous proximal articulation, a broad and transversely widened proximal end, lateral grooves which are completely enclosed by bone proximally and which open ventrally as distinct foramina, and often the presence of pronounced rugosity of the proximolateral and proximodorsal surfaces. In conjunction with their delicately built crania and numerous small and simplified peg-like teeth, alvarezsaurids have drawn ecological comparisons to extant myrmecophages, likely preying upon wood-dwelling insects living within fallen logs. However, little is known about alvarezsaurian ontogeny. Here we describe two new alvarezsaurid manual D-I unguals from the upper Maastrichtian Hell Creek Formation of eastern Montana. These newly discovered manual unguals, together with the three previously described unguals of the Hell Creek Formation alvarezsaurid, form a progressive size series which is notably accompanied with the progressive expression of more extensively developed derived characteristics as size increases, providing increased resolution to the sequence of ontogenetic change of alvarezsaurid manual unguals, and represent the only described alvarezsaurian and alvarezsaurid ontogenetic series. This ontogenetic series indicates that the ventral foramina enclose earliest and become more deeply enclosed through growth, followed by transverse widening of the proximal articular end, which occurs asymmetrically with the ventral aspect widening

before the dorsal aspect, alongside development of the proximal rugosities first as low, subparallel ridges and finally into well-developed spur-like projections. The ontogenetic changes noted here occur in features of the claws which have been inferred as being adaptations for their hypothesized ecological functions, including the highly ginglymous and broad proximal articulation and enclosed ventral foramina, and as such the ecology and feeding behavior of alvarezsaurids can be hypothesized as stimulating this ontogenetic change in the functional manual unguals.

## **Quantitative Methods**

### **USING COMBINED METHODS TO REASSESS THE PHYLOGENETIC AFFINITIES OF THE SOUTH AMERICAN NATIVE UNGULATES**

Wilson, Oscar, Asher, Robert J.

Department of Zoology, University of Cambridge, Bath, U.K.

The South American Native Ungulates (SANUs) were a diverse group of mammals endemic to South America with a stratigraphic range from the Paleocene to the Pleistocene. Their phylogenetic affinity has been debated, with molecular data suggesting a Perissodactyl affinity and morphology less clear. Our work increases the sampling of SANU taxa for 3660 morphological characters, as well as including three crown perissodactyls to further test the hypothesis of perissodactyl affinity. This morphological data has been concatenated with collagen and DNA sequences for the most comprehensive reassessment to date of the position of the SANUs within placental mammals. In particular, through inclusion of five of the seven major SANU orders, this combined approach explicitly aims to test the assumption of SANU monophyly. In addition, to assess the impact of taphonomy on the position of the SANUs within eutherian phylogeny, we perform artificial extinction experiments, using each of our 47 fossil taxa as a template on which to construct 'fossil phenotypes' for 47 extant taxa. In addition, predicted ancestor experiments are applied to an entirely fossil taxon for the first time, to understand the effect on phylogeny relative to the consensus. The phylogenetic affinity of the SANUs has major implications for understanding their origin and dispersal to the South American continent. Using the R package BioGeoBears, we assess the possible biogeographic patterns based on our phylogeny. This research will allow greater understanding of the history of this enigmatic group of fossil mammals, as well as provide methods that may be applied to other fossil groups with unknown affinity.

## **Symposium: Dietary Reconstruction**

## IMPROVING DIETARY RECONSTRUCTION USING DENTAL MICROWEAR TEXTURE ANALYSIS COMBINED WITH STABLE ISOTOPE ANALYSIS - FROM EXPERIMENTAL TO FOSSIL APPLICATION

Winkler, Daniela E.<sup>1</sup>, Clauss, Marcus<sup>3</sup>, Schulz-Kornas, Ellen<sup>4</sup>, Kaiser, Thomas M.<sup>5</sup>, Codron, Daryl<sup>2</sup>, Leichliter, Jennifer N.<sup>1</sup>, Weber, Katrin<sup>1</sup>, Weber, Michael<sup>1</sup>, Tütken, Thomas<sup>1</sup>

<sup>1</sup>Geology, Johannes Gutenberg University of Mainz, Mainz, Germany, <sup>2</sup>University of the Free State, Bloemfontein, South Africa, <sup>3</sup>University of Zurich, Zürich, Switzerland, <sup>4</sup>University of Leipzig, Leipzig, Germany, <sup>5</sup>University of Hamburg, Hamburg, Germany

The study of extinct vertebrates' biology often starts with a key aspect of their ecology: dietary preference. Dietary reconstruction allows us to understand trophic interactions and to draw conclusions about habitat preferences (e.g., open vs. closed habitat). Depending on how a fossil assemblage is analyzed (different taxa, populations, stratigraphic successions), diet can reveal not only niche specialization or intraspecific variability and competition, but also climate changes or seasonality. Beyond tooth shape, microscopic tooth wear and stable isotope analysis ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ,  $\delta^{44}\text{Ca}$ ) are well-known approaches to infer dietary preferences of fossil species. Both approaches resolve different mechanical and chemical food properties and are widely applied but rarely combined. Here we present how dental microwear texture analysis (DMTA) can be improved by controlled feeding experiments and studies of museum specimens. We further complement DMTA by stable isotope analysis (SIA) in selected modern and fossil applications to improve dietary reconstructions. Even though DMTA is a common method, its' temporal resolution has not been experimentally tested. In a staggered sampling approach with rats we show that a new informative DMTA signal needs at least 2-3 weeks to form and overprint a pre-existing signal, hereby providing the first experimentally documented time period of the so called 'last-supper' effect. Further feeding experiments contribute to the long-lasting debate on how both external mineral abrasives (grit, dust) and internal amorphous silica abrasives in plant tissue (phytoliths) affect microscopic tooth wear and indicate how to untangle the two effects in natural settings. Moreover, we find that DMTA caused by natural plant feeds does not only depend on phytolith content, but also on the hydration state of the plant tissue. In extant lizards and crocodiles, we find that DMTA reflects dietarily informative wear, even in absence of thorough oral food processing. In fossil crocodiles and theropods we find evidence for non-carnivorous dietary preferences in a Cretaceous heterodont crocodile and show that food processing in Tyrannosauridae was more

comparable to crocodiles than to lizards. Preliminary  $\delta^{44}\text{Ca}$  results support DMTA-based reconstructions of trophic relationships, and can help to further resolve dietary nuances, e.g., bone consumption in carnivores. Combined DMTA and SIA ( $\delta^{44}\text{Ca}$ ) provides an informative toolbox for refined dietary reconstruction.

**Funding Sources** This project received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research & innovation programme, grant agreement No 681450.

## Mesozoic Herpetology

### A SPECIALIZED RESPIRATORY SYSTEM IN PLESIOSAURS (SAUROPTERYIA): BREATHING WITH THE LONG NECK

Wintrich, Tanja<sup>1</sup>, Vanhoeffler, Jakob<sup>2</sup>

<sup>1</sup>Institute of Anatomy, Bonn, Germany, <sup>2</sup>Faculty of Mathematics and Natural Science, Bonn, Germany

Plesiosaurs are enigmatic marine reptiles known from the Late Triassic to the Late Cretaceous and represent the most derived group of sauropterygians. Among plesiosaurs, there are several lineages showing an extremely long neck, which raises different biomechanical questions dealing with use and function, up to the breathing mechanism. Furthermore, for aquatic tetrapods, buoyancy control is an important adaptation to support the body in the water column. The respiratory system and its influence on buoyancy control have been discussed only briefly, and no mathematical approach has been taken so far. However, the breathing mechanism and therefore the respiratory system of highly aquatic tetrapods has to be specialized in different ways to enable life in a pelagic environment. Here, we follow different mathematical approaches based on the metabolism (work of breathing), the trachea, and the morphology of the skull and trunk, in order to reconstruct the breathing mechanism, respiratory system, and lung volume in plesiosaurs, and then discuss the most plausible respiratory anatomy. Furthermore, we find support for the hypothesis of a functional secondary palate from the reconstructed respiratory system as well as for the use of gastroliths, especially in the Elasmosauridae. In addition to this, we calculated the center of mass to reconstruct buoyancy control in plesiosaurs. In general, we studied four different long-necked plesiosaurs (*Cryptoclidus*, *Albertonectes*, *Rhaeticosaurus*, *Rhomaleosaurus*) and included *Augustasaurus* as the most derived plesiosaur for which the entire neck is known. Our results demonstrate that the lung volume was larger than suspected for an

aquatic tetrapod. However, plesiosaurs showed an adaption similar to that of marine turtles, which have shifted the lung to the dorsal side of the trunk. The influence of the long trachea on breathing is not as great as suggested before. However, especially in the elasmosaurid, the long neck influences the center of mass. This supports the hypothesis of gastroliths functioning in buoyancy control in elasmosaurs. Furthermore, based on an ancestral state reconstruction, we show that the specialized plesiosaurian respiratory systems probably evolved in early sauropterygians.

## Quantitative Methods

### A WORKFLOW FOR PRODUCING AND ANALYSING MUSCULOSKELETAL MODELS AND SIMULATIONS IN COMPARATIVE BIOMECHANICS

Wiseman, Ashleigh<sup>1</sup>, Cuff, Andrew R.<sup>2</sup>, Bishop, Peter<sup>1</sup>, Michel, Krijn B.<sup>1</sup>, Demuth, Oliver E.<sup>1</sup>, Hutchinson, John R.<sup>1</sup>

<sup>1</sup>Structure and Motion Laboratory, Royal Veterinary College, Hatfield, U.K., <sup>2</sup>Centre for Anatomical and Human Sciences, Hull York Medical School, York, U.K.

Biomechanical models can offer unique insights into animal musculoskeletal function, which can in turn provide the basis for simulating extinct animal movement. Modelling musculoskeletal function in extinct forms first ideally requires modern forms to be explored, modelled and analysed for validation purposes. For example, to model the locomotory behavior of extinct archosaurs (e.g., the quadrupedal ‘rauisuchian’ *Batrachotomus*) we first need to capture subject-specific movement of a comparable living archosaur (e.g., *Crocodylus*). In this study, we collected marker-based XROMM (biplanar high-speed X-ray video) and ground reaction force data for five *C. niloticus* across a range of speeds and limb postures. Dissection data provided muscle architectural properties. CT data were collected from three specimens; one for segmental mass/inertial properties, one for skeletal form, and another was iodine-stained for muscle visibility. The latter was used to generate muscle lines of action in Rhinoceros 4.0. Maya 2019 was used to create a rigged model using an inverse kinematic constraint approach. Alongside inertial properties and muscle architecture, the rigged model was fed into OpenSim 3.3. Inverse dynamics was used to calculate external joint moments. A dynamic crocodylian routine using direct collocation estimated how those joint moments related to muscle forces throughout the gait cycle. The simulations were used to investigate

how muscle fiber lengths changed across a stride and how they varied with changing limb posture (i.e., a sprawling walk versus a high walk). Results reveal a wide diversity of muscle functions, with different muscles operating on different parts of their force-length curve during locomotion, which altered significantly when limb posture was changed. The result is a three-dimensional, subject-specific musculoskeletal model and simulation with the potential for integrated fore- and hindlimb locomotor dynamics of a quadrupedal species. The model has provided quantitative insight into important aspects of crocodylian limb muscle fiber function during different locomotor behaviors. These data and simulation results provide a rigorous framework which can inform simulations to estimate, for the first time, well-validated, integrative quadrupedal locomotor dynamics of extinct archosaurs and to reconstruct muscle-, limb- and organism-level details of locomotor biomechanics and its evolution. **Funding Sources** ERC Horizon 2020 Advanced Investigator Grant (695517, to J.R.H.).

## Romer Prize

### A PALEOBIOGEOGRAPHIC HYPOTHESIS OF ARVICOLINE RODENT ORIGINATION AND DISPERSAL USING THE FIRST TIME-CALIBRATED PHYLOGENY FOR THE CLADE

Withnell, Charles B.

Jackson School of Geosciences, The University of Texas at Austin, Austin, Texas, U.S.A.

Arvicoline rodents (voles, lemmings, and muskrats) are important taxa for characterizing the North American Land Mammal Ages (NALMAs) of the Pliocene and Pleistocene. They were the basis for finer-scale temporal and spatial resolution and were used to generate five arvicoline divisions of the Blancan NALMA and three for the Irvingtonian, although some of those divisions are now abandoned. The rich fossil record of arvicolines has never been reconciled with modern phylogenetic methodologies, because that record consists almost exclusively of isolated teeth or partially preserved tooth rows. I present a molecular phylogeny of arvicoline rodents, based on five genes and including 134 species. I used Parsimony, Maximum Likelihood, and Bayesian inference methodologies to frame hypotheses of arvicoline rodent relationships. I incorporated seven fossil calibrations in my Bayesian analysis. Calibrations were spread throughout the tree and yield a hypothesized age of origination of the clade in the Miocene at 6.5 Ma, and the subsequent evolution of all the extant clades by 1 Ma. My approach is novel, because I successfully used isolated teeth to inform my molecular phylogeny, even though some of those fossils were not identified to species. The time-calibrated

Bayesian phylogeny was then incorporated into the R program BioGeoBEARS to give a probabilistic hypothesis for ancestral range reconstructions at nodes. My primary objective was to model arvicoline dispersal across the Bering Land Bridge connecting Asia to North America. Results suggest an Asian origination for the clade, with at least eight immigration events into North America, and one from North America to Asia. My data indicate an origination of *Lemmiscus* at 5 Ma and the origination of the *Synaptomys* clade (including *Mictomys*) at 3.8 Ma. The Blancan V division is defined by the immigration of bog lemmings (*Synaptomys sensu lato*), previously thought to be 2.5 Ma. My results indicate that bog lemmings evolved and dispersed into North America much earlier than that, and corroborate a previously problematic report of bog lemmings from the Hagerman Fossil Beds at 3.93 Ma. These results leave the Blancan undifferentiated from 2.5 Ma to the start of the Irvingtonian at 1.9 Ma. My data also independently corroborate fossil discoveries of the sagebrush vole at Hagerman Fossil Beds, (3.75 Ma) earlier than the widespread appearance of *Lemmiscus* in late Irvingtonian faunas.

**Funding Sources** Funding for this project was provided by the Jackson School of Geosciences, The University of Texas at Austin.

### Marine Reptile Diversity & Biology

#### A NEW ICHTHYOSAURID (REPTILA: ICHTHYOSAURIA) FROM THE BLUE LIAS FORMATION (HETTANGIAN–SINEMURIAN, LOWER JURASSIC) OF WARWICKSHIRE, U.K., WITH IMPLICATIONS FOR THE TAXONOMY AND PHYLOGENY OF ICHTHYOSAURIDAE

Wolniewicz, Andrzej S.  
Institute of Paleobiology, Polish Academy of Sciences,  
Warsaw, Poland

Ichthyosauridae is a monophyletic ichthyosaur group known almost exclusively from the Lower Jurassic of the U.K. The most recent taxonomic review recognized two valid genera within the clade – *Ichthyosaurus*, represented by six species, and *Protoichthyosaurus*, comprising two species. However, our understanding of ichthyosaurid taxonomy is hindered by the paucity of comprehensive, anatomical descriptions of the abundant fossil material and insufficient knowledge of the effects of intraspecific and interspecific variation and taphonomy on morphological character states. Here, I present a new ichthyosaurid from the Blue Lias Formation (Hettangian–Sinemurian, Lower Jurassic) of Warwickshire, U.K., represented by an almost complete, three-dimensionally preserved skull and mandible in occlusion. The new taxon represents one of the largest ichthyosaurids reported to date and is diagnosed by

a unique combination of morphological character states, which include a moderate overbite and several ichthyosaurian plesiomorphies, previously unreported in Ichthyosauridae – the anterior terrace of the supratemporal fenestra, a posterior process of the postorbital and a posterior process of the jugal. In order to test the phylogenetic position of the new taxon relative to other ichthyosaurids, I performed an expanded, specimen-level phylogenetic analysis of Ichthyosauridae, based on a previously published dataset. The resulting cladogram confirms the placement of the new taxon within the group, but its exact phylogenetic position relative to other ichthyosaurids remains unresolved. Furthermore, our phylogenetic analysis also recovers several partial specimens previously referred to *Protoichthyosaurus* to demonstrate closer phylogenetic affinity with the new taxon than with *Protoichthyosaurus*. This has implications for the systematics of Ichthyosauridae and enables a critical revision of several cranial characters used in previous studies of ichthyosaurid taxonomy. My results demonstrate the importance of specimen-based phylogenetics in vertebrate paleontology and encourage additional work on the anatomy, taxonomy and phylogeny of Ichthyosauridae.

**Funding Sources** Natural Environment Research Council (NERC) PhD studentship (NE/L501530/1).

### Colbert Poster Prize/Paleogene Mammals

#### NEW FOSSIL SPECIMENS OF *PALAEOAMASIA KANSUI* AND PHYLOGENETIC REVISION OF EMBRITHOPODA

Wood, Melissa C.<sup>1</sup>, Beard, K. Christopher<sup>3</sup>, Sanders, William J.<sup>2</sup>

<sup>1</sup>Department of Geophysical Sciences, University of Chicago, Chicago, Illinois, U.S.A., <sup>2</sup>Museum of Paleontology, University of Michigan, Ann Arbor, Michigan, U.S.A., <sup>3</sup>University of Kansas, Lawrence, Kansas, U.S.A.

Embrithopoda is an extinct order of Afrotheria (Mammalia) whose evolutionary and biogeographic history is complicated by extremely fragmentary fossil remains. Its constituents are recognizable by unique pseudolophodont upper molars, which are most extreme in *Arsinoitherium*, a genus known from the latest Eocene and throughout much of the Oligocene of Afro-Arabia. Older Eurasian embrithopods in the genera *Crivadiatherium*, *Hypsamasia*, and *Palaeoamasia* are more poorly represented in the fossil record than *Arsinoitherium*. As a result, attempts to phylogenetically assess relationships within Embrithopoda have produced poorly supported topologies. Many of these previous phylogenies have placed the Turkish embrithopod *Palaeoamasia kansui* as a basal member of Embrithopoda due to its less developed

pseudolophodonty with respect to *Arsinoitherium*, implying a Eurasian ancestry of embrithopods that contradicts expectations for evolutionary origins of afrotherian orders. Here we describe new Lutetian (43 Ma) material of *P. kansui* from the Uzuncarsidere Formation of Central Turkey, including a nearly complete palate comprising the most complete dental series known of this species. It exhibits features that are unexpectedly derived for embrithopods, including enlarged, procumbent incisors, and a diastema anterior to P2. Our new observations on this palate, as well as on 30 isolated teeth and jaw fragments of *P. kansui*, provide the impetus for a revised, comprehensive, phylogenetic analysis of the order and a review of its species-level taxonomy. The new phylogeny contains 205 characters for the six embrithopod genera and two outgroups (*Phosphatherium* and *Phenacolophus*) and reveals minimal variation among described embrithopod specimens from Turkey. These results support a taxonomic revision in which nearly all Turkish embrithopod specimens are designated as *P. kansui*. This species exhibits a unique mix of plesiomorphic and derived features and is therefore not a primitive taxon. Instead, it represents a separate evolutionary trajectory than that in Africa and appears to have colonized Eurasia from Afro-Arabia via sweepstakes dispersal. Our new phylogeny serves as a template for future discovery of embrithopod material and may be informative for the study of relationships within Afrotheria as a whole.

**Funding Sources** This project was supported by NSF grants EAR-1543684 and EAR-1923294.

## Dinosaur Systematics, Diversity & Ecology

### SAURO-THROAT: THE FIRST OCCURRENCE OF A RESPIRATORY INFECTION IN A NON-AVIAN DINOSAUR

Woodruff, Cary<sup>1</sup>, Wolff, Ewan<sup>2</sup>, Wedel, Mathew J.<sup>3</sup>, Witmer, Lawrence<sup>4</sup>

<sup>1</sup>Royal Ontario Museum/Great Plains Dinosaur Museum, Toronto, Ontario, Canada, <sup>2</sup>Montana State University, Bozeman, Montana, U.S.A., <sup>3</sup>Western University of Health Sciences, Pomona, California, U.S.A., <sup>4</sup>Ohio University, Athens, Ohio, U.S.A.

Infectious diseases affect all vertebrate species today, and there is every reason to believe that this has evolutionarily always been the case. Other than repaired fractures, osteoarthritis and periosteal reaction, the vertebrate fossil record has limited evidence of other types of disease. This difficulty in paleontological diagnoses mainly stems from 1) the inability to conduct modern medical testing (e.g., biopsy, immunology), 2) because the vertebrate fossil record is predominated by osseous tissues, soft-tissue

pathologic structures are less likely to be preserved, and 3) many osseous lesions are not very diagnostically specific. However, here reported for the first time is a respiratory disorder in a dinosaur. Identified from an immature diplodocid sauropod collected from the Lower O'Hair Quarry within the undivided Morrison Formation of southwest Montana, this specimen presents irregular bony pathologic structures stemming from the pneumatic features in the anterior cervical vertebrae. As these dinosaurs show well-understood osteological correlates indicating that respiratory tissues (i.e., non-vascularized pulmonary air sacs) were incorporated into the post-cranial skeleton and thus likely had an 'avian-style' form of respiration (i.e., unidirectional airflow through the lungs), it is most parsimonious to identify these pathologic structures as stemming from a respiratory infection. Numerous avian respiratory disorders are known today, and thus comparisons were made to the fossil case. While several extant avian infections produce symptoms consistent with what is seen in the fossil, the most agreeable and parsimonious is airsacculitis with associated osteomyelitis (bone infection). From actinobacterial to fungal in origin, airsacculitis is extremely prevalent and the most common respiratory disorder in birds today. While we cannot at this time precisely pinpoint the specific infectious agent that caused the airsacculitis, this diagnosis establishes the first fossil record of this disease. Additionally, it allows us increased insight into the medical disorders of dinosaurs from a phylogenetic perspective and represents a further data point in understanding what ailments, diseases, and disorders plagued the 'terrible lizards.'

## Macroecology & Macroevolution

### CAN A FRAGMENTED PAST BE TRUSTED? ASSESSING BIAS AND PHYLOGENETIC SIGNAL IN THE SQUAMATE FOSSIL RECORD

Woolley, Charles H.<sup>1</sup>, Thompson, Jeffrey R.<sup>2</sup>, Wu, Yun-Hsin (Becky)<sup>1</sup>, Bottjer, David J.<sup>1</sup>, Smith, Nathan D.<sup>3</sup>

<sup>1</sup>Department of Earth Sciences, University of Southern California, Los Angeles, California, U.S.A., <sup>2</sup>Department of Genetics, Evolution and Environment, University College London, London, U.K., <sup>3</sup>Dinosaur Institute, Natural History Museum of Los Angeles County, Los Angeles, California, U.S.A.

Although squamates have an extensive fossil record spanning >242 million years, a substantial number of fossil squamate generic and specific diagnoses are based on isolated and often incompletely-preserved skeletal specimens. This apparent bias represents a major hurdle in understanding squamate evolution through geologic time, and is a consistent source of uncertainty in determining the

phylogenetic placement of fossil squamate taxa. The present study: 1) characterizes bias in fossil data currently available from a pivotal period in squamate evolution (Late Cretaceous) in multiple museum collections, and 2) assesses the phylogenetic ‘fidelity’ of this data by measuring phylogenetic signal in fossil squamate skeletal elements ‘overrepresented’ in museum collections. To quantify taphonomic/sampling bias, we sampled 480 skeletal specimens in Late Cretaceous squamate collections at four major North American natural history collections. We determined that 31.1% of observed specimens are tooth-bearing, 41.7% are dermal (osteoderms), 13.6% are axial (vertebrae + ribs), 11.3% are appendicular, and 2.3% are non-tooth-bearing cranial (skull). This sample distribution reflects a clear bias toward tooth-bearing elements of the skull and osteoderms. To determine the effect of this bias on squamate phylogeny, we used metrics of homoplasy (Consistency Index, CI) and retained synapomorphy (Retention Index, RI) in individual morphological characters corresponding to ‘underrepresented’ and ‘overrepresented’ skeletal elements in the squamate fossil record. We applied these metrics to two recent comprehensive squamate morphological phylogenetic datasets that reflect the two competing hypotheses of squamate evolutionary relationships. Rigorous statistical comparisons of character CI and RI values across both datasets reveal that characters corresponding to ‘overrepresented’ skeletal elements in the squamate fossil record show similar levels of CIs and RIs to characters from ‘underrepresented’ anatomical elements. This demonstrates that phylogenetic character data from the biased squamate fossil record is not any more likely to provide misleading evidence of phylogenetic relationships than character data from the rest of the skeleton. Critically, this result is recovered regardless of hypothesis of squamate higher-level evolutionary relationships. These preliminary results add confidence to our ability to accurately infer the phylogenetic relationships of fossil squamates.

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### **Dinosaur Systematics, Diversity & Ecology**

#### **TESTING SIZE-FREQUENCY DISTRIBUTIONS AS A METHOD OF ONTOGENETIC AGING: A LIFE HISTORY ASSESSMENT OF HADROSAURID DINOSAURS FROM THE DINOSAUR PARK FORMATION OF ALBERTA, CANADA, WITH IMPLICATIONS FOR HADROSAURID PALEOECOLOGY AND ONTOGENETIC SEGREGATION**

Wosik, Mateusz<sup>1</sup>, Chiba, Kentaro<sup>2</sup>, Therrien, François<sup>3</sup>, Evans, David<sup>4</sup>

<sup>1</sup>Biology, Misericordia University, Dallas, Pennsylvania, U.S.A., <sup>2</sup>Okayama University of Science, Okayama, Japan, <sup>3</sup>Royal Tyrrell Museum, Drumheller, Alberta, Canada, <sup>4</sup>Royal Ontario Museum, Toronto, Ontario, Canada

Hadrosaurid dinosaurs, the dominant large-bodied terrestrial herbivores in most Late Cretaceous Laurasian ecosystems, have an exceptional fossil record consisting of many ontogenetic series, making them an ideal clade with which to conduct life history studies. Previous research considered the Dinosaur Park Formation (DPF) of Alberta as an attritional, or time-averaged, sample and interpreted a size-frequency distribution of long bones collected from the DPF with three size classes to suggest that hadrosaurids from the DPF attained near-asymptotic body size in under three years. This conflicted with previously published osteohistological estimates of 6+ years for penecontemporaneous hadrosaurids from the Two Medicine Formation (TMF) of Montana, suggesting either extreme variation in hadrosaurid growth rates or that size-frequency distributions and/or osteohistology and growth modeling inaccurately estimate ontogenetic age.

We tested the validity of the previously proposed size-age relationship of hadrosaurids from the DPF by significantly increasing the sample size and combining data from size-frequency distributions and osteohistology across multiple long bone elements. The newly constructed size-frequency distributions typically revealed four relatively distinct size-frequency peaks that, when integrated with the osteohistological data, aligned with growth marks. The yearling size class was heavily underrepresented in this newly generated DPF size-frequency distribution. If not due to preservation, this suggests that either juvenile (<2 years of age) hadrosaurids from the DPF had increased survivorship following an initially high nestling mortality rate, or that yearlings were segregated from adults. A growth curve analysis revealed that asymptotic body size was attained in approximately 7 years across the multi-taxic sample, which is consistent with hadrosaurids from the TMF. These data suggest size-frequency distributions of attritional samples underestimate age and overestimate growth rates, but when paired with osteohistology can provide unique insights into life history that may be otherwise unobtainable.

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### **Fishes & Chondrichthyans: Evolution & Distribution**

#### **FIRST RECORD OF AN EDENTULOUS SUSPENSION-FEEDING PACHYCORMIFORM FISH FROM THE LOWER CRETACEOUS OF AUSTRALIA**

Wretman, Lovisa<sup>3</sup>, Liston, Jeff<sup>1</sup>, Kear, Benjamin<sup>2</sup>

<sup>1</sup>Preservation & research, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada, <sup>2</sup>Museum of Evolution, Uppsala University, Uppsala, Sweden, <sup>3</sup>Department of Organismal Biology, Uppsala University, Uppsala, Sweden

Pachycormiforms are an extinct radiation of Mesozoic actinopterygian fishes that occupy a key transitional position along the Holostei-Teleostei stem. The group first appears in the fossil record with an explosive diversification into two morphologically distinct lineages: ‘toothless’ suspension-feeders (SFP) including the famously gigantic *Leedsichthys*; and ‘tusked’ carnivorous pursuit predators, such as the superficially sword-fish like *Protosphyraena*. Pachycormiforms characteristically trended towards reduced ossification in the skeleton, especially amongst the larger-bodied suspension-feeding forms, which tend to be represented by fragmentary and enigmatic remains. Nevertheless, pachycormiform fossils have been recognized worldwide in strata of Early–Late Jurassic and Late Cretaceous age. In contrast, stratigraphically intermediate Early Cretaceous pachycormiforms are virtually unknown, with the exception of the *Protosphyraena*-like taxon *Australopachycormus* from the late Albian of Australia. Here we report on a new Early Cretaceous pachycormiform taxon from the late Albian Allaru Mudstone of northwestern Queensland in Australia. Surprisingly, this specimen is edentulous and consists of a skull with the anterior half of the body, representing an individual of about 1.0–1.5 m SL – approximately equivalent in length to the Dresden juvenile specimen of *Asthenocormus*. Significantly, the Allaru Mudstone pachycormiform is both the first SFP identified from Australia, and the first Early Cretaceous SFP globally. Moreover, while our multiple cross-referencing parsimony and Bayesian phylogenetic analyses decisively place it as a basally branching member of the suspension-feeding clade, the Allaru Mudstone pachycormiform possesses a curious character state mosaic incorporating traits that are more consistent with pursuit predator pachycormiform taxa of equivalent body-size. This observation raises questions about whether Cretaceous pachycormiforms manifested repeated convergence, or perhaps mask a more complex evolutionary history of secondarily-derived extreme feeding specializations.

## Permo-Triassic Tetrapods

### ESTIMATING BODY MASS IN NON-MAMMALIAN SYNAPSIDS: A TALE OF TWO METHODS

Wright, Mark<sup>1</sup>, Cavanaugh, Timothy<sup>2</sup>, Pierce, Stephanie E.<sup>1</sup>

<sup>1</sup>Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts, U.S.A., <sup>2</sup>Harvard Extension School, Harvard University, Cambridge, Massachusetts, U.S.A.

Body mass heavily influences locomotor performance in terrestrial animals and is thus a key trait for reconstructing the potential locomotor behaviors of extinct animals. Although extensive work has gone into understanding body size evolution in archosaurs, less attention has been given to the mammalian stem lineage, the non-mammalian synapsids (NMS). Reconstructing body mass evolution in NMS can provide insight into their evolutionary dynamics and how body size influenced locomotor ecology during mammalian evolution. Here, we compare limb bone circumference scaling coefficients from the literature with a volumetric reconstruction method to estimate body mass in four NMS: the ‘pelycosaur’ *Ophiacodon uniformis*, *Dimetrodon milleri*, and *Edaphosaurus boanerges*, and the dicynodont *Dinodontosaurus turpior*. Full body 3D skeletal models were created from museum mounts using photogrammetry, and each model was divided into 15 regional segments. Using a Python script, we estimated a minimum mass by generating convex hulls around each segment to calculate its volume and then added these values together to estimate the whole-body volume of each specimen. We then used two segment density measurements (horse = 893 kg/m<sup>3</sup> and crocodile = 1080 kg/m<sup>3</sup>) to calculate a minimum and maximum body mass estimate for each specimen. Our preliminary results show that the limb bone scaling method and the volumetric approach estimate comparable body mass ranges for the smaller synapsid species: *Ophiacodon* (limb = 24–42 kg; vol = 17–20 kg), *Dimetrodon* (limb = 33–57 kg; vol = 33–40 kg), and *Edaphosaurus* (limb = 45–78 kg; vol = 78–94 kg). However, the two methods estimate vastly different body mass ranges for the heaviest species *Dinodontosaurus* (limb = 877–1519 kg; vol = 196–237 kg), with limb bone scaling predicting a body mass 4–7 times greater than the volumetric model. This latter result is consistent with recent studies that compared these methods in two large-bodied synapsids, the dinocephalian *Tapinocanius* and the dicynodont *Lisowicia*. Although further data are needed, we hypothesize that limb bone scaling may overestimate body mass in large synapsids due to bone shape allometry and that volumetric reconstructions may provide more conservative estimates. Moving forward, we aim to sample a much wider range of NMS, in addition to extant amniotes, to investigate the relationship between body size, posture, and locomotion during the evolution of mammals.

## Quantitative Methods

### FROM MICROFOSSILS TO MOLARS: TESTING THE APPLICATION OF THE SOFTWARE

## PACKAGE AUTOMORPH TO FOSSIL MAMMAL TEETH

Wright, Susannah, Vietti, Laura A., Clementz, Mark  
Geology & Geophysics, University of Wyoming, Laramie,  
Wyoming, U.S.A.

Teeth represent a significant portion of the fossil mammal record and are often useful for assigning taxonomic determinations of a specimen. However, due to subtle differences in tooth morphology among mammal species, teeth are often difficult to identify without a high degree of familiarity. AutoMorph, a software package developed in 2017 by Hsiang and colleagues, may provide a semi-automated method to determine the taxonomic identity of fossil mammal teeth. AutoMorph is an open-source, high-throughput software package that can rapidly extract 2D and 3D morphological data from both standard and focal-stacked images. This software was developed to automate the taxonomic identification of foraminifera from deep-sea sediments and has also successfully been used to identify marine invertebrates and ichthyoliths. However, no published works have applied AutoMorph to the fossil mammal tooth record. Here, I present a study exploring AutoMorph's usefulness for studies of small fossil mammal teeth. I selected and imaged the occlusal surfaces of upper and lower molars from 530 Wasatchian-aged fossil mammal specimens from three clades: condylarths, primates, and rodents. AutoMorph processed these images, generating occlusal outlines and measurements for nine 2D variables. These results were analyzed in a two-part study with the goals of: (1) determining and refining the process of using AutoMorph with images of fossil mammal teeth, and (2) determining AutoMorph's usefulness for taxonomic differentiation and identification of specimens. Results from the first part of this study show that AutoMorph can extract precise occlusal outlines and 2D measurements from images of fossil mammal teeth. Discriminant and principal component analyses in the second part of this study were able to differentiate taxa at various taxonomic levels; however, results were inconsistent across the studied clades. Results do indicate that AutoMorph may highlight size and shape trends that may be indicative of niche sharing and/or competition. This software may still have important applications for collections-scale studies of fossil mammal teeth, and future studies should explore the applicability of AutoMorph's 3D-measurement module.

**Funding Sources** Institute of Museum and Library Services: Museums for America Grant.

### Mesozoic Herpetology

#### A NEW NOTHOSAUROID (SAUROPTERYGIA) FROM CHINA

Wu, Xiao-Chun<sup>1</sup>, Shang, Qing-Hua<sup>2</sup>, Li, Chun<sup>2</sup>  
<sup>1</sup>Paleobiology, Canadian Museum of Nature, Ottawa, Ontario, Canada, <sup>2</sup>Lower Vertebrate Lab, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China

Sauropterygia, which flourished in the Mesozoic sea, is a diverse group of aquatic diapsid reptiles that consists of Placodontiformes and Eosauropterygia. The latter includes the European pachypleurosaurs, a number of pachypleurosaurs-like forms from China, and the clades Nothosauroida and Pistosauroida (the latter incorporating the Plesiosauroidea). Although interrelationships among many subgroups of the Eosauropterygia have been a subject to debate for years, the monophyly of the Nothosauroida is broadly accepted. This group includes *Simosaurus*, *Paludidraco*, *Germanosaurus*, *Nothosaurus*, and *Lariosaurus*, which are all known in Europe. Since 2000, new species of *Nothosaurus* or *Lariosaurus* have been continuously described in China, but no single genus of the Nothosauroida has been discovered in the country so far. Here we report a new nothosauroid represented by two skeletons from the Ladinian Zhuganpo Member of the marine Falang Formation in southwest China. The new nothosauroid is unique in having an unusually short tail shorter than the skull-neck region in length. Its skull is diagnostic in having a wide and constricted snout, a large supratemporal fossa slightly larger than the orbit, and a parietal table strongly constricted posteriorly. Postcranial specializations also include a short trunk with 14 dorsal vertebrae, an extremely massive and broadened mid-diaphysis of the humerus, and a strongly expanded proximal head of the ulna. In addition, the postcranial skeleton is strongly pachyostotic, which may indicate a slow mode of swimming underwater and a benthic carnivorous feeding habit for the new form. Phylogenetically, it forms the sister taxon of the *Nothosaurus*–*Lariosaurus* clade within Nothosauroida. The discovery of this new nothosauroid not only reveals a local faunal diversity and expands the known range of sauropterygian lifestyles during the late Middle Triassic, but also provides a chance to test the phylogenetic relationships of the Eosauropterygia hypothesized by previous studies.

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### Bird Biology & Evolution

#### TOOTH CYCLING AND REPLACEMENT PATTERNS OF CRETACEOUS ORNITHOMORPH BIRDS

Wu, Yun-Hsin (Becky)<sup>1</sup>, Chiappe, Luis M.<sup>2</sup>, Bottjer, David J.<sup>1</sup>, Bailleul, Alida<sup>3</sup>

<sup>1</sup>Geological Sciences, University of Southern California, Los Angeles, California, U.S.A., <sup>2</sup>Dinosaur Institute, Natural History Museum of Los Angeles County, Los Angeles, California, U.S.A., <sup>3</sup>Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China

Most Mesozoic birds have teeth and many of them are found with multiple generations of tooth cycling. The earliest reports of tooth replacement in birds came from observations on *Ichthyornis* during the 19<sup>th</sup> century, data leading to the suggestion that *Ichthyornis* had vertical tooth replacement with lingual root resorption, similar to the condition in other dinosaurs and crocodylians. In 1999, Martin and Stewart argued that such vertical replacement supported a sister-group relationship between birds and crocodylians. Nonetheless, this inference was based on the incomplete representation of avian tooth cycles (i.e., lacking a complete ontogenetic history). Here we present new  $\mu$ CT data of two ornithuromorph avian specimens, *Ichthyornis dispar* (FHM-2503) and *Yanornis martini* (IVPP 13358), which preserve replacement teeth in different tooth cycling stages, thus revealing the ontogeny of their teeth. Comparisons of these data to CT scans of American alligators (*Alligator mississippiensis*) and previous studies of *Coelophysis*, *Allosaurus*, and tyrannosaurids reveal a different resorption behavior of the odontoclasts in ornithuromorphs. Whereas crocodylians, non-avian theropods, and ornithuromorphs share replacement teeth formed lingually, which move labially and invade the space of the functional tooth's root, alligators and ornithuromorphs start resorbing the root of functional teeth during earlier developmental stages than the studied non-avian theropods. Yet, unlike alligators, during the resorption process, the crowns of growing teeth in *Ichthyornis* approach tightly the roots of functional teeth, a pattern that also results in functional teeth having a significant portion of their labial roots remaining even as the replacement teeth reach the alveolar margin. Consequently, the pattern of tooth cycling in *Ichthyornis*, although different from that of studied non-avian dinosaurs, is also different from that of crocodylians. The well-preserved tooth families in these avian specimens also reveal the conserved alternating tooth replacement pattern of other archosaurs. The new data show that this pattern is not synchronized among tooth families and is asymmetrical in *Yanornis*. Our results thus provide novel data on the tooth cycling of Mesozoic birds, contributing to unravelling the mechanisms of dental renewal in archosaurs and what controls them.

## Quantitative Methods

## USING 2D DENTAL GEOMETRIC MORPHOMETRICS TO IDENTIFY MODERN *PEROGNATHUS* AND *CHAETODIPUS* SPECIMENS (RODENTIA, HETEROMYIDAE)

Wyatt, Megan R.<sup>1</sup>, Hopkins, Samantha S.<sup>2</sup>, Davis, Edward B.<sup>2</sup>

<sup>1</sup>Department of Ecology and Evolution, Stony Brook University, Stony Brook, New York, U.S.A., <sup>2</sup>Department of Earth Sciences, University of Oregon, Eugene, Oregon, U.S.A.

The Heteromyidae (pocket mice and kangaroo rats) are a group of extant small rodents abundant in North American Cenozoic fossil assemblages. Two genera of heteromyids, *Chaetodipus* and *Perognathus*, share similar tooth morphology. Previous genetic studies show these extant genera likely diverged in the early Miocene (~20 million years ago). However, the *Chaetodipus* fossil record starts in the Pleistocene (~2 million years ago) while the *Perognathus* fossil record begins in the middle Miocene, near the time suggested by molecular divergence. Studies have previously found these two genera are not distinguishable from each other using descriptive dental morphology alone. In this study, we asked whether two-dimensional geometric morphometrics performed on either complete dentition or isolated premolars can accurately identify *Chaetodipus* and *Perognathus* specimens to the genus and species-level. We developed a landmarking scheme based on features that are consistent through wear and recognizable in the fossil record, and could be subset for analyses on individual molars. We landmarked the occlusal surface of the upper and lower tooth rows of modern *Chaetodipus* (n = 83) and *Perognathus* specimens (n = 80), including 12 of the 26 extant species across the two genera. We used the R packages 'geomorph' and 'Morpho' to run a canonical variates analysis to investigate whether principal component variation could predict known taxonomic identifications. The morphospace using complete dentition can identify specimens to genus with 90–92% accuracy and to species with 36%–100% accuracy. Body size and biogeographic ranges explained species-level misidentification more than phylogenetic relationships of the species. Specifically, *Perognathus parvus*, the largest *Perognathus* species in the analysis, was most frequently misidentified as *Chaetodipus*. We found an isolated premolar provides sufficient information for genus-level identification (69%–84% accuracy), but not for species-level identification (26%–56% accuracy). The morphospace suggests the anterior–posterior length and transverse width ratios of the premolars are diagnostic for genus identification. This morphospace of modern specimens can be used to identify the fossil dentition of *Chaetodipus* and *Perognathus* specimens already in museum collections and refine our existing knowledge of heteromyid occurrences in North America.

## Macroecology & Macroevolution

### COMPETITION AND TAPHONOMY IN THE STRUCTURING OF LATE CRETACEOUS DINOSAUR COMMUNITIES IN NORTH AMERICA

Wyenberg-Henzler, Taia C.<sup>1</sup>, Mallon, Jordan<sup>2</sup>

<sup>1</sup>Earth Sciences, Carleton University, Okotoks, Alberta, Canada, <sup>2</sup>Palaeobiology, Canadian Museum of Nature, Ottawa, Ontario, Canada

Body size distribution in most dinosaur communities was negatively skewed (as opposed to normal or positively skewed, as in most mammal communities). Abundance modeling of dinosaur communities has showed that competitive pressure from immature megaherbivores may have limited the abundance of small ornithischian species, producing this negatively skewed distribution. However, these models assume competition at like body sizes, and do not otherwise account for any ecomorphological differences that might have existed.

We examined the potential for competition between immature megaherbivores and small ornithischians from the Late Cretaceous of North America using cranial morphometrics and beak shape as ecomorphological proxies. Principal components analyses and rarefied testing show overlap within the reconstructed ecomorphospace and no significant differences in component scores between leptoceratopsids and juvenile megaherbivores, indicating competition may have occurred between these taxa. Thescelosaurids and pachycephalosaurids were otherwise isolated in ecomorphospace. We also predicted that, on the competition hypothesis, immature megaherbivores should outnumber small ornithischians under taphonomically equivalent circumstances. We used femoral counts and associated lithological and taphonomic information to show that megaherbivores generally outnumbered small ornithischians, as predicted by the competition hypothesis. However, the results for isolated and sandstone occurrences showed statistically similar abundances of small ornithischians and megaherbivores. Our results support some small role for competition in the structuring of size distributions of Late Cretaceous dinosaur communities, but it is likely that taphonomic size bias also contributed to the negatively skewed distribution observed today.

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#### Quantitative Methods

### INCLUDING DISTORTED SPECIMENS IN ALLOMETRIC ANALYSES: USING GENERALIZED LINEAR MIXED MODELS TO ACCOUNT FOR SAMPLE DEFORMATION

Wynd, Brenen<sup>1</sup>, Uyeda, Josef<sup>2</sup>, Nesbitt, Sterling J.<sup>1</sup>

<sup>1</sup>Geosciences, Virginia Tech, Blacksburg, Virginia, U.S.A., <sup>2</sup>Biological Sciences, Virginia Tech, Blacksburg, Virginia, U.S.A.

Allometry, patterns of relative change in body parts, has been applied to reconstructing how clades exhibit scaling patterns representing evolutionary constraint on phenotype, or in the patterns of ontogeny. Recording allometry through measurements is one of the few methods available to reconstruct ontogenies in extinct taxa. However, many fossil specimens are deformed during fossilization, changing their morphology. Deformation can influence recovered allometric patterns by outlier effects, which can lead to recovered patterns that do not represent the biology of the organism. The remedy for this is to remove distorted measurements from analyses; however, this removes individual variation and limits the number of samples amenable to study. The issue lies in the method, not the specimens. Both linear regression and reduced major axes are sensitive to outliers, as opposed to a generalized linear mixed model (GLMM) which can code specimens as distorted. To test the efficacy of a GLMM, we performed a simulation study based on measurements of a sample of the cynodont, *Exaeretodon argentinus*. We estimated between 10 and 25 measurements of the skull from a normal distribution. We then used these simulated data to generate a feature estimate, based on estimated skull length, and coefficient of allometry (slope), y intercept, and residuals taken from a regression analysis of *E. argentinus*. To estimate the effects of distortion, we added variation to half of our sample using a binomial distribution. We tested three models, with 1,000 repetitions each: linear regression without added variation, linear regression with added variation, and GLMM with added variation. We found that a linear regression of 10 non-deformed samples performed nearly equivalent to a GLMM of 15 samples including added variation. To validate these findings, we performed a nonparametric bootstrap analysis on two datasets, *E. argentinus* crania (n = 15) and *Tawa hallae* femora (n = 28). Results of the bootstrap analysis support our simulations such that the GLMM is better able to reconstruct patterns of allometry in samples with deformation. Though somewhat negligible for large datasets, for smaller sample sizes (10 < n < 20) where removing measurements or entire specimens can greatly influence results, this method can reconstruct allometric patterns including deformed specimens. Our study suggests that a GLMM can better reconstruct patterns of allometry over a linear regression, given fossil datasets.

#### Late Cenozoic Mammalian Macroecology & Macroevolution

### A LONGER FUSE FOR THE SPREAD OF C4-DOMINATED ECOSYSTEMS IN NORTH AMERICA

Yann, Lindsey T.<sup>1</sup>, Feranec, Robert<sup>3</sup>, Pagnac, Darrin<sup>4</sup>, Browne, Ian D.<sup>2</sup>

<sup>1</sup>Waco Mammoth National Monument, National Park Service, Waco, Texas, U.S.A., <sup>2</sup>OSU Center for Health Sciences, Tulsa, Oklahoma, U.S.A., <sup>3</sup>New York State Museum, Albany, New York, U.S.A., <sup>4</sup>Geology and Geologic Engineering, South Dakota School of Mines & Technology, Rapid City, South Dakota, U.S.A.

C<sub>4</sub> grasslands were not widespread until the late Miocene rapid increase in C<sub>4</sub> ecosystems (RICE; ~7 Ma), but molecular clock data suggest that C<sub>4</sub> vegetation arose in the Oligocene. This disparity in ages likely means that C<sub>4</sub> vegetation was present on the landscape much earlier than the fossil record indicates. Recent investigations of phytoliths and stable carbon isotope values indicate C<sub>4</sub> vegetation was present at specific localities during 'The Great Transformation' in North America, including sites in southern California. While landscapes were C<sub>3</sub> dominated, the early presence of C<sub>4</sub> vegetation has evolutionary implications, including the onset of hypsodonty in ungulates. Identifying C<sub>4</sub> vegetation signals within the Barstow Formation may identify the locus of a later Miocene spread and can reveal when the C<sub>4</sub> expansion 'fuse' was lit before the late Miocene RICE. Fifty-four Barstow Formation specimens were bulk sampled for  $\delta^{13}\text{C}$  stable isotope analysis and were compared with previously published data. Skyline Quarry (14.94 Ma) was used as a control to compare values between this work (range: -9.7‰ to -7.8‰; mean: -8.5‰) and published data (range: -8.5‰ to -7.8‰; mean: -8.1‰). Overlap of  $\delta^{13}\text{C}$  values suggests the datasets are comparable, and C<sub>4</sub> consumption is seen in southern Californian specimens despite varying researchers and lab analyses. Previous work on equids from the Barstow Formation showed the presence of C<sub>4</sub> vegetation in diets at 15.75 Ma, but these new data indicate C<sub>4</sub> was also present at the following quarries: Rak (15.79 Ma), Oreodont (15.81 Ma), Sunset (15.91 Ma), and Steepside (15.92 Ma). Data from Steepside Quarry push the consumption of C<sub>4</sub> vegetation back approximately 170,000 years to 15.92 Ma with equid  $\delta^{13}\text{C}$  values as high as -6.0‰ (mean: -7.4‰). Over the course of nearly 20 years, three different labs and numerous researchers have produced consistent results that support the presence of measurable amounts of C<sub>4</sub> vegetation on the southern California landscape. While medial Miocene ecosystems were still dominated by C<sub>3</sub> grasses, C<sub>4</sub> vegetation was a measurable part of equid diets in southern California as early as 15.92 Ma. This work, paired with recent phytolith research, pushes the fossil record closer to the age indicated by molecular data. The extension in C<sub>4</sub> utilization suggests that the influence of C<sub>4</sub> plant characteristics, like bundle sheath cells, cannot be ignored when studying the evolution of hypsodonty in the early medial Miocene.

## Mesozoic Herpetology

### CRANIAL MORPHOLOGY OF THE LOWER TRIASSIC ICHTHYOSAURIFORM *CHAOHUSAURUS BREVIFEMORALIS* (REPTILIA: ICHTHYOSAURIFORMA) BASED ON DIGITAL RECONSTRUCTIONS

Yin, Ya-Lei

School of Earth and Space Sciences, Peking University, Beijing, Beijing, China

*Chaohusaurus* is one of the most basal ichthyosauriforms, only known from the Early Triassic of South China, and mostly recovered from the Nanlinghu Formation (Olenekian) of Majiashan Quarry, Chaohu City, Anhui Province. Although many specimens of *Chaohusaurus* have been reported, knowledge of its cranial morphological information is still limited or equivocal, especially in the braincase, palate, and cheek regions, which are partially concealed by matrix. In this study, I redescribe a three-dimensionally preserved skull with four articulated cervical vertebrae of a specimen (GMPKU-P-3086) of *C. brevifemoralis*, with the assistance of CT scans. New anatomical information of *C. brevifemoralis* is revealed, such as two ascending processes on the basisphenoid lateral to the pituitary fossa and a single row of teeth on the palatine. Previously uncertain or misidentified characters of *C. brevifemoralis* are further identified and rectified, respectively. The suborbital fenestra is absent due to the lateral and caudal enlargement of the palatine. The frontal doesn't participate in the formation of the anterior margin of the upper temporal fenestra, despite previous interpretations. A retroarticular process is present, and the articular actually articulates with the quadrate condyle through its antero-medial surface rather than postero-medial surface. This study firstly provides a complete cheek region of Early Triassic ichthyosauriforms. The jugal is uncontacted by the strut-like quadratojugal both externally and internally, reinforcing that the lateral open embayment of ichthyosauriforms is homologous with the lower temporal fenestra of other diapsids. Because *Chaohusaurus* is one of the basal ichthyosauriforms, these findings are significant for comparative and phylogenetic studies of this clade.

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## Symposium: Paleoneurology

### OLFACTORY GENE EVOLUTION IS UNUSUALLY RAPID ACROSS TETRAPODA AND OUTPACES CHEMOSENSORY PHENOTYPIC CHANGE

Yohe, Laurel R., Fabbri, Matteo, Hanson, Michael, Bhullar, Bhart-Anjan S.  
Earth and Planetary Sciences, Yale University, New Haven, Connecticut, U.S.A.

Chemosensation is the most ubiquitous sense in animals, enacted by the products of complex gene families that detect environmental chemical cues and larger-scale sensory structures that process these cues. While there is a general conception that olfactory receptor genes evolve rapidly, the universality of this phenomenon across vertebrates, and its magnitude, are unclear. The supposed correlation between molecular rates of chemosensory evolution and phenotypic diversity of chemosensory systems is largely untested. We combine comparative genomics and sensory morphology to test whether olfactory receptor genes and olfactory phenotypic traits evolve at faster rates than other genes or traits. Using published genomes, we identified olfactory receptors in 21 tetrapods, including amphibians, reptiles, birds, and mammals and compared their rates of evolution to those of orthologous non-chemosensory protein-coding genes. We found that, for all clades investigated, most chemosensory receptor genes evolve nearly an order of magnitude faster than other protein-coding genes, with many olfactory genes showing signatures of diversifying selection. This rapid rate of evolution suggests that chemoreceptor genes are in 'evolutionary overdrive', perhaps evolving in response to the ever-changing chemical space of the environment. To obtain complementary morphological data, we stained whole fixed specimens with iodine,  $\mu$ CT-scanned the specimens, and digitally segmented chemosensory and non-chemosensory brain regions. We then estimated phenotypic variation within traits and among tetrapods. While we found considerable variation in chemosensory structures, they were no more diverse than non-chemosensory regions. We suggest chemoreceptor genes evolve so quickly in reflection of an ever-changing chemical space, whereas chemosensory phenotypes and processing regions are more conserved because they use a standardized or constrained architecture to receive and process a range of chemical cues.

**Funding Sources** National Science Foundation Postdoctoral Fellowship in Biology.

**Dinosaur Systematics, Diversity & Ecology**

#### **A SMALL AND MEDIUM-SIZED ORNITHOPOD TRACKSITE FROM THE LOWER CRETACEOUS HAMAN FORMATION, SOUTH KOREA**

Yoon, Han Sang<sup>1</sup>, Lee, Yuong-Nam<sup>1</sup>, Jung, Seung-Ho<sup>2</sup>, Kong, Dal-Yong<sup>2</sup>, Kim, Su-Hwan<sup>1</sup>, Son, Minyoung<sup>1</sup>

<sup>1</sup>School of Earth and Environmental Sciences, Seoul National University, Seoul, Korea (the Republic of),

<sup>2</sup>National Research Institute of Cultural Heritage, Daejeon, Korea (the Republic of)

A new dinosaur tracksite with footprints of small and medium-sized ornithopods was discovered in the Lower Cretaceous Haman Formation (Albian), Gunbuk-myeon, Haman-gun, South Gyeongsang Province of South Korea, in 2018. The tracksite (33 m<sup>2</sup>) consists exclusively of 54 ornithopod footprints (five short trackways and 32 isolated footprints) within three track-bearing horizons partially exposed on the small creek bottom. Lithofacies and sedimentary structures of the track-bearing horizons and overlying strata imply a marginal lacustrine setting. All tracks are mesaxononic tridactyl pes prints with wide and blunt, short, digital impressions and a large, rounded heel pad impression. No manus prints are observable in the tracksite. The average pes length and width are 18.7 cm and 17.2 cm respectively (average L/W ratio 1.09). The average stride, pace lengths and pace angulation of trackways are 132.5 cm, 66.7 cm, and 170.4° respectively. The average divarication angle of tracks was measured as 28.3° between digits II and III and 29.3° between digits III and IV. All tracks show inward (negative) rotation, with an average angle of 7.0°. The morphological features of the footprints are most likely attributable to ichnogenus *Caririchnium*. The relatively small pes size (lengths range from 13–27 cm) indicates that trackmakers were juvenile to subadult ornithopods. Footprints on each horizon show preferred orientations, suggesting their gregarious behavior. Notably, there are no large-sized ornithopod footprints at all, which is an uncommon phenomenon compared to other ornithopod tracksites with age-mixed or adult-only ornithopod community. The absence of the adult ornithopod tracks would be interpreted as the spatial segregation of ornithopod population based on their ages and formation of the juvenile-only community without parental care.

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#### **Marine Reptile Diversity & Biology**

#### **BRAINS, VEINS, AND SINUSES: ENDOCRANIAL ADAPTATIONS OF THE LAND-TO-SEA TRANSITION IN THALATTOSUCHIAN CROCODYLOMORPHS**

Young, Mark T.<sup>1</sup>, Schwab, Julia A.<sup>1</sup>, Dufeu, David<sup>2</sup>, Dollman, Kathleen<sup>3</sup>, Witmer, Lawrence<sup>4</sup>, Herrera, Yanina<sup>5</sup>, Walsh, Stig<sup>6</sup>, Zanno, Lindsay E.<sup>7</sup>, Xu, Xing<sup>8</sup>, Brusatte, Stephen<sup>1</sup>

<sup>1</sup>School of GeoSciences, University of Edinburgh, Edinburgh, Scotland, U.K., <sup>2</sup>Marian University, Indianapolis, Indiana, U.S.A., <sup>3</sup>University of the Witwatersrand, South Africa, South Africa, <sup>4</sup>Ohio University, Athens, Ohio, U.S.A., <sup>5</sup>UNLP, La Plata,

Argentina, <sup>6</sup>National Museum of Scotland, Edinburgh, U.K., <sup>7</sup>North Carolina State University, Raleigh, North Carolina, U.S.A., <sup>8</sup>Institute of Vertebrate Paleontology & Paleoanthropology, Beijing, China

During their 230 million-year evolutionary history, crocodylomorphs evolved from gracile terrestrial forms, into large-bodied semi-aquatic taxa and bizarre pelagic animals. In order to investigate the land-to-sea transition seen in *Thalattosuchia*, and the evolution of the pelagic metriorhynchids, our team CT-scanned and digitally segmented the cranial endocasts of 16 extinct and extant crocodylomorphs. Our results document that early diverging crocodylomorphs ('sphenosuchians') had distinct brain, vasculature, and sinus morphologies, noticeably different from extant species. However, protosuchian-grade taxa had the entire suite of pneumatic structures seen in extant crocodylians, suggesting crocodylian sinus patterns originated over 200 million years ago. Interestingly, 'protosuchians' had highly pneumatic crania, far more so than extant species with pneumatization of the laterosphenoids and frontals. *Thalattosuchians* had a unique array of endocranial vasculature and pneumatic anatomies; with hypertrophy of venous sinuses and vasculature canal endocasts. Compared to the circulatory patterns of extant species, *thalattosuchians* would have had far greater blood flow entering and exiting the orbital and nasal regions. This corresponds to their proportionally large orbits, and hints that the salt glands observed in *Metriorhynchidae* evolved at the base of *Thalattosuchia*. All *thalattosuchians* had less extensive cranial pneumatic sinus systems when compared to 'sphenosuchians', 'protosuchians' and extant species. Rather than having discrete diverticula, the sinuses were confluent with the tympanic cavity and hard to individualize. The lack of the intertympanic diverticula suggests *thalattosuchians* had poor acoustic coupling of the middle ears, with limited directional hearing when compared to extant species. Our results suggest that some of the major soft tissue adaptations that underpinned the metriorhynchid radiation into the pelagic realm occurred much earlier in *thalattosuchian* evolution, prior to the reorganization of the post-cranial skeleton. This corresponds to our already published work on the inner ears: the major endocranial changes occurred at the base of *Thalattosuchia*, with incremental changes occurring towards and within *Metriorhynchidae*.

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## Quantitative Methods

## MORPHOLOGICAL INFORMATION CHALLENGES CHARACTER EQUAL WEIGHTING AND INDEPENDENCE

Yu, Congyu<sup>1</sup>, Jiangzuo, Qigao<sup>2</sup>, Tschopp, Emanuel<sup>1</sup>, Wang, Haibing<sup>2</sup>, Norell, Mark<sup>1</sup>

<sup>1</sup>Division of Paleontology, American Museum of Natural History, New York, New York, U.S.A.,

<sup>2</sup>Paleomammalogy, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, Beijing, China

Paleontology studies morphology. However, some basic questions such as what a character is, how to weight each character, and what the independence is between characters, are still debated. A morphological character is often coded to describe morphological variation that distinguishes taxa but with more or less consistency across a target group. Existing definitions of morphological characters seem to be more descriptive than definitional. There is little theoretical support in morphological character selection and weighting not only because fossil records are fragmentary but also because researchers rarely assess how much information, rather than data, is in each character. Here, we analyze existing morphological character matrices of a variety of vertebrate groups including different dinosaur lineages, mammals, and lizards. We calculate the information, information entropy, and mutual information in each matrix. The results show considerable variation of information entropy between morphological characters, indicating equal weighting may not be appropriate in phylogenetic analysis. Phylogenetic analysis using matrices weighted by information entropy show generally better results than non-weighting and implied weighting. Mutual information results between characters show widely existing dependence without significant variation across body parts, which challenges the independent character assumption.

## Dinosaur Systematics, Diversity & Ecology

### A PROBABLE LARGEST SAUROPODOMORPH DINOSAUR FROM THE EARLY JURASSIC OF YUNNAN PROVINCE, CHINA

Zhang, Qian-Nan<sup>1</sup>, Jia, Lei<sup>2</sup>, You, Hai-Lu<sup>2</sup>

<sup>1</sup>Beijing Museum of Natural History, Beijing, China,

<sup>2</sup>IVPP, Beijing, China

Non-sauropodan sauropodomorphs were the dominant high-browsing herbivores from the Norian until the end of the Early Jurassic, when replaced by true sauropods. Most of them came from Gondwana, primarily discovered in South America and southern Africa. The Lufeng Formation of China has been recognized for its diversity of sauropodomorph dinosaurs at that time, especially for non-

sauropodan sauropodomorphs. Here we describe a new specimen (ZLJ0011) of non-sauropodan sauropodiform, which was excavated from the Lower Jurassic Lufeng Formation, very close to the locality of *Panguraptor lufengensis*. This specimen is represented by a partially preserved skeleton, including the skull with lower jaw and seven cervical vertebrae. It is diagnosed by a unique combination of autapomorphic characters, such as a wider anterodorsal process of the nasal at its base; posterior-most neurovascular foramen of the lateral maxillary row smaller than the others; shape of the supraoccipital is semilunate and wider than high; lingual concavities of the teeth present; and presence of a lateral expansion at the anterior end of the dorsal surface of the cervical neural spines. As compared with other sauropodomorph material from Lufeng, both its skull and cervicals are larger, and no currently known taxa here have been found with a big head but small body. Our phylogenetic analysis recovers the new specimen as a member of sauropodiforms, forming a sister group with *Yumnanosaurus*, but the two differ greatly in both cranial and cervical characters based on morphological and comparative studies. We used the BioGeoBEARS package in R to do a biogeographic analysis. Though the results of ancestral area reconstruction for sauropodomorphs from Lufeng Formation are ambiguous, the interrelationships of Lufeng taxa seems to repeat the patterns seen in North American counterparts, indicative of multiple dispersal events from different parts of Pangaea. Due to the lack of substantial evidence of dinosaurs around eastern and southeastern Asia, the Lufeng Formation saurischian fauna dominated by diverse sauropodiforms may well represent the earliest biogeographic occurrence of dinosaurs in this region.

### Permo-Triassic Tetrapods

#### SIZE DOES NOT CORRELATE WITH MATURITY IN A SAMPLE OF ADULT SPECIMENS OF THE PHYTOSAUR *RUTIODON CAROLINENSIS*

Ziesemer, Elizabeth  
Biology, Carthage College, Milwaukee, Wisconsin, U.S.A.

Phytosaurs were a clade of basal archosaurs from the Late Triassic. Studies of growth in the clade are limited but juveniles are of small size and have a short snout and large orbits compared to the skull length. *Rutiodon carolinensis*, a species from the Carnian, lived in what is now North Carolina; its relatively high sample size makes it ideal to recover a growth series using quantitative cladistic analysis. The goals of this study were to (1) obtain a growth series, (2) test the correlation between maturity and size, and (3) test for evidence of sexual dimorphism. Six specimens (represented by whole or partial skulls) were coded based on 13 characters from phylogenetic studies. The skulls in this study range from ~500–700 mm in

length, and so the data set lacks juveniles. The character matrix was analyzed in PAUP and an ontogram with 6 growth stages and a tree length of 21 was recovered, the Consistency Index is 0.81 and the Homoplasy Index is 0.19. Stage 1 is not supported by unambiguously optimized synontomorphies; Stage 2 is defined by a wide squamosal and an orbit length of over 60 mm long. Stage 3 is diagnosed by an antorbital fenestra that is over 100 mm long. Stage 4 is diagnosed by a skull length over 700 mm, snout length over 450 mm, and the parietosquamosal complex is rectangular in shape. Stage 5 is diagnosed by a skull width of over 150 mm. Stage 5 was represented by two specimens, and to break the tie an artificial adult was added by coding the synontomorphies at their internode and run in a second analysis; that resulted in multiple ontograms, leaving the issue unresolved. Maturity was then assessed by counting the number of changes from the root of the ontogram, where USNM 5373 was found to have a distance of nine synontomorphies, in contrast to USNM 214513 with only seven changes. The 6<sup>th</sup> stage is diagnosed by a triangular antorbital fenestra and the jugal contributing to the rim of the orbit. Evidence for sexual dimorphism was not seen in this taxon because the ontogram does not split into two separate branches of male and female variants. Finally, the correlation between size and maturity was tested quantitatively. A Shapiro–Wilk normality test returned a p-value of 0.39 for the size measurement ranks and 0.96 for the growth stages, indicating the data are normally distributed. The Spearman Rank test found no correlation between size and growth stage ( $p = 0.872$ ); therefore, size is an unreliable proxy for maturity among adult *R. carolinensis*.

### Marine Reptile Diversity & Biology

#### HOW TO MAKE MONSTERS: CLADISTIC ANALYSIS OF ONTOGENY IN FOUR MOSASAUR TAXA RECOVERED ANCESTRAL PATTERNS OF MOSASAURID SKULL GROWTH

Zietlow, Amelia R.  
Comparative Biology, Richard Gilder Graduate School, Milwaukee, Wisconsin, U.S.A.

Mosasaurs were large, globally distributed aquatic lizards that lived during the Late Cretaceous. Despite numerous specimens of varying maturity, a detailed growth series has not been proposed for any mosasaur taxon. Four taxa, *Tylosaurus proriger*, *T. kansansensis/nepaeolicus*, *Tethysaurus nopcsai*, and *Mosasaurus hoffmannii*, have robust fossil records that span a wide range of sizes and are thus ideal for studying ontogeny. Growth series provide an opportunity to test taxonomy, sexual dimorphism, congruence between size and maturity, and recover ancestral patterns of growth.

The goals of this project were to use quantitative cladistic analysis to (1) recover the growth series of the four taxa; (2) evaluate whether total skull length (TSL) or quadrate height (QH) are appropriate proxies for relative maturity; (3) test for sexual dimorphism; (4) test the hypothesis that *T. kansasensis* are juveniles of *T. nepaeolicus*; (5) test the hypothesis that the presence of a frontal crest in *T. proriger* is paedomorphic; and (6) identify conserved patterns of growth in mosasaurs.

Fifty-nine hypothetical growth characters were identified, including size-dependent, size-independent, and phylogenetic characters. A growth series was recovered for each taxon: *T. proriger*, 14 growth stages (Consistency Index (CI) = 0.7, Homoplasy Index (HI) = 0.3); *T. nepaeolicus/kansasensis*, 11 stages (CI = 0.6, HI = 0.4); *Te. nopcsai*, three stages (CI = 1, HI = 0); and *M. hoffmannii*, five stages (CI = 0.8, HI = 0.2). The results supported the synonymy of *T. kansasensis* with *T. nepaeolicus* and that *T. kansasensis* are juveniles of *T. nepaeolicus*. A Spearman rank-order test resulted in a significant ( $p < 0.05$ ) correlation between size (TSL and QH) and maturity for all taxa except in *M. hoffmannii* (TSL  $p = 0.9$ , QH  $p = 0.6$ ), which is an artifact of small sample size. Evidence for sexual dimorphism was not found.

Eleven growth changes were shared across the phylogenetic hierarchy: premaxillary rostrum becomes knobbed, quadrate infrastapedial process grows in and broadens, quadrate suprastapedial process lengthens and thickens, and dentary predental process develops a dorsal ridge (*Tylosaurus*); quadrate tympanic ala rim becomes defined and quadrate articular condyle becomes rounded (Russellosaurinae); TSL and QH increase, quadrate anteroventral corner develops, QH increases relative to TSL, quadrate articular condyle ossifies, and dentary tooth row decreases relative to dentary length (Mosasauridae).

## Quantitative Methods

### THE *HESPEROMYS* PROJECT: A NEW DATABASE OF TETRAPOD NOMENCLATURE

Zijlstra, Jelle S.

Hesperomys Project, San Mateo, California, U.S.A.

I present the *Hesperomys* Project, a new database covering the nomenclature and taxonomy of extinct and extant tetrapods. The aim of this database is to provide comprehensive data for all available names, including synonyms. Taxonomically, the focus is on mammals, but several other groups of tetrapods are also well covered, including saurischian dinosaurs, pterosaurs, crocodylians, and caecilians. Currently, there is original description data

for 90% of fossil mammals, type localities for 55%, and type specimens for 41%. In total, the database contains over 85,000 names.

Type specimens are listed with the institution in which they are deposited, and type localities are provided with high geographical and stratigraphic precision. The database contains nearly a thousand distinct institutions and more than 4000 fossil type localities. All names are placed in a taxonomic classification that aims to represent the current state of the literature and clearly distinguishes dubious from accepted names.

The database is useful as a tool for researchers studying the taxonomy of particular groups, and also as a data source for statistics about historical rates of species descriptions, the distribution of type specimens, and similar questions.

## Dinosaur Systematics, Diversity & Ecology

### BIOSTRATIGRAPHIC CORRELATION OF UPPER KAROO-AGE FOSSILS FROM THE MPANDI FORMATION OF SENTINEL RANCH, TULI BASIN, ZIMBABWE

Zondo, Michel<sup>1</sup>, Choiniere, Jonah N.<sup>2</sup>, Barrett, Paul M.<sup>3</sup>

<sup>1</sup>Palaeontology, Natural History Museum, Bulawayo, Bulawayo, Zimbabwe, <sup>2</sup>Geology, University of Witwatersrand, Johannesburg, Gauteng, South Africa, <sup>3</sup>Earth Sciences, Natural History Museum, London, London, U.K.

The Mpandi Formation is the sole upper Karoo-aged fossiliferous unit in the Tuli Basin of Zimbabwe, and based on the co-occurrence of the early branching sauropodomorph dinosaur genus *Massospondylus*, it is correlated with the Elliot Formation of South Africa. Previous Mpandi paleontological fieldwork also identified the presence of the wastebasket sauropodomorph taxon '*Euskelosaurus*.' In the traditional upper-Karoo biozonation, the '*Euskelosaurus*' Assemblage Zone was considered to be Upper Triassic, and the *Massospondylus* biozone was considered to be Lower Jurassic, a result generally upheld by recent reassessment, which suggests these biozones are up to 20 million years apart from each other. This suggests that the Mpandi Formation, despite only presenting a few tens of meters of outcrop thickness, may contain Elliot Formation correlatable beds that span the Triassic-Jurassic boundary, but this has only been tested in a preliminary fashion. My working group at the Natural History Museum of Zimbabwe has been conducting ongoing fieldwork at the Sentinel Ranch locality aimed at improving our knowledge of Mpandi vertebrates. Among the findings of this work are several dinosaur fossils bearing autapomorphic features that allow identification to relatively low taxonomic levels, including cf. *Melanorosaurus*, cf. *Pulanesaura*, and cf.

*Massospondylus*. The identities of these new specimens enable higher-precision correlation with the better studied strata of the Main Karoo Basin and suggest that, although relatively thin, the Mpandi has a temporal span extending from the middle part of the lower Elliot Formation to at least the lower part of the upper Elliot Formation. This may indicate a cryptic unconformity within the Mpandi Formation, its diachronous deposition due to faulting, or the co-occurrence of taxa that are separated by millions of years in the main Karoo Basin.