



THE SOCIETY OF VERTEBRATE PALEONTOLOGY

# VIRTUAL MEETING CONFERENCE PROGRAM

NOVEMBER 1-5, 2021

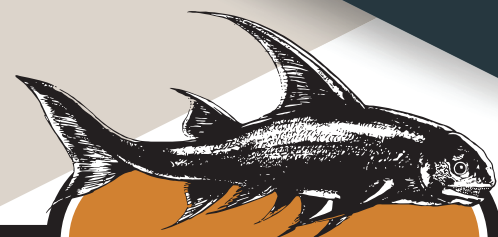


SVP

SOCIETY OF  
VERTEBRATE  
PALEONTOLOGY

81ST ANNUAL MEETING

[www.vertpaleo.org](http://www.vertpaleo.org)



SOCIETY OF  
VERTEBRATE  
PALEONTOLOGY

2021 ANNUAL MEETING

VIRTUAL

# WELCOME TO VIRTUAL!

Dear Delegates,

Welcome to our 81st Annual Meeting, and our second virtual one. While I know we all would have preferred to be able to return to our in-person format, ongoing pandemic concerns made it too uncertain for us to move ahead with our plans for Minneapolis this year. Last year was our first virtual meeting, and one of the biggest benefits of this format was accessibility to a wider audience including many more students than can ordinarily attend in person. We have done our best to respond to your feedback from last year, have added networking opportunities, and we look forward to seeing how they work. In spite of the challenges we have all faced this year, it is exciting to still be able to welcome you to the SVP annual meeting, to share our research and our enthusiasm for vertebrate paleontology.

We are delighted that you are joining us this fall, in what continues to be difficult circumstances for many. All of us involved with organizing this meeting appreciate your ongoing dedication in the face of the challenges presented by lack of access to specimens, labs, and of engaging virtually. We appreciate the time and effort that you have put into your presentations, delivering the workshops and platform events, and we thank you all for the efforts.

As we did last year, we ask that you exercise empathy in interaction with your colleagues, and recognize that many attendees may face pandemic restrictions on their work that are different from your experience. We are glad to be in a position to continue to share our ideas and our work in vertebrate paleontology with one another, and to work together to discuss ways to make pressing issues in our field better.

Welcome, and I hope that you enjoy the 81st Annual Meeting, and that next year we will see you in person in Toronto.



**Jessica Theodor**

SVP President

## THANK YOU TO OUR COMMITTEE!

Thank you to the committee members whose efforts ensured an SVP meeting experience during another unusual year!

### 2021 Program Committee

Mark Uhen, Co-Chair	Jonah Choiniere	Andrew Farke	Josh Miller
Lindsay Zanno, Co-Chair	Brian Choo	Bryan Gee	Alison Murray
Ken Angielczyk	Thomas Cullen	Seb Groh	Brandon Peacock
Victoria Arbour	Larisa de Santis	Advait Jukar	John Rowan
Arnau Bolet	Liping Dong	Brandon Kilbourne	Matt Smith
Kirstin Brink	Alton Dooley	Amber MacKenzie	Jasmina Wiemann
Jennifer Botha Brink	Jaelyn Eberle	Philip Mannion	
Judd Case	Dana Ehret	Win McLaughlin	

### 2021 Virtual Planning Committee

Larisa DeSantis	Selina Robson	Mark Uhen
Margaret Lewis	Elliot Smith	Ted Vlamis
Ali Nabavizadeh	Jessica Theodor	Lindsay Zanno

## SVP 2021 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, Colbert Poster Prize, Preparators', and Education & Outreach presentations.

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# SESSION THEMES

## SVP SESSION THEMES

Avialan Evolution & Biology  
Biomechanics & Functional Morphology  
Colbert Poster Prize  
Crocodylomorph & Pterosaur  
Dinosaur Systematics, Diversity, & Biology  
Education & Outreach  
Fishes Evolution & Distribution  
Holocene & Pleistocene Mammalian Faunas  
Late Cenozoic Mammalian Evolution & Ecology  
Macroecology & Macroevolution  
Mammalian Skeletal Morphology  
Marine Mammals  
Mesozoic & Paleogene Mammals  
Non-Avian Theropod Systematics, Biology, & Evolution  
Paleohistology & Paleopathology  
Permo-Triassic Ecosystems  
Preparators'  
Quantitative Paleontological Methods  
Romer Prize  
Stem Tetrapod, Squamate, & Amphibian Diversity & Biology  
Symposium: Vertebrate Dental Ecomorphology  
Taphonomy, Paleoenvironments, & Stratigraphy  
Turtle & Marine Reptile Diversity & Biology

All session themes are allocated their own live networking session, except for the following themes which have been combined into the following networking session: Mammalian Skeletal Morphology and Marine Mammals.

### THE ALFRED SHERWOOD ROMER PRIZE SESSION

Hear from new voices in paleontology on Tuesday, November 2, from 10:00am to 12:00pm EDT. Twelve 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, November 5, from 4:00pm to 4:45pm EDT.

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

View the posters from which the 2021 Edwin H. and Margaret M. Colbert Prize winner will be chosen, and participate in the live networking session on Thursday, November 4, from 10:00am to 11:00am EDT. These students offer fresh viewpoints in Vertebrate Paleontology.

### PREPARATORS' SESSION

Join this live networking session on Wednesday, November 3, 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.

## ANNUAL BUSINESS MEETING

This live session will be held on Wednesday, November 3, from 4:30pm to 5:30pm EDT.

## 2021 SVP AWARDS PRESENTATION

We are excited to announce an innovation to our virtual awards presentation that will facilitate greater engagement between our attendees and the content about our 2021 Awardees. This year, SVP's virtual meeting platform will include a section devoted to the 2021 awards, allowing attendees to access on demand content about each of the 2021 Awardees throughout the four weeks that the platform is open.

## DIVERSITY SESSIONS

This year, we will be offering four 60-minute diversity sessions on distinct topics each day beginning Tuesday, November 2 through Friday, November 5. 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, NOVEMBER 2 12:30PM - 1:30PM EDT

*Diverse Racial and Ethnic Backgrounds*

### WEDNESDAY, NOVEMBER 3 6:00PM - 7:00PM EDT

*LGBTQIA+*

### THURSDAY, NOVEMBER 4 11:00AM - 12:00PM EDT

*Disabilities and Neurodiversity*

### FRIDAY, NOVEMBER 5 6:00PM - 7:00PM EDT

*Mental Health*

## STUDENT AND POSTDOC ROUNDTABLE EXCHANGE SESSIONS

This year, we will be offering four 60-minute Student and Postdoc Roundtable Exchange sessions from Tuesday, November 2 through Friday, November 5. These sessions will be held on Zoom using breakout rooms (each for a different topic) with timed rotations among the rooms to best simulate the format of an in-person meeting. Some popular topics will be offered multiple times during the week. See below for the schedule of sessions:

### Tuesday, November 2, 6:00pm - 7:00pm EDT

- Visiting Museums
- Applying for Postdocs
- Family and Work/Life Balance
- Science Communication
- Research Abroad

### Wednesday, November 3, 10:00AM - 11:00AM EDT

- Applying for Postdocs
- Government Jobs
- Fossil Preparation Jobs
- Field Work
- Consulting Jobs

### Thursday, November 4, 6:00PM - 7:00PM EDT

- Applying for Graduate School
- Museum Jobs
- Paleontology Outreach
- Field Work
- Meet the SVP Leadership

### Friday, November 5, 11:00AM - 12:00PM EDT

- Applying for Graduate School
- Government Jobs
- Science Communication
- Academic Jobs
- Coding (it's not scary!)

# EXHIBIT HOURS

*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 25 through Sunday, November 21. Live engagement with exhibits is scheduled to occur between Tuesday, November 2 through Friday, November 5 during the following hours:

### **TUESDAY, NOVEMBER 2,**

12:00pm – 1:00pm EDT

### **WEDNESDAY, NOVEMBER 3,**

10:30am – 11:30am EDT

### **THURSDAY, NOVEMBER 4,**

11:30am – 12:30pm EDT

### **FRIDAY, NOVEMBER 5,**

11:30am – 12:30pm EDT

There are three key components to the 2021 SVP Virtual Meeting:

**Pre-recorded talks and posters,** grouped into themes, available for viewing 24/7 Sunday, October 25 through Sunday, November 21.

**Asynchronous moderated Q&A** associated with each presentation available Monday, November 1 through Friday, November 5. 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, Monday, November 1 through Friday, November 5.

## THANK YOU TO OUR FEATURED SPONSOR!



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At Indiana University Press, we want to publish books that will matter twenty or even a hundred years from now—books that make a difference today and will live on into the future through their reverberations in the minds of teachers and writers.

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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! TUESDAY, NOVEMBER 1 - FRIDAY, NOVEMBER 5

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.

## SOCIAL MEDIA GUIDELINES

Follow SVP and comment about the upcoming Annual Meeting using hashtag #2021SVP. Please follow the following 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 #2021SVP. We look forward to seeing your thoughts and discussion online!

## SVP CODE OF CONDUCT (REVISED, 2021)

SVP is committed to providing an inclusive and welcoming environment for all members, during the Annual Meeting and beyond. We will uphold the society's value of non-discrimination in conference spaces, outside of conferences spaces, and in online discourse. We will treat other members equally and respectfully, regardless of age or seniority. Respectful conduct is expected of all members towards others, even from laboratories or research groups in direct competition.

We will treat every member of the community respectfully and acknowledge others for work contributed; this includes not only professional scientists but also technicians, volunteers, collaborators external to its own lab or institution. We will not tolerate harassment, discrimination, bullying or coercive manipulation in any form, and we will consider such behavior to constitute scientific misconduct.

### 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.

## REPORTING AN ALLEGATION OF CODE OF CONDUCT VIOLATION

If you witness or experience prohibited behavior, SVP provides several ways that you can submit a report. Allegations of misconduct must be submitted in writing (see "What to include in a report") via one of the following:

1. Anonymous or non-anonymous reports may be submitted through the NAVEX Platform accessible through the SVP website.
2. Non-anonymous reports may be submitted to the Ethics Committee using safesvp@vertpaleo.org.
3. Non-anonymous reports may also be submitted in writing to:

Chair of Ethics Committee  
Society of Vertebrate Paleontology  
7918 Jones Branch Drive, Suite 300  
McLean, VA 22102 USA

## WHAT TO INCLUDE IN AN ALLEGATION REPORT:

All allegations must be made in writing in one of the three ways described in the previous section. Allegation reports must contain the following:

1. Unless this is an anonymous report via the NAVEX

Platform, the name and affiliation of the individual(s) submitting the allegation.

2. Name(s) of individuals alleged to have engaged in the prohibited behavior(s), if known, or as much identifying information as possible.
3. If there is a victim (and if this is not an anonymous report by the victim), then include the name of the victim(s) and affiliation when possible.
4. Description of the allegation that includes the date(s) and circumstances of the alleged ethics violation. This should include the type of prohibited behavior(s) as defined in the Code of Ethics that is being alleged. Include names and affiliations of witnesses, when possible.
5. Any documentation or other relevant items with a description of how each item relates to the allegation.
6. A statement of any real or perceived conflicts of interest related to any party named in the allegation (e.g., reporters, victims, alleged perpetrators, witnesses) and any members of the Ethics Committee or Executive Committee to ensure a fair and unbiased process.

Allegations may be returned if they do not contain the above information.

## WHAT IF YOU NEED IMMEDIATE HELP DURING AN SVP EVENT?

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).

If you are experiencing or witness prohibited behavior that is not an immediate threat to public safety during an SVP event (meeting, fieldtrip, symposium, online event, etc.), but you need to report DURING the event to stop the observed behavior, please alert the leader of that event immediately (e.g., fieldtrip leader, online event organizer) and, as soon as possible, contact the Vice President/Chair of the Ethics Committee Margaret Lewis (Margaret.Lewis@stockton.edu) or email safesvp@vertpaleo.org. Once you are able, please submit an official written report documenting what happened using one of the above three listed methods of reporting and including "What to Include in an Allegation Report".

# PROGRAM AT A GLANCE

## MONDAY, OCTOBER 25

START	END	TITLE
8:00 AM EDT	through Sun, Nov 21 at 11:59pm EDT	Launch of virtual platform online, including Welcome Message from the President, asynchronous pre-recorded posters, talks, exhibits
2:00 PM EDT	3:00 PM EDT	Public Lecture: "Human Origins told from Afar: Recent fossil discoveries from Woranso-Mille (Afar Rift, Ethiopia) and mid-Pliocene hominin evolution" Yohannes Haile-Selassie

## MONDAY, NOVEMBER 1

9:00 AM EDT	5:00 PM EDT	Workshop #1: Introduction to the Paleobiology Database
1:00 PM EDT	5:00 PM EDT	Workshop #2: Digital Morphology and Shape Analysis with SlicerMorph
3:00 PM EDT	5:00 PM EDT	Workshop #3: Inclusive Science Communication
5:00 PM EDT	8:00 PM EDT	Workshop #4: Optimizing GatherTown for Interactive Science Education

## TUESDAY, NOVEMBER 2

9:30 AM EDT	10:00 AM EDT	Coffee Break w/ Interactive Networking <b>New this year!</b>
10:00 AM EDT	12:00 PM EDT	Romer Prize: <b>Live Q&amp;A with Attendees</b>
12:00 PM EDT	1:00 PM EDT	Visit with Exhibitors
12:30 PM EDT	1:30 PM EDT	Diversity Session #1: Diverse Racial and Ethnic Backgrounds
1:00 PM EDT	2:00 PM EDT	Fishes Evolution & Distribution Networking Session
2:00 PM EDT	2:30 PM EDT	Stem Tetrapod, Squamate, & Amphibian Networking Session
2:30 PM EDT	3:00 PM EDT	Break (on your own)
3:00 PM EDT	4:00 PM EDT	Symposium: Vertebrate dental ecomorphology: Tooth traits that reflect ecology <b>Networking Session</b>
4:00 PM EDT	4:45 PM EDT	Non-Avian Theropod Systematics, Biology, & Evolution <b>Networking Session</b>
4:45 PM EDT	5:15 PM EDT	Coffee Break w/ Interactive Networking <b>New this year!</b>
5:00 PM EDT	6:00 PM EDT	NSF Research & Training Opportunities for Vertebrate Paleontologists
6:00 PM EDT	7:00 PM EDT	Student & Post Doc Session #1: Visiting Museums, Applying for Postdocs, Family and Work/Life Balance, Science Communication, Research Abroad
7:00 PM EDT	7:45 PM EDT	Mammalian Skeletal Morphology & Marine Mammals <b>Networking Session</b>

## WEDNESDAY, NOVEMBER 3

9:30 AM EDT	10:00 AM EDT	Coffee Break w/ Interactive Networking <b>New this year!</b>
10:00 AM EDT	11:00 AM EDT	Student & Post Doc Session #2: Applying for Postdocs, Government Jobs, Fossil Preparation Jobs, Field Work, Consulting Jobs
10:30 AM EDT	11:30 AM EDT	Visit with Exhibitors
11:30 AM EDT	12:15 PM EDT	Permo-Triassic Ecosystems <b>Networking Session</b>
12:15 PM EDT	12:45 PM EDT	Avialan Evolution and Biology <b>Networking Session</b>
12:45 PM EDT	1:30 PM EDT	Break (on your own)
1:30 PM EDT	2:15 PM EDT	Preparators' <b>Networking Session</b>
2:15 PM EDT	3:15 PM EDT	Late Cenozoic Mammalian Evolution & Ecology <b>Networking Session</b>
3:15 PM EDT	3:30 PM EDT	Break (on your own)
3:30 PM EDT	4:15 PM EDT	Mesozoic & Paleogene Mammals <b>Networking Session</b>

## WEDNESDAY, NOVEMBER 3 (CONTINUED)

4:15 PM EDT	4:30 PM EDT	Break (on your own)
4:30 PM EDT	5:30 PM EDT	Annual Business Meeting
5:30 PM EDT	6:00 PM EDT	Coffee Break w/ Interactive Networking <b>New this year!</b>
6:00 PM EDT	7:00 PM EDT	Diversity Session #2 LGBTQIA+

## THURSDAY, NOVEMBER 4

9:30 AM EDT	10:00 AM EDT	Coffee Break w/ Interactive Networking <b>New this year!</b>
10:00 AM EDT	11:00 AM EDT	Colbert Poster Prize <b>Networking Session</b>
11:00 AM EDT	12:00 PM EDT	Diversity Session #3: Disabilities and Neurodiversity
11:30 AM EDT	12:30 PM EDT	Visit with Exhibitors
12:30 PM EDT	1:00 PM EDT	Break (on your own)
1:00 PM EDT	2:00 PM EDT	Paleopathology & Paleohistology <b>Networking Session</b>
2:00 PM EDT	2:45 PM EDT	Macroecology & Macroevolution <b>Networking Session</b>
2:45 PM EDT	3:00 PM EDT	Break (on your own)
3:00 PM EDT	3:30 PM EDT	Turtles & Marine Reptile Diversity & Biology <b>Networking Session</b>
3:30 PM EDT	4:30 PM EDT	Crocodylomorph & Pterosaur <b>Networking Session</b>
4:30 PM EDT	6:00 PM EDT	Break (on your own)
6:00 PM EDT	7:00 PM EDT	Student & Post Doc Session #3: Applying for Graduate School, Museum Jobs, Paleontology Outreach, Field Work, Meet the SVP Leadership
7:00 PM EDT	7:30 PM EDT	Coffee Break w/ Interactive Networking <b>New this year!</b>
8:00 PM EDT	9:00 PM EDT	Holocene and Pleistocene Mammalian Faunas <b>Networking Session</b>

## FRIDAY, NOVEMBER 5

9:30 AM EDT	10:00 AM EDT	Coffee Break w/ Interactive Networking <b>New this year!</b>
10:00 AM EDT	11:00 AM EDT	Biomechanics & Functional Morphology <b>Networking Session</b>
11:00 AM EDT	12:00 PM EDT	Student & Post Doc Session #4: Applying for Graduate School, Government Jobs, Science Communication, Academic Jobs, Coding (it's not scary!)
11:30 AM EDT	12:30 PM EDT	Visit with Exhibitors
12:30 PM EDT	1:00 PM EDT	Break (on your own)
1:00 PM EDT	1:45 PM EDT	Taphonomy, Paleoenvironments, & Stratigraphy <b>Networking Session</b>
1:45 PM EDT	2:30 PM EDT	Quantitative Paleontological Methods <b>Networking Session</b>
2:30 PM EDT	3:00 PM EDT	Break (on your own)
3:00 PM EDT	4:00 PM EDT	Dinosaur Systematics, Diversity, & Biology <b>Networking Session</b>
4:00 PM EDT	4:45 PM EDT	Education & Outreach <b>Networking Session</b>
4:45 PM EDT	5:15 PM EDT	Coffee Break w/ Interactive Networking <b>New this year!</b>
6:00 PM EDT	7:00 PM EDT	Diversity Session #4: Mental Health
7:00 PM EDT		End of Live Programming; Online Q&A available until Sunday, November 21

## SUNDAY, NOVEMBER 21

11:59 PM EST		Platform closes down completely at midnight EST
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EDITOR-IN-CHIEF:  
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## SPECIAL ISSUES

The *Anatomical Record* regularly publishes special and thematic issues on topics of current interest. Articles from many of these issues are freely accessible via the journal's home page, where you can find our most recent Special Issue on Blind Snakes



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

**TUESDAY, NOVEMBER 2, 2021, 10:00AM EDT-12:00PM EDT  
ROMER PRIZE: LIVE Q&A NETWORKING SESSION**

### **TALKS**

**M. Fabbri.** RADIATION OF AQUATIC PREDATORY DINOSAURS

**T. Green.** GROWTH AND SEX: EVOLUTIONARY AND DEVELOPMENTAL ANALYSES OF FORM-FUNCTION RELATIONSHIPS IN THE CRANIAL ORNAMENTATIONS OF NON-AVIAN AND AVIAN DINOSAURS

**P. Medina-González.** DOES SIMILAR MORPHOLOGIES MEAN THE SAME MOVEMENT CAPABILITIES? MORPHOFUNCTIONAL SPACES FOR *CARAGUATYPOTHERIUM MUNOZI* (NOTOUNGULATA; MESOTHERIIDAE) AND *NOTOSTYLOPS MURINUS* (NOTOUNGULATA; NOTOSTYLOPIDAE)

**N.M. Morales Garcia.** THE FEEDING ECOLOGY OF MESOZOIC MAMMALS: A BIOMECHANICAL APPROACH

**A. Pearson.** CEREBRAL REORGANIZATION IN OLD WORLD MONKEYS (CERCOPITHECOIDEA): NEW APPROACHES QUANTIFYING TEMPORAL LOBE EVOLUTION

**D.M. Reuter.** UNPACKING MAMMALIAN OMNIVORE MACROECOLOGY AND MACROEVOLUTION WITH APPLICATIONS TO THE FOSSIL RECORD

**J.P. Rule.** HOW SEALS CONQUERED THE WORLD: INFERRING THE DISPERSAL CAPABILITIES OF ANCIENT TRUE SEALS (FAMILY PHOCIDAE)

**D. Smith Paredes.** THE DEVELOPMENT OF THE TETRAPOD LIMB MUSCULATURE

**C. Torres.** BIRD NEUROCRANIAL AND BODY MASS EVOLUTION ACROSS THE END-CRETACEOUS MASS EXTINCTION: A UNIQUELY AVIAN RESHAPING OF THE BRAIN LEFT ALL OTHER DINOSAURS BEHIND

**M.L. Turner.** INSIDE THE “BLACK BOX” OF THE CRUROTARSAL ANKLE AND INSIGHTS INTO THE PEDAL ORIGINS OF LOCOMOTOR DIVERSITY IN ARCHOSAURS

**L.N. Weaver.** BONE HISTOLOGY OF MULTITUBERCULATE MAMMALS POINTS TO A LIFE HISTORY STRATEGY SIMILAR TO THAT OF PLACENTALS, NOT MARSUPIALS

**C.D. Whalen.** A BAYESIAN TIP-DATED PHYLOGENY OF STEM VERTEBRATES, TOTAL-GROUP CYCLOSTOMES, AND STEM GNATHOSTOMES

**TUESDAY, NOVEMBER 2, 2021, 1:00PM EDT-2:00PM EDT  
FISHES EVOLUTION & DISTRIBUTION NETWORKING SESSION**

**POSTERS**

**J.G. Allen, K. Shimada.** RELATIVE ABUNDANCE BY TAXA IN A UNIQUE LATE CRETACEOUS BONEBED FROM WESTERN KANSAS, USA, LIKELY REVEALING A MORE ACCURATE REPRESENTATION OF THE 'NIOBRARA VERTEBRATE FAUNA'

**D. Broussard, E.B. Daeschler, C. Burrow, J. Trop, P. Zippi, T. Hess.** NEW RECORDS OF LATE DEVONIAN ISCHNACANTHIFORM ACANTHODIANS FROM THE CATSKILL FORMATION OF NORTH-CENTRAL PENNSYLVANIA, USA

**C. Duffin, B. Lauer, R. Lauer, E. Popov, D. Ward.** CHIMAEROID EGG CAPSULES FROM THE LATE JURASSIC LITHOGRAPHIC LIMESTONES OF SOUTHERN GERMANY

**S.Z. Gibson, N. Gammel, M. Julius, A. Simons.** NEW DISCOVERY OF PLEISTOCENE-AGE FOSSIL FISHES (OSTARIOPHYSI: CYPRINIFORMES) FROM SOUTHWESTERN MINNESOTA

**J.M. Hodnett, R.S. Toomey, R.A. Olson, D.K. Elliott, J. Wood, J. Tweet, V.L. Santucci.** THE LATE MISSISSIPPIAN (VISÉAN) CHONDRICHTHYAN ASSEMBLAGE OF THE ST. LOUIS FORMATION AT MAMMOTH CAVE NATIONAL PARK, KENTUCKY

**S.M. Ott, S.Z. Gibson.** A MASS DEATH ASSEMBLAGE OF JUVENILE SEMIONOTIFORM FISHES (NEOPTERYGII: HOLOSTEI) FROM THE REDONDA FORMATION, DOCKUM GROUP, NEW MEXICO

**K. Shimada, J.J. Wood, P.C. Sternes.** COMMENTS ON THE BODY FORM OF THE EXTINCT MEGATOOTH SHARK, *OTODUS MEGALODON*, BASED ON EXTANT LAMNIFORM SHARKS

**J.B. Stout.** LAST FISH IN THE RHEIC OCEAN: PRELIMINARY REPORT ON EARLY CARBONIFEROUS CHONDRICHTHYANS FROM NORTHEAST TENNESSEE AND SOUTHWEST VIRGINIA

**J.J. Wood, B.A. Schumacher, K. Shimada.** FOSSIL MARINE VERTEBRATES FROM THE JUANA LOPEZ MEMBER OF THE UPPER CRETACEOUS CARLILE SHALE IN SOUTHEASTERN COLORADO, USA

**TALKS**

**J.V. Andrews, M. Friedman, J. Schein.** A NEW DANIAN SQUIRRELFISH (ACANTHOMORPHA: HOLOCENTRIDAE) REVEALS EXTENSIVE SURVIVORSHIP ACROSS THE CRETACEOUS-PALEOGENE BOUNDARY

**A. Capobianco, M. Friedman.** FOSSILS REVEAL LONG-DISTANCE MARINE DISPERSALS AND MAJOR ENVIRONMENTAL TRANSITIONS IN THE BIOGEOGRAPHIC HISTORY OF BONYTONGUE FISHES (OSTEOGLOSSOMORPHA)

**A.M. Caron, K. Tietjen, M.I. Coates.** REVISITING *TRAWDENIA PLANTI*: ENDOSKELETAL DATA AND A FRESH LOOK AT ACTINOPTERYGIAN ROOTS

**F. Charest, Z. Johanson, R. Cloutier.** FROM ALLOMETRY TO LIFE-HISTORY – ONTOGENETIC SALTATORY PATTERNS IN THE LATE DEVONIAN JAWED STEM-GNATHOSTOME *BOTHRIOLEPIS CANADENSIS*

**K. Criswell, J. Gillis, J. Head.** EVOLUTION AND DEVELOPMENT OF AXIAL SKELETAL REGIONALISATION IN GNATHOSTOMES: INSIGHTS FROM FISHES

**J.P. Downs, J. Barbosa, E.B. Daeschler.** A NEW SPECIES OF *EUSTHENODON* (SARCOPTERYGII; TETRAPODOMORPHA) AND OTHER TRISTICHOPTERIDS FROM THE CATSKILL FORMATION OF PENNSYLVANIA, USA

**T. El Hossny, E. Samankassou, M. Friedman, L. Cavin.** A LONGIROSTRINE TELEOST FISH FROM THE LATE CRETACEOUS OF LEBANON, AND ITS IMPACT ON THE PHYLOGENY OF TSELFATIIFORMES

**S. El-Sayed, M. Friedman, R.P. Speijer, B.S. Salem, H.M. Sallam.** A NEW MARINE FISH FAUNA DATING TO THE LATEST DANIAN EVENT (LDE – 62.2 MA) OF THE EASTERN DESERT, EGYPT

**R.T. Figueroa, M. Friedman.** A NEW CARBONIFEROUS–PERMIAN RAY-FINNED FISH (OSTEICHTHYES: ACTINOPTERYGII) HIGHLIGHTS THE MORPHOLOGICAL DIVERSITY OF ENDOCRANIAL ANATOMY OF LATE PALEOZOIC ACTINOPTERYGIANS

**E.J. Hilton, L. Grande.** NEW STURGEONS FROM THE LATE CRETACEOUS HELL CREEK FORMATION OF NORTH AMERICA, WITH NOTES ON THE CRETACEOUS RECORD OF THE FAMILY ACIPENSERIDAE

**C. Kevrekidis, S.B. Penk, M. Altner, B. Ruthensteiner, A.F. Cerwenka, B. Reichenbacher.** NEW FOSSILS FROM THE MIDDLE-LATE MIOCENE OF KENYA ILLUMINATE THE HISTORY OF CICHLID FISHES LIVING IN ALKALINE LAKES

**J. Liston, L. Costeur.** PLANKTIVORES BITE BACK: REEXAMINATION OF MAXILLAE ENDS EDENTULOUS PACHYCORMID CLADE

**J. Liu, J. Zhang.** PALEOCENE-EOCENE JIANGHANICHTHYIDS (TELEOST, OSTARIOPHYSI, CYPRINIFORMES) FROM SANSUI BASIN, CHINA ARE THE OLDEST KNOWN CYPRINIFORMS

**K. Matsui, Y. Kimura.** MAMMALIAN-LIKE TOOTH REPLACEMENT IN A PYCNODONT FISH JAW

**R.L. McKeeby, M. Gottfried.** USING GEOMETRIC MORPHOMETRICS AND OUTLINE ANALYSIS TO DELINEATE ONTOGENETIC HETERODONTY IN RECENT AND FOSSIL WHITE SHARK (*C. CARCHARIAS*) TEETH.

**J. Stack, M. Gottfried.** A PERMIAN ACTINOPTERYGIAN FROM THE MINNEKAHTA LIMESTONE OF SOUTH DAKOTA, USA

**TUESDAY, NOVEMBER 2, 2021, 2:00PM EDT-2:30PM EDT  
STEM TETRAPOD, SQUAMATE, & AMPHIBIAN NETWORKING SESSION**

**POSTERS**

**C.A. Boyd.** A NEW RHINEURID (SQUAMATA: AMPHISBAENIA) FROM THE OLIGOCENE (WHITNEYAN) BRULE FORMATION OF NORTH DAKOTA

**J. Creighton, J. Anderson.** MORPHOLOGICAL ANALYSIS OF A NECTRIDEAN LEPOSPONDYL, *DICERATOSAURUS*, FROM LINTON AND FIVE POINTS, OHIO.

**M.A. EL-Hares, S. El-Sayed, E. Erik R. Seiffert, H.M. Sallam.** A NEW HERPETOFAUNAL ASSEMBLAGE (AGAMIDS AND RANOIDS) FROM THE LATE EOCENE LOCALITY BQ-2 OF THE FAYUM DEPRESSION, EGYPT.

**D. Flores, C.J. Bell, W. Godwin, P.J. Lewis.** THE FIRST RECORD OF *LAMPROPELTIS* FROM MCFADDIN BEACH, TEXAS

**M.R. Forcellati, J.G. Napoli, A.R. Zietlow, D. Meyer, C.J. Raxworthy, M. Norell.** CRANIAL OSTEOLOGY OF *PELTOSAURUS*, BASED ON MICROCT SCANS OF TWO EXQUISITE SKULLS

**J. Head, A.M. Lawing, L. Flynn.** SNAKES FROM THE CHITARWATA FORMATION (OLIGOCENE-EARLY MIOCENE) OF PAKISTAN: FOSSIL EVIDENCE FOR THE EARLY HISTORY OF *ACROCHORDUS*.

**A.M. Kufner, D.M. Lovelace.** DIMINUTIVE ‘*METOPOSAURUS*’ *BAKERI* MATERIAL IS MORPHOLOGICALLY DISTINCT FROM STRATIGRAPHICALLY YOUNGER SMALL-BODIED METOPOSAURIDS

**TALKS**

**J.D. Daza, K. Smith, J. Arias, A. Bauer.** THE SURPRISING LONGEVITY OF STEM-GEKKOTAN LINEAGES

**S.J. ElShafie.** DOES REPTILE BODY SIZE TRACK ENVIRONMENTAL TEMPERATURE WITHIN LOCAL ASSEMBLAGES OR ACROSS CONTINENTAL INTERIORS?

**E.J. Hillan, K. Criswell, J. Head.** REGIONALIZATION OF THE SQUAMATE RIBCAGE IN THE EVOLUTION OF THE SNAKE BODY FORM

**A. Howard, J. Head.** INFERRING HOMOPLASY IN CRANIAL MORPHOLOGY ASSOCIATED WITH FOSSORIALITY IN SNAKES

**J.J. Jacisin, A.M. Lawing.** MIDDLE TRUNK VERTEBRAL SHAPE AND THE ECOMETRICS OF LOCOMOTION AND TEMPERATURE IN NORTH AMERICAN SNAKES

**B. Kligman, M. Stocker, A. Marsh, S. Nesbitt, W. Parker.** NEW LATE TRIASSIC STEM-CAECILIAN FROM SOUTHWESTERN NORTH AMERICA STRENGTHENS EVIDENCE FOR LISSAMPHIBIAN MONOPHYLY, AND ILLUMINATES THE ANATOMICAL, FUNCTIONAL, AND GEOGRAPHIC ORIGINS OF LIVING CAECILIANS



**D. Marjanović.** THE ORIGIN OF AMNIOTA IN PHYLOGENETIC CONTEXT

**D. Meyer, C.D. Brownstein, J. Gauthier.** COMPUTED TOMOGRAPHY REVEALS A JURASSIC STEM-GEKKOTAN FROM THE MORRISON FORMATION

**B.K. Otoo, M.I. Coates.** OLD THINGS ARE NEW AGAIN: *WHATCHEERIA*, *AYTONERPETON*, AND A TOURNAISIAN TETRAPOD CROWN

**A. Palci, S. Onary, K. Smith, M. Rabi, O. Wings, M. Lee.** NEW BOOID SNAKES FROM THE MIDDLE EOCENE (LUTETIAN) FOSSIL KONSERVAT LAGERSTÄTTE GEISELTAL, SAXONY-ANHALT, GERMANY

**C. So, A.M. Kufner, D.M. Lovelace.** COMPARATIVE CRANIAL ALLOMETRY AND ONTOGENY OF A DIMINUTIVE BURROWING STEREO SPONDYL

**TUESDAY, NOVEMBER 2, 2021, 3:00PM EDT-4:00PM EDT**  
**SYMPOSIUM: VERTEBRATE DENTAL ECOMORPHOLOGY: TOOTH TRAITS THAT REFLECT ECOLOGY NETWORKING SESSION**

### **TALKS**

**E. Fulwood, G. Yapuncich, D.M. Boyer.** TRENDS IN NORTH AMERICAN PRIMATE ECOMORPHOLOGICAL DISPARITY IN RESPONSE TO CLIMATE FLUCTUATIONS OVER THE EOCENE

**D. Grossnickle, L.N. Weaver, K. Jäger, J. Schultz.** ANTERIORLY DIRECTED MOLAR OCCLUSION IS UNIQUE TO THERIAN MAMMALS AND MAY HAVE FACILITATED THEIR DIETARY DIVERSIFICATION

**J.S. Keller, L.S. Garcia, C.E. Martinez, S.D. Newsome, S.K. Lyons, F.A. Smith.** MICROMAMMAL DENTAL ECOMORPHOLOGY FROM THE PLEISTOCENE TO THE PRESENT AT HALL'S CAVE, TEXAS

**S.A. Martinez, K.M. Jenkins, B. Bhullar.** DENTAL MORPHOLOGY OF PROCOLOPHONIDAE AND IMPLICATIONS FOR PERMO-TRIASSIC POST-EXTINCTION RECOVERY

**R. Messec, J.S. Keller, J. Moore.** HIGH INTRASPECIFIC MOLAR VARIATION IN NORTH AMERICAN EOCENE–OLIGOCENE RODENTS

**R.R. Messer, T. Curtis, M. Belmaker.** EFFECTS OF DEMOGRAPHY AND MORPHOLOGY ON VOLE (*MICROTUS* SPP.) MESOWEAR: IMPLICATIONS FOR PALEOECOLOGICAL RECONSTRUCTIONS

**P.E. Morse, J.D. Pampush, E.J. Fuselier, R.F. Kay.** WHERE'S THE POINT? DENTAL SURFACE SHARPNESS ARISING FROM CONVEX VERSUS CONCAVE OCCLUSAL MORPHOLOGY AND IMPLICATIONS FOR INTERPRETATION OF FOSSIL PRIMATE DIET

**S. Pineda-Munoz, P. Polly.** DIETARY GENERALISM AND ITS IMPLICATIONS TO PALEOECOLOGY, DENTAL MORPHOLOGY AND WEAR

**K.R. Selig, S. López-Torres, A. Burrows, M. Silcox.** DENTAL TOPOGRAPHIC ANALYSIS OF LIVING AND FOSSIL LORISOIDS: A NEW SIGNAL FOR EXUDATE FEEDING IN LORISES AND GALAGOS

**N.S. Vitek, P.E. Morse, S.G. Strait, D.M. Boyer, J.I. Bloch.** TRANSIENT CHANGES IN RELATIVE CROWN AREA AND ENAMEL THICKNESS IN THE INSECTIVOROUS MAMMAL *MACROCRANION* DURING THE PALEOCENE–EOCENE THERMAL MAXIMUM

**E.T. Whiting, D.L. Fox, A.K. Hastings, J.I. Bloch.** DIETARY RECONSTRUCTIONS OF PALEOGENE FOSSIL LIZARDS FROM THE WESTERN INTERIOR OF NORTH AMERICA USING THREE-DIMENSIONAL DENTAL TOPOGRAPHY ANALYSIS AND A MODERN COMPARATIVE DATASET OF EXTANT PLEURODONT SQUAMATES

**TUESDAY, NOVEMBER 2, 2021, 4:00PM EDT-4:45PM EDT  
NON-AVIAN THEROPOD SYSTEMATICS, BIOLOGY, & EVOLUTION NETWORKING  
SESSION**

**POSTERS**

**K.L. Atkins-Weltman, P. O'Connor, E. Snively.** ESTIMATING MASS PROPERTIES OF *ANZU WYLIEI*, WITH PARAMETERIZED RECONSTRUCTION OF THE RESPIRATORY SYSTEM

**B.B. Britt, D. Chure, P. Currie, A. Holmes, B. Theurer, R. Scheetz.** A NEW DEINONYCHOSAURIAN THEROPOD FROM THE MID-CRETACEOUS (ALBIAN) MUSSENTUCHIT MEMBER OF THE CEDAR MOUNTAIN FORMATION IN DINOSAUR NATIONAL MONUMENT, NORTHEASTERN UTAH, USA

**C.D. Brownstein, J.G. Napoli, A. Ruebenstahl, M.R. Forcellati, M. Norell.** DIMINUTIVE THEROPODS FROM APPALACHIA AND THE EARLY EVOLUTION OF THE AVIAN BRAINCASE

**T.D. Carr.** *TYRANNOSAURUS REX*: AN ENDANGERED SPECIES

**E. Isasmendi, P. Sáez-Benito, F. Torcida Fernández-Baldor, J. Canudo, A. Torices, X. Pereda-Suberbiola.** PALEOBIODIVERSITY OF THEROPOD DINOSAURS OF THE LOWER CRETACEOUS CAMEROS BASIN, NORTHERN SPAIN

**R.E. Nottrodt.** MORPHOMETRIC ANALYSIS OF NORTH AMERICAN ORNITHOMIMID MANUAL AND PEDAL UNGUALS: CAN UNGUAL SHAPE BE USED TO DISTINGUISH BETWEEN TAXA?

**J.T. Voris, F. Therrien, D. Zelenitsky.** ORIGIN AND DISPERSAL OF DERIVED TYRANNOSAURINES (THEROPODA: TYRANNOSAURIDAE) IN ASIAMERICA: INSIGHT FROM A MIDDLE CAMPANIAN TYRANNOSAURINE FROM ALBERTA, CANADA

**TALKS**

**K.E. Chapelle, M. Norell, D.P. Ford, C. Hendrickx, V.J. Radermacher, A. Balanoff, L.E. Zanno, J.N. Choiniere.** A CT-BASED REVISED DESCRIPTION AND PHYLOGENETIC ANALYSIS OF THE SKULL OF THE BASAL MANIRAPTORAN *ORNITHOLESTES HERMANNI* OSBORN 1903

**C.J. Hohman, D. Varricchio.** ONTOGENETIC IMPLICATIONS OF TWO DISTINCT DROMAEOSAURID MAXILLAE FROM THE CRETACEOUS (CAMPANIAN) TWO MEDICINE FORMATION OF MONTANA, U.S.A.

**T.R. Holtz.** MESOZOIC MEAT-EATER MARKETPLACE: ASSESSING THEROPOD GUILD EVOLUTION BEYOND BODY SIZE

**E. Lessner, C. Holliday.** LIMITED POTENTIAL FOR TRIGEMINAL-INNERVED SENSORY BEHAVIORS AMONG DINOSAURS

**C.R. Marshall, D. Latorre, C. Wilson, T.M. Frank, K. Magoulick, J. Zimmt, A. Poust.** ON THE STANDING POPULATION SIZE OF *TYRANNOSAURUS REX*, THE TOTAL NUMBER THAT EVER LIVED, AND ITS ABSOLUTE PRESERVATION RATE

**A.T. McDonald, D.G. Wolfe, A.C. Dooley.** NEW DATA ON THE TYRANNOSAURID DINOSAUR *DYNAMOTERROR*, INCLUDING A MORE COMPLETE SKELETON, FROM THE MENEFEE FORMATION (MIDDLE CAMPANIAN) OF NEW MEXICO, USA: IMPLICATIONS FOR TYRANNOSAURID EVOLUTION IN SOUTHERN LARAMIDIA

**M. Powers, M. Norell, P. Currie.** EXAMINATION OF MORPHOLOGICAL VARIATION ACROSS *VELOCIRAPTOR MONGOLIENSIS* SPECIMENS REVEALS A NEW SPECIES WITH POSSIBLE ECOMORPHOLOGICAL VARIATION IN SNOUT DIMENSIONS

**V.J. Radermacher, V. Fernandez, W.J. de Klerk, K.E. Chappelle, J.N. Choiniere.** SYNCHROTRON  $\mu$ CT SCANNING REVEALS NOVEL CRANIAL ANATOMY OF THE ENIGMATIC EARLY CRETACEOUS SOUTH AFRICAN COELUROSAUR, *NQWEBASAURUS THWAZI*

**A. Ruebenstahl, J.G. Napoli, B. Bhullar, A.H. Turner, M. Norell.** TWO NEW EUDROMAEOSAURS FROM KHULSAN (CENTRAL MONGOLIA) REVEAL MODERN-LIKE FAUNAL PREDATORY STRUCTURE AMONG NON-AVIAN DINOSAURS

**B.S. Salem, M.C. Lamanna, P. O'Connor, G.M. El-Qot, F. Shaker, W.A. Thabet, S. El-Sayed, H.M. Sallam.** FIRST DEFINITIVE RECORD OF ABELISAURIDAE FROM THE BAHARIYA FORMATION, BAHARIYA OASIS, WESTERN DESERT OF EGYPT INCREASES DIVERSITY OF LARGE-BODIED THEROPODS IN THE MIDDLE CRETACEOUS OF NORTHEASTERN AFRICA

**TUESDAY, NOVEMBER 2, 2021, 7:00PM EDT-7:45PM EDT  
MAMMALIAN SKELETAL MORPHOLOGY & MARINE MAMMALS NETWORKING  
SESSION**

### **MAMMALIAN SKELETAL MORPHOLOGY**

#### **POSTERS**

**A. Grass.** VISUALIZATION OF SLOTH UNGUAL VASCULATURE

**A.M. Lawson, S.S. Hopkins.** NEW SKULL MATERIAL OF *HAPLOMYS* (RODENTIA, APLODONTIIDAE) GIVES WAY TO NEW MORPHOLOGICAL DETAILS

**V.L. Naples, M. Haji-Sheikh.** *BARBOUROFELIS FRICKI*—THE HEAD BONE IS CONNECTED TO THE NECK BONE OR HOW TO REBUILD A UNIQUE CAT

**A. Martín-Serra, B. Figueirido.** INFLUENCE OF CONSTRAINT AND ADAPTATION ON MORPHOSPACE OCCUPATION PATTERNS OF THE CARNIVORAN APPENDICULAR SKELETON

**J.M. Theodor, S.V. Robson.** THE PETROSAL MORPHOLOGY OF *HEPTACODON OCCIDENTALIS* (ANTHRACOTHERIIDAE)

### **TALKS**

**R.J. Asher.** SKULLS, LATITUDE, AND 'RACE': HISTORICAL ATTEMPTS TO UNDERSTAND HUMAN CRANIAL VARIATION

**K. Le Verger, L. Gonzalez Ruiz, G. BILLET.** COMPARATIVE ANATOMY OF INTRACRANIAL OSSEOUS CANALS AND ALVEOLAR CAVITIES PROVIDE FURTHER CLUES ON THE RELATIONSHIPS BETWEEN GLYPTODONTS AND ARMADILLOS (XENARTHRA, CINGULATA)

**D. Rhoda, K.D. Angielczyk.** MORPHOLOGICAL DIVERSIFICATION ALONG AN ALLOMETRIC LINE OF LEAST RESISTANCE IN THE RUMINANT SKULL

**S.V. Robson, J.M. Theodor.** MORPHOLOGICAL VARIATION IN THE PETROSAL OF SOME EXTINCT AND EXTANT CAMELIDS

**J.S. Silviria.** STRAIGHTENING THE HORSE'S MOUTH? NON-DENTAL MANDIBULOMETRY IN DERIVED EQUIDS, AND THE ORIGIN OF *EQUUS CABALLUS*

**R.B. Sulser, R.D. MacPhee.** AN ISLAND APART: ENDOCAST VARIATION WITHIN THE TENRECOMORPHA

### **MARINE MAMMALS**

### **POSTERS**

**A. Ashraf, M. AbdelGawad, A. Zakaria.** THE FIRST RECORD OF A COMPLETE SIRENIA FROM THE MIDDLE EOCENE FOSSILIFEROUS LIMESTONE IN THE EASTERN DESERT, EGYPT

**N.A. Brand, M.D. Uhen.** TACKLING THE MYSTICETE MYSTERY: COMBINING DISPARATE MATRICES TO EXAMINE THE EVOLUTION OF FEEDING MODES IN EARLY BALEEN WHALES

**A.S. Gohar, M.S. Antar, S. El-Sayed, H.M. Sallam.** FROZEN IN TIME: UNIQUELY PRESERVED PROTOCETID WHALE ENTOMBED INSIDE DECORATIVE LIMESTONE FROM THE MIDDLE EOCENE OF EGYPT

**T. Okamura, Y. Akune, T. Mori, T. Morisaka, W. Otomo, I. Wakabayashi, S. Watanabe, K. Yoda.** THE RELATIONSHIP BETWEEN THE POSTURE OF FLIPPERS AND THE PRESENCE OF DORSAL FINS LEADING TO THE RECONSTRUCTION OF THE DORSAL FIN IN SMALL CETACEANS: THE CONTRIBUTION OF FINS TO LATERAL/DIHEDRAL INHERENT STABILITY

**I.S. Zalmout, Y.A. Al-Mufarreh, S.A. Soubhi, M.A. Haptari, A.I. Nabhan, A.M. Memesh, M.H. Aljahdali, P.D. Gingerich.** FIRST RECORD OF AN UPPER EOCENE ARCHAEOCETE FROM THE RASHRASHIYAH FORMATION, AL-JAWF REGION, NORTHWESTERN SAUDI ARABIA

## TALKS

**E.A. Buchholtz.** FUNCTIONAL AND ONTOGENETIC IMPLICATIONS OF STERNAL STRUCTURE IN MYSTICETE CETACEANS

**M. Clementz, B. Carrapa.** RISING FROM THE ASHES: LINKING ANDEAN VOLCANISM, DIATOMS, AND MARINE MAMMAL DIVERSITY WITH THE LATE MIOCENE COOLING EVENT

**S. Davydenko.** REEXAMINATION OF AN EOCENE CETACEAN *EOCETUS SCHWEINFURTHI* (CETACEA, PROTOCETIDAE): NEW DATA ON MORPHOLOGY, PHYLOGENY AND FEEDING STRATEGY

**A.M. Glass, M.D. Uhen.** NEW CORRELATIONS BETWEEN CRANIOFACIAL AND INNER EAR MORPHOLOGIES FOR ECHOLOCATION AND FEEDING IN ODONTOCETES

**A. Lanzetti, V. Fernandez, B. Clark, A. Goswami.** DEVELOPING A TASTE: CONNECTING SKULL SHAPE ONTOGENY AND EVOLUTION OF DIFFERENT FEEDING ADAPTATIONS IN CETACEA USING 3D GEOMETRIC MORPHOMETRICS

**E.C. Rohlicek, R.W. Boessenecker, V.M. Arbour.** EVIDENCE FOR OLIGOCENE CETACEAN DIVERSITY IN THE SOOKE FORMATION (CARMANAH GROUP) OF VANCOUVER ISLAND, BRITISH COLUMBIA, CANADA

## WEDNESDAY, NOVEMBER 3, 2021, 11:30AM EDT-12:15PM EDT PERMO-TRIASSIC ECOSYSTEMS NETWORKING SESSION

## POSTERS

**S. Chambi-Trowell, D.I. Whiteside, M. Skinner, M.J. Benton, E.J. Rayfield.** TRICKY TRIASSIC TRILOPHOSAURS: WERE THE REPTILES *TRICUSPISAUROS THOMASI* AND *VARIODENS INOPINATUS* REPRESENTATIVES OF TRILOPHOSAURIDAE IN EUROPE?

**A. Marsh, W. Parker, S. Nesbitt, B. Kligman, M. Stocker, E. Patellos.** A NEW SPECIES OF CARNIVOROUS AZENDOHSAURID (ARCHOSAURIFORMES) FROM THE CHINLE FORMATION OF PETRIFIED FOREST NATIONAL PARK

**I. Pugh, A.B. Heckert.** MULTIPLE SUPERNUMERARY CARINAE IN REVUELTIAN (TRIASSIC:MID-LATE NORIAN) PHYTOSAUR TEETH FROM THE BULL CANYON FORMATION OF EAST-CENTRAL NEW MEXICO, U.S.A.

## TALKS

**K.D. Angielczyk, B.R. Peacock, R.M. Smith, C.A. Sidor, J.K. Lungmus, S. Nesbitt, S.L. Olroyd, J. Steyer, M. Stocker, S. Tolan.** THE MANDIBLE OF *COMPSODON HELMOEDI* (THERAPSIDA, ANOMODONTIA), WITH NEW RECORDS FOR THE RUHUHU BASIN, TANZANIA

**L. Czepinski, D. Drozd, T. Szczygielski, M. Talanda, W. Pawlak, A. Lewczuk, A. Rytel, T. Sulej.** AN UPPER TRIASSIC TERRESTRIAL VERTEBRATE ASSEMBLAGE FROM THE FORGOTTEN KOCURY LOCALITY (POLAND) WITH A NEW AETOSAUR TAXON

**D. Drozd, T. Sulej.** NOTES ON VARIATION IN PELVIC DEVELOPMENT OF THE LATE TRIASSIC AETOSAUR *STAGONOLEPIS OLENKAE* FROM NORTHERN PANGAEA

**B.M. Gee, C.A. Sidor.** TEMNOSPONDYLS ON ICE: NEW INSIGHTS FROM THE TRIASSIC OF ANTARCTICA

**E.R. Goldsmith, M. Stocker.** ONTOGENETIC INSIGHTS BASED ON A REDESCRIPTION OF THE CRANIAL MORPHOLOGY OF AN IMMATURE ‘*REDONDASAURUS*’ (ARCHOSAURIFORM: PHYTOSAURIA)

**D.K. Hoffman, S. Nesbitt, K.D. Angielczyk, C.A. Sidor, M. Stocker, R.M. Smith, N.J. Tabor, C. Van Beek.** A NEW PSEUDOSUCHIAN ARCHOSAUR FROM THE MIDDLE TRIASSIC OF TANZANIA AND THE EARLY EVOLUTION OF SUCHIANS

**L. Janzen, J. Müller, H. Sues, G. Sobral.** A NEW SPHENODONTIAN FROM THE LATE TRIASSIC OF GERMANY

**B.R. Peacock, K.D. Angielczyk, J.K. Lungmus, J.A. McIntosh, C.A. Sidor, R.M. Smith, S. Tolan, P. Viglietti, M. Whitney.** RHYNCHOSAUR RELATIVITY: NEW STENAULORHYNCHINES FROM THE MID-LUANGWA BASIN, ZAMBIA, AND THE EVOLVING BIOSTRATIGRAPHY OF VERTEBRATE ASSEMBLAGES AT THE MIDDLE-LATE TRIASSIC BOUNDARY

**A.C. Pritchard.** REVISED PHYLOGENETIC ANALYSIS OF PERMO-TRIASSIC DIAPSID SUPPORTS KUEHNEOSAURIDS AS BASAL ARCHOSAURIFORMS

**T. Sethapanichsakul, M.J. Benton.** A JUVENILE RHYNCHOSAUR SPECIMEN FROM THE OTTER SANDSTONE FORMATION OF SOUTHERN ENGLAND (ANISIAN, MIDDLE TRIASSIC)

**T. Szczygielski, T. Sulej.** A NEW STAHLCKERIID FROM POLAND

**K. To, M. Stocker, S. Nesbitt.** TRACING THE ARCHOSAURIAN BEAK USING THE LATE TRIASSIC ARCHOSAURIFORM, *TRILOPHOSAURUS BUETTNERI*

**P. Viglietti, A. Rojas, M. Rosvall, B. Davis, K.D. Angielczyk.** A NETWORK-BASED BIOSTRATIGRAPHIC FRAMEWORK FOR THE BEAUFORT GROUP (KAROO SUPERGROUP), SOUTH AFRICA

**WEDNESDAY, NOVEMBER 3, 2021, 12:15PM EDT-12:45PM EDT  
AVIALAN EVOLUTION & BIOLOGY NETWORKING SESSION**

## **POSTERS**

**T. Tanaka, R. Takasaki, K. Chiba, S. Hayashi, K. Brink, M. Buuvei, K. Tsogtbaatar.** A HESPERORNITHIFORM FROM THE UPPER CRETACEOUS NEMEGT FORMATION IN THE GOBI DESERT OF SOUTHWEST MONGOLIA: IMPLICATIONS FOR PALEOECOLOGY OF INLAND HESPERORNITHIFORMS

## TALKS

**E. Alger-Meyer, T.A. Gates.** SURVEY OF CORNIFIED TISSUE COVERINGS IN BIRD BILLS WITH IMPLICATIONS FOR HADROSAURID DINOSAUR RECONSTRUCTIONS

**J. Benito, A. Chen, B. Bhullar, D.J. Field.** 40 NEW SPECIMENS OF *ICHTHYORNIS* PROVIDE UNPRECEDENTED INSIGHT INTO THE POSTCRANIAL MORPHOLOGY OF CROWNWARD STEM GROUP BIRDS

**B.R. Chapman, L.E. Wilson.** CONTROLS ON THE CAMPANIAN DISTRIBUTION OF *HESPERORNIS* (AVES: HESPERORNITHIFORMES) IN THE WESTERN INTERIOR SEAWAY

**A. Chen, R.B. Benson, D.J. Field.** TOWARDS A COMPREHENSIVE ANATOMICAL MATRIX FOR CROWN BIRDS: PHYLOGENETIC INSIGHTS FROM THE PECTORAL GIRDLE AND FORELIMB SKELETON

**O.E. Demuth, J. Benito, D.J. Field.** THREE-DIMENSIONAL RECONSTRUCTION OF VERTEBRATE MORPHOLOGY AND QUANTIFICATION OF TAPHONOMIC DEFORMATION

**D.J. Field, J. Benito, P. Kuo, J. Jagt.** MESOZOIC FOSSIL INSIGHT INTO THE PALAEOGNATH-NEOGENATH ANATOMICAL DICHOTOMY

**L. King, M.E. Kirchner-Smith, D. Landi.** THE NEUROANATOMY, OLFACTORY ABILITY, AND TROPHIC ECOLOGY OF *TERATONIS MERRIAM* (AVES: TERATORNITHIDAE)

**J.A. Moretti, E. Johnson.** SMALL RAILS (AVES: GRUIFORMES: RALLIDAE) FROM THE LATE PLEISTOCENE AND EARLY HOLOCENE OF THE SOUTHERN HIGH PLAINS OF TEXAS.

**J. O'Connor, M.C. Lamanna, J. Harris, H. Hu, A. Bailleul, M. Wang, H. You.** FIRST AVIAN SKULLS FROM THE LOWER CRETACEOUS XIAGOU FORMATION, GANSU, CHINA

**E. Steell, J.M. Nguyen, R.B. Benson, D.J. Field.** COMPARATIVE MORPHOLOGY OF THE PASSERINE CARPOMETACARPUS: IMPLICATIONS FOR INTERPRETING THE FOSSIL RECORD OF CROWN PASSERIFORMES

**D. Williams, D. Burnham, L. Gurche.** REPORT OF A DIVING BIRD FROM THE HELL CREEK FORMATION, GARFIELD COUNTY, MONTANA

**WEDNESDAY, NOVEMBER 3, 2021, 1:30PM EDT-2:15PM EDT  
PREPARATORS' NETWORKING SESSION**

## POSTERS

**V. Carrió.** EVALUATION ON THE PROCEDURES FOR THE REMOVAL OF ADHESIVES USED FOR FOSSIL SPECIMENS FROM THE 19<sup>TH</sup> CENTURY EXHIBITIONS AT THE NATIONAL MUSEUMS OF SCOTLAND

**L.D. Collins, B.S. Dooley, A.T. McDonald, M.N. Mendleson.** PALEO TOOLS VS. THE STONE COMPANY AIR SCRIBES: AN UNOFFICIAL USAGE GUIDE

**M. Ferrer Ventura, A. Torices, X. Mar-Barberà, P. Navarro-Lorbés, R. San Juan-Palacios.** AN APPROACH TO USE CYCLODODECANE AS PROTECTION FOR MECHANICAL MATRIX REMOVAL OF A THEROPOD TOOTH

**E. Gorscak, D.E. Ehrlich.** EXPLORATORY RETRODEFORMATION METHOD ON COMPRESSED FOSSILS USING SLICED SURFACE CONTOURS: A CASE STUDY ON THE OBLIQUELY COMPRESSED METAPODIALS OF AN EGYPTIAN TITANOSAURIAN SAUROPOD DINOSAUR

**S. Van Hauwermeiren, A. Hellemond.** PREPARATION OF THE NIEUWDONK COLLECTION (BERLARE, BELGIUM): A WINDOW INTO THE LAST GLACIAL AND INTERGLACIAL FAUNAS OF THE FLEMISH VALLEY

**L. Vietti, A.B. Shaffer, T.J. Kerr.** APPLICATION OF FULL COLOR 3D PRINTERS TO FOSSIL PREPARATION, RESEARCH, AND COLLECTIONS MANAGEMENT AT THE UNIVERSITY OF WYOMING

### **TALKS**

**C. Byrd, E. Biedron, J. Woodward, C. Green.** MOVING AN OVERSIZE COLLECTION DURING A PANDEMIC

**J. Cavigelli, J. Van Veldhuizen.** YET ANOTHER TECHNIQUE FOR CURATING MICROMAMMAL FOSSILS THAT EMPHASIZES COST, VISIBILITY, TIME AND STORAGE EFFICIENCY, SPECIMEN AND DATA PROTECTION

**J. Foster, S.D. Sroka, T.F. Howells.** PALEONTOLOGICAL RADIATION AND RADON MONITORING: A CASE STUDY FROM THE UTAH FIELD HOUSE OF NATURAL HISTORY

**M. Fox.** MOUNTING FOSSIL SPECIMENS FOR MICRO-CT SCANNING

**J. Groenke, P. O'Connor.** PREPARATION AND RECONSTRUCTION OF *FALCATAKELY FORSTERAE*, AN ENANTIORNITHINE BIRD FROM THE UPPER CRETACEOUS MAEVARANO FORMATION OF MADAGASCAR

**J. Hook.** MARINE FOSSILS FROM THE COALEDO FORMATION: A CASE STUDY ILLUSTRATING THE WORKFLOW TO PREPARE AND SHIP AN UNCURATED COLLECTION

**C.G. Levitt-Bussian, A.E. Wilkins, A.W. Johnson, T.J. Mareck.** HARNESSING THE POWER OF COMMUNITY SCIENCE TO DIGITIZE, TRANSCRIBE, AND IMPORT PREPARATION INFORMATION INTO A COLLECTIONS MANAGEMENT DATABASE SYSTEM

**E. Lund, L. Herzog, L.E. Zanno.** COLLECTION AND PREPARATION OF A *TRICERATOPS PRORSUS* SKULL PROVIDES UNIQUE OPPORTUNITIES FOR SCIENCE COMMUNICATION AND EDUCATION IN MATERIALS AND METHODS IN PALEONTOLOGY

**C. Lutz, C. Lash.** UTILIZING OLD AND NEW TECHNIQUES TO BRING NEW LIFE TO OLD DISPLAYS

**M.K. Macias, C. Shi, A. Montenegro, A. Ollendorf.** ACCESSIONING A LARGE FOSSIL COLLECTION FROM THE FAIRMEAD LANDFILL LOCALITY, CITY OF CHOWCHILLA, MADERA COUNTY, CALIFORNIA



**M. Pinsdorf.** FOSSIL PREPARATION CONTINUES AT THE SMITHSONIAN INSTITUTION NATIONAL MUSEUM OF NATURAL HISTORY DURING COVID-19 PANDEMIC

**D. Wagner, J. Lively, M. Brown.** CONSERVATION OF A MOLD AND FIRE-DAMAGED MOSASAUR SPECIMEN

**WEDNESDAY, NOVEMBER 3, 2021, 2:15PM EDT-3:15PM EDT  
LATE CENOZOIC MAMMALIAN EVOLUTION & ECOLOGY NETWORKING SESSION**

**POSTERS**

**A. DeMers, J. Hunter.** INFERRING ARCHAIC UNGULATE DIETS USING TWO-DIMENSIONAL DENTARY MORPHOLOGY

**C.M. Janis, A. O'Driscoll, H. Richards.** DID MIOCENE DIDACTYL STHENURINE KANGAROOS WALK LIKE THE PLIO-PLEISTOCENE MONODACTYL ONES?

**S.E. Jasinski, S.G. Abbas.** BIODIVERSITY AND CARNIVORAN FAUNAL DYNAMICS IN SOUTHWESTERN ASIA AND NORTH AMERICA DURING THE MIOCENE–PLIOCENE

**W.D. Lambert, R.E. Eshelman, G.S. Morgan, S.J. Godfrey.** A NEW GENUS OF GOMPHOTHERE (MAMMALIA, PROBOSCIDEA, GOMPHOTHERIIDAE) FROM THE MIOCENE CHOPTANK FORMATION OF VIRGINIA, AND A REVIEW OF BARSTOVIAN AND CLARENDONIAN GOMPHOTHERES FROM THE CHESAPEAKE BAY REGION

**G.M. Semprebon, C.M. Janis.** WHAT WAS THE MAIN DRIVER OF HYPSONDONTY ACQUISITION IN NORTH AMERICAN UNGULATES?

**T. Tsubamoto, N. Handa.** REAPPRAISAL OF A SUPPOSED CHALICOTHERIID (MAMMALIA, PERISSODACTYLA) FEMUR FROM THE PLIOCENE OF CENTRAL MYANMAR

**TALKS**

**S. Bartolini Lucenti, L. Rook.** *CANIS FEROX* REVISITED WITH DIETARY INFERENCES ON *EUCYON* SPECIES

**I. Bonilla-Salomón, Ā. Luján, M. Ivanov, M. Sabol.** *ALIVERIA* SP. NOV. AMONG OTHER SCIURID REMAINS (MAMMALIA, RODENTIA) FROM THE EARLY MIOCENE OF MOKRÁ-QUARRY (MORAVIA, CZECH REPUBLIC) AND ITS LOCOMOTOR ADAPTATIONS

**L. DeSantis, K. Black, M. Archer, S. Hand.** TREE-CLIMBING IN SEARCH OF FRUIT: PALEOECOLOGY OF THE DIPROTODONTID *NIMBADON LAVARACKORUM*

**E. Galbrun, J.S. Hermansen, I. Zliobaite.** PROBING THE MAMMALIAN FOSSIL RECORD FOR PATTERNS OF COMPETITIVE EXCLUSION USING COMPUTATIONAL RANDOMIZATION EXPERIMENTS

**L.A. Gonzales, M. Arnal, L. Angel Valdivia, P.E. Morse, M.R. Borths, P.R. Fleming, J. Martinez, R.F. Kay.** FIRST EARLY MIOCENE CAVIOMORPH ASSEMBLAGE FROM LOW LATITUDES OF SOUTH AMERICA

**I.A. Kerr, G.J. Prideaux, A.B. Camens, T.H. Worthy.** POSTCRANIAL TRAITS DIFFERENTIATE SPECIES OF THE LATE CENOZOIC KANGAROO GENUS *PROTEMNODON* BETTER THAN TEETH

**C. Lopez-Aguirre, S. Hand, A. Link, M. Silcox.** NICHE PARTITIONING BETWEEN CONGENERIC SPECIES WITHIN A RICH MIOCENE NEOTROPICAL BAT COMMUNITY FROM COLOMBIA

**K.M. Loughney, C. Badgley, R. Feng, A. Bahadori, W. Holt, E. Rasbury.** LARGE- AND SMALL-MAMMAL RICHNESS OF THE BASIN AND RANGE THROUGH CHANGING CLIMATE SINCE 36 MA

**J.B. Rossie, S. Cote.** NEW FOSSIL APE MATERIAL FROM THE LOTHIDOK FORMATION, NORTHERN KENYA

**K. Travouillon, R. Beck, J.A. Case.** PERAMELEMORPHIAN (BANDICOOT AND BILBIES) DIVERSITY OF THE ETADUNNA AND WIPAJIRI FORMATIONS, LATE OLIGOCENE TO EARLY–MIDDLE MIOCENE, SOUTH AUSTRALIA

**WEDNESDAY, NOVEMBER 3, 2021, 3:30PM EDT-4:15PM EDT  
MESOZOIC & PALEOGENE MAMMALS NETWORKING SESSION**

**POSTERS**

**S.F. Al Ashqar, M. Borths, A. Sileem, S. El-Sayed, E. Seiffert, H.M. Sallam.** THE CRANIUM OF *APTERODON* (HYAINAILOURIDAE, APTERODONTINAE) FROM ONE OF THE YOUNGEST VERTEBRATE-BEARING LOCALITIES (EARLY OLIGOCENE) IN THE FAYUM DEPRESSION, EGYPT

**J.A. Case.** A NEW LATE OLIGOCENE PYGMY POSSUM (BURRAMYIDAE) FROM THE LAKE EYRE BASIN, SOUTH AUSTRALIA

**E. Froehlich, S.S. Hopkins.** *RUDIOMYS* (RODENTIA, APLDONTIDAE) FROM THE JOHN DAY FORMATION OF OREGON

**J. Grubbs, J.F. Genise, K.A. Nichols, T. Bown.** DETERMINING INSECT PREY OF EARLY EOCENE PRIMATES FROM TRACE FOSSILS, WILLWOOD FORMATION, BIGHORN BASIN, WYOMING, USA

**F. Habib, M. AbdelGawad, A. Sileem, G. Abdel-Gawad, Y. Salama.** LATERAL DISTRIBUTION OF THE PALEOGENE *ARSINOITHERIUM* IN AFRICA AND THE AFRO-ARABIAN REGION

**E. Huang, G.S. Bever.** STILL EXPLORING CONFLICTING MOLECULAR AND MORPHOLOGICAL SIGNALS IN THE PHYLOGENETIC ASSESSMENT OF FOSSILS—A CRITICAL LOOK AT THE EARLY HISTORY OF PRIMATES

**T. Okoshi, S. Kodaira, K. Chiba, M. Saneyoshi, A. Takahashi, M. Natori, B. Mainbayar, K. Tsogtbaatar.** A NEW MAMMAL FOSSIL FROM THE UPPER CRETACEOUS BAYNSHIRE FORMATION, GOBI DESERT, MONGOLIA

**L. Perales-Gogenola, G. Merceron, A. Badiola, A. Gómez-Olivencia, X. Pereda-Suberbiola.** WHAT DID THE PALAEOOTHERIID *PLAGIOLOPHUS* FEED FROM?—A STUDY ON ITS EVOLUTIONARY ECOLOGY AND PALEODIET THROUGH TIME AND SPACE

**E.M. St Clair, D.M. Boyer, K. Beard.** REASSESSMENT OF THE DENTAL REDUCTION SEQUENCE IN PLESIADAPIDAE (MAMMALIA, PLESIADAPIFORMES) AND IMPLICATIONS FOR EVOLUTIONARILY CONSERVED PATTERNS OF LOSS OF VESTIGIAL STRUCTURES

**S.P. Zack, T. Penkrot.** NEW MATERIAL OF *LOPHIPARAMYS* (MAMMALIA, RODENTIA), INCLUDING TARSALS, FROM THE WILLWOOD FORMATION (EARLY EOCENE)

## **TALKS**

**P. dePolo, G. Funston, S. Shelley, T. Williamson, J. Wible, S. Brusatte.** THE FIRST JUVENILE OF *PANTOLAMBDA BATHMODON* (MAMMALIA, PANTODONTA) FROM THE SAN JUAN BASIN, NEW MEXICO, USA

**G. Funston, P. dePolo, S. Shelley, J. Wible, T. Williamson, S. Brusatte.** LIFE HISTORY OF AN ARCHAIC PLACENTAL MAMMAL, *PANTOLAMBDA BATHMODON* (PLACENTALIA, PANTODONTA)

**B.T. Hovatter, S.G. Chester, G. Wilson Mantilla.** NEW RECORDS OF EARLIEST TORREJONIAN (TO1) PLESIADAPIFORMS FROM NORTHEASTERN MONTANA, USA, PROVIDE WINDOW INTO THE EARLY DIVERSIFICATION OF STEM PRIMATES

**A. Huttenlocker, S.A. Singh, A.C. Henrici, S.S. Sumida.** A CARBONIFEROUS SYNAPSID JAW WITH CANINIFORM TEETH AND A REAPPRAISAL OF MANDIBULAR SIZE-SHAPE HETERODONTY IN THE ORIGIN OF MAMMALS

**M.F. Jones, Q. Li, X. Ni, K. Beard.** THE EARLIEST ASIAN BATS AND IMPLICATIONS FOR EVOLUTION AND BIOGEOGRAPHY OF EOCENE BATS

**M.S. Juhn, J. Aramkul, M. Balisi, E. Doughy, A. Friscia, A. Howenstine, C. Jacquemetton, J. Marcot, S. Nugen, B. Van Valkenburgh.** NORTH AMERICAN MAMMAL PREDATOR DIVERSITY AND FUNCTIONAL TRAIT RESPONSE TO CLIMATE CHANGE ACROSS THE PALEOGENE

**R.F. Kay, M. Arnal, W. Salenbien, L. Angel Valdivia, P.E. Morse, M.R. Borths, P.R. Fleming, J. Martinez, L.A. Gonzales.** PALEOGENE RODENTS OF THE HUAYABAMBA FORMATION, OF THE ALTO RÍO MADRE DE DIOS AND ITS TRIBUTARIES, AMAZONIAN PERU

**T. Sulej.** EVOLUTION OF DENTITION IN MAMMALIAMORPHA

**J.D. Wilson, E. Huang, G.S. Bever.** PUSHING THE LOWER LIMITS OF BODY SIZE: BODY MASS ESTIMATES FOR THE STEM-THERIAN EUTRICONODONTA

**A.F. Wroblewski, B. Gulas-Wroblewski.** FIRST, BIGGEST, AND OLDEST: A COMPLEX, UPPER PALEOCENE MAMMAL TRACKSITE REVEALS IMPORTANT EVOLUTIONARY INSIGHTS

THURSDAY, NOVEMBER 4, 2021, 10:00AM EDT-11:00AM EDT  
COLBERT POSTER PRIZE NETWORKING SESSION

**POSTERS**

**H.M. Avrahami, T.A. Gates, L.E. Zanno.** A COMPARISON OF BAYESIAN AND PARSIMONY OPTIMALITY CRITERIA FOR THE ANALYSIS OF NEORNITHISCHIAN PHYLOGENIES

**I. Bonilla-Salomón, S. Čermák, Ā. Luján, M. Ivanov, M. Sabol.** THE LATEST RECORDS OF *MELISSIODON DOMINANS* FROM THE EARLY MIOCENE OF MOKRÁ-QUARRY (MORAVIA, CZECH REPUBLIC)—PRELIMINARY RESULTS

**R. Buchmann, T. Rodrigues.** BIOMECHANICS BEYOND BONES: INFERENCES ABOUT THE SOFT TISSUE OF THE PTEROSAUR NECK

**E. Carlisle, D. Silvestro, P. Donoghue.** THE ORIGIN OF PLACENTAL MAMMALS ACCORDING TO THE FOSSIL RECORD

**R. Carr, L.E. Wilson.** ASSESSING THE DISTRIBUTION OF CRANIAL KINESIS AMONG MOSASAUROIDS (SQUAMATA)

**O. Cirilli, L. Pandolfi, L. Rook, R.L. Bernor.** EVOLUTION OF THE OLD WORLD *EQUUS* AND ORIGIN OF THE ZEBRA-ASS CLADE

**A. Demers-Potvin, D. Cortés Parra, H. Bui, A. Smith, H. Larsson, H.P. Street, M. Parra Ruge.** ELASMOSAURIDS THROUGH TIME: A COLLABORATION ACROSS THE AMERICAS

**B.A. Ehrman, J.M. Theodor.** REVISIONS TO THE LATE UINTAN MAMMALS OF THE SWIFT CURRENT CREEK LOCALITY, SASKATCHEWAN

**S. Finch, M. D'Emic.** PATTERNS IN THE SCALING OF AMNIOTE DENTINE APPPOSITION

**G.W. Flora, J.J. Eberle.** DESCRIPTION OF A NEW UINTATHERE SKULL (MAMMALIA, DINOCERATA) FROM THE UINTA FORMATION, PICEANCE CREEK BASIN, COLORADO AND ITS TAXONOMIC IMPLICATIONS

**J. Grimes, R. Terry.** MORPHOLOGICAL VARIATION IN GREAT BASIN HETEROMYIDS: THE ROLE OF BODY SIZE AND DIETARY STRATEGY IN DRIVING MANDIBULAR SIZE AND SHAPE OVER THE LAST 13,000 YEARS

**J.C. Hoefflich, J.I. Bloch.** A TRANSITIONAL DRUM FISH FROM THE LATE MIOCENE OF FLORIDA

**J.C. Johnson.** THE HIGH VALLEY PROJECT: NEW FOSSIL VERTEBRATE LOCALITIES FROM THE WHITE RIVER GROUP OF NORTHEASTERN COLORADO

**J.K. Juranek, K. Shimada.** A NEW MID-CENOMANIAN FISH FAUNA FROM SOUTHEASTERN NEBRASKA, USA

**N. Kim, S. Choi, Y. Lee, S. Zhang.** A RELATIONSHIP BETWEEN EGGSHELL THICKNESS AND MICROSTRUCTURE TO SHOW A POSSIBLE MECHANISM FOR HATCHING OF THICK-SHELLED DINOSAUR EGGS

**D. Landi, L. King, M.E. Kirchner-Smith.** THE CRANIAL ENDOCAST OF *BREAGYPS CLARKI* (AVES: CATHARTIDAE) AND THE EVOLUTION OF CONDOR OLFATORY LOBES

**K. Mata, A. Shiinoki, N. Noriega, J. Cohen, W. Binder.** TOOTH BE TOLD: THE ADVANTAGES OF DIGITAL MEASUREMENTS FOR THE MORPHOMETRIC ANALYSIS OF THREE RANCHO LA BREA CARNIVORES

**P.L. McInerney, T.H. Worthy.** A COMMON AND SEVERE BONE INFECTION IN THE DROUGHT-RIDDEN POPULATION OF THE AUSTRALIAN PLEISTOCENE GIANT, *GENYORNIS NEWTONI* (AVES, DROMORNITHIDAE)

**C.V. Miller, M. Pittman.** THE DIET OF FOSSIL BIRDS AND A NEW FRAMEWORK FOR ITS RECONSTRUCTION

**C. Nicholl, E. Hunt, D. Ouarhache, P. Mannion.** A NEW CROCODYLIFORM FROM THE MID-CRETACEOUS KEM KEM GROUP OF MOROCCO DEMONSTRATES HEIGHTENED DIVERSITY IN THE PEIROSAURID LINEAGE

**A.K. Parker, J. Head.** REPTILE BODY SIZE HISTORIES IN THE TURKANA BASIN: INFLUENCES OF LOCAL HABITAT CHANGE

**A.W. Peng, S.S. Hopkins.** MORPHOLOGICAL AND ECOLOGICAL EVOLUTION IN ASIAN RODENTIA

**W.A. Reyes.** PALEONEUROANATOMY OF THE OTISCHALKIAN STAGONOLEPIDOID AETOSAUR *LONGOSUCHUS MEADEI* (ARCHOSAURIA: PSEUDOSUCHIA) FROM THE UPPER TRIASSIC DOCKUM GROUP OF WEST TEXAS

**A.J. Snyder, E. Snively, K. Brink.** TOOTH BIOMECHANICS USING 2D FINITE ELEMENT ANALYSIS IN *DIMETRODON* (SYNAPSIDA, SPHENACODONTIDAE)

**S. Tada, R. Matsumoto, T. Hanai, Y. Iwami, N. Tomita, T. Tsuihiji.** EVOLUTIONARY PROCESS TOWARD ENDOTHERMY IN DINOSAURIA ELUCIDATED BASED ON NASAL STRUCTURES

**A. Traynor, A.R. LeBlanc, K.D. Angielczyk.** CHANGES IN EMPLACEMENT PATTERN AND ORGANIZATION OF THE PALATAL DENTITION ACCOMPANIED THE EVOLUTION OF HERBIVORY IN EDAPHOSAURIDAE (SYNAPSIDA, EUPELYCOSAURIA)

**M.C. Vallejo-Pareja.** MORPHOLOGICAL VARIATION IN GREENHOUSE FROGS (*ELEUTHERODACTYLUS*, ELEUTHERODACTYLIDAE) AND DIVERSITY IN THE FOSSIL RECORD OF FLORIDA.

**A.R. Zietlow.** *TYLOSAURUS* THROUGH TIME: CLADISTIC ANALYSIS OF ONTOGENY RECOVERED EVIDENCE OF PERAMORPHY-DRIVEN ANAGENESIS IN NORTH AMERICAN TYLOSAURINES

**THURSDAY, NOVEMBER 4, 2021, 1:00PM EDT-2:00PM EDT  
PALEOPATHOLOGY & PALEOHISTOLOGY NETWORKING SESSION**

**POSTERS**

**E.V. Araújo, R. Bantim, J.M. Sayão, B. Holgado, M. Sena, A.S. Brum, E. I. Souza, L. C. Weinschütz, A.W. Kellner.** THE MICROSTRUCTURE AND SKELETOCHRONOLOGY OF *CAIUAJARA DOBRUSKII* (PTEROSAURIA, PTERODACTYLOIDEA, TAPEJARINAE)

**S. Baag, Y. Lee.** BONE HISTOLOGY ON *KOREACERATOPS HWASEONGENSIS* FROM KOREA

**T. Chinzorig, K.A. Beguesse, G. Phillips, L.E. Zanno.** A PATHOLOGICAL METATARSAL OF A LARGE-BODIED ORNITHOMIMID (DINOSAURIA: THEROPODA) DINOSAUR FROM THE UPPER CRETACEOUS EUTAW FORMATION (UPPER SANTONIAN) OF MISSISSIPPI, U.S.A.

**R.V. Germano, F.H. Barbosa, T. Rodrigues.** PREDOMINANCE OF LUMBAR AND CAUDAL PATHOLOGIES IN THE GIANT GROUND SLOTH *EREMOTHERIUM LAURILLARDI*

**C. Griffin, C. Colleary.** THE OSTEOHISTOLOGY OF HYOID ELEMENTS PRESERVES A RECORD OF GROWTH IN ARCHOSAURS

**H.M. Maddox, S.K. Drumheller, M. Stocker, T.L. Adams, C.R. Noto.** DIFFERENTIATING BITE MARKS AND SHELL DISEASE IN MODERN AND FOSSIL TURTLES USING COMPUTED TOMOGRAPHY

**N.S. Ong, B.J. Hart-Farrar, H. Woodward-Ballard.** OSTEOHISTOLOGICAL DESCRIPTION OF OSTRICH AND EMU LONG BONES, WITH COMMENTS ON POTENTIAL GROWTH MARKS

**N.S. Ong, R.B. Irmis, C.G. Levitt-Bussian.** THE HISTOLOGY OF ORNAMENTED TRIONYCHOID SHELLS FROM THE KAIPAROWITS FORMATION OF UTAH

**J. Slowiak, T. Szczygielski.** SHELL HISTOLOGY OF THE TRIASSIC TURTLE, *PROTEROCHERSIS POREBENSIS*, PROVIDES NOVEL INSIGHTS ABOUT SHELL ANKYLOSIS

**TALKS**

**T. Aureliano, A. Ghilardi, M.A. Fernandes, P. Sander, F. Ricardi-Branco.** AIR SACS ATTACHMENT OR TENDON SCARS? DISTINCTION BETWEEN SOFT TISSUE TRACES IN A TITANOSAUR VERTEBRA

**J. Benoit, L. Norton, C. Browning.** EVIDENCE OF INTRASPECIFIC FACE-BITING IN GORGONOPSIA (SYNAPSIDA, THERAPSIDA)?

**M. Bhat, A. Chinsamy, J. Parkington.** BONE HISTOLOGY AND LIFE HISTORY OF FOSSILISED ANGULATE TORTOISES (TESTUDINES: TESTUDINIDAE) FROM SOUTH AFRICA

**J. Botha, J.N. Choiniere, R.B. Benson.** OSTEOHISTOLOGY OF SOUTH AFRICAN SAUROPODIFORMS PROVIDES INFORMATION ABOUT THE TRANSITION TO SAUROPODAN GROWTH STRATEGIES

**A. Canoville, M.H. Schweitzer, L.E. Zanno.** REEVALUATING PURPORTED MEDULLARY BONE IN SELECT NON-AVIAN DINOSAURS

**B.J. Hart-Farrar, E. Snively, H. Woodward-Ballard.** ORTHOGONAL VASCULAR HISTOLOGY OF GROWTH SERIES IN THE ORNITHISCHIAN DINOSAURS *CENTROSAURUS* AND *MAIASAURA* COMPARED TO THE THEROPOD *GORGOSAURUS*

**E.M. Jevnikar, L.E. Zanno.** BIMODAL TRAJECTORIES AND UNRESOLVED EARLY GROWTH STAGES IN *TYRANNOSAURUS REX* GROWTH

**C. Nacarino-Meneses, A. Chinsamy.** ENAMEL HISTOLOGY AND DENTAL GROWTH IN THE EXTINCT CAPE ZEBRA

**D.J. Simon, D. Evans.** OSTEOHISTOLOGY SUPPORTS IMMATURE ONTOGENETIC STATUS OF NORTH AMERICAN OVIRAPTOROSAURS *APATORAPTOR PENNATUS* AND *CHIROSTENOTES PERGRACILIS*

**J. Slowiak, T. Szczygielski, B.M. Rothschild, D. Surmik.** A HADROSAUROID WITH AGE-RELATED DISEASES BRINGS A NEW PERSPECTIVE ON DINOSAUR SENESCENCE

**R.S. Sombathy, M. D'Emic.** RECONSTRUCTING GROWTH AND BODY SIZE IN *ALLOSAURUS* ACROSS ITS PALEOLATITUDINAL RANGE IN NORTH AMERICA

**M. Whitney, S. Pierce.** THE COMPARATIVE OSTEOHISTOLOGY OF *GREERERPETON* AND *PROTEROGYRINUS* (TETRAPODA) FROM THE CARBONIFEROUS OF NORTH AMERICA

**L.E. Wilson.** OSTEOHISTOLOGY OF *PROTOSTEGA GIGAS* (TESTUDINES: PROTOSTEGIDAE) REVEALS UNIQUE LIFE HISTORY STRATEGIES

**THURSDAY, NOVEMBER 4, 2021, 2:00PM EDT-2:45PM EDT  
MACROECOLOGY & MACROEVOLUTION NETWORKING SESSION**

**TALKS**

**E.R. Bender, T.A. Gates.** COMPARISON OF THE THRESHOLD MODEL AND PHYLOGENETIC GENERALIZED LEAST SQUARES IN CORRELATION ANALYSES OF DISCRETE TRAITS

**J.J. Caledo, T.M. Smiley.** A DATABASE OF RODENT BODY MASS FOR THE END OLIGOCENE THROUGH PLIOCENE

**T.M. Cullen, S. Zhang, J. Spencer, B. Cousens.** STABLE STRONTIUM ANALYSES INDICATE HABITAT USE AND FEEDING DIFFERENCES IN CO-OCCURRING LARGE HERBIVORES IN THE LATE CRETACEOUS OF WESTERN NORTH AMERICA

**M. D'Emic.** EVOLUTION OF BODY MASS IN SAUROPOD DINOSAURS

**N. Freymueller, D. DeMar, C. Dwyer, A. Farnsworth, I. Fendley, K. Gaines, C.P. Hedberg, J.S. Keller, J. Moore, C. Myers, D. Perriguet, R. Rovelli, K. Schroeder, J.S. Silviria, G. Wilson Mantilla, J. Witts.** THE FATE OF THE HELL CREEK TETRAPOD BIOTA: ECOLOGICAL NICHE MODELING REVEALS GEOGRAPHIC AND ENVIRONMENTAL HABITAT CHANGES FOR 106 GENERA ACROSS THE END-CRETACEOUS MASS EXTINCTION

**S. Hellert, G. Lloyd, D. Grossnickle, K.D. Angielczyk, C. Kammerer.** THE INFLUENCE OF ANCESTRAL BODY SIZE ON ECOMORPHOLOGICAL TRENDS IN SYNAPSID RADIATIONS

**C. Hendrickx, N. Brocklehurst, P. Currie, M. Romano.** NON-AVIALAN THEROPOD ECOSPACE DRIVEN BY EXTINCTION EVENTS, ORIGIN OF FLIGHT, AND RADIATION OF FLOWERING PLANTS

**S.S. Hopkins, A.W. Peng.** THE EFFECTS OF ECOSYSTEM CHANGE ON SMALL MAMMAL COMMUNITY ECOLOGY: A HOLARCTIC VIEW

**A.A. Kilmury, K. Brink.** DIVERSITY AND PROPOSED BIOZONES OF VERTEBRATES FROM THE LATE CRETACEOUS WESTERN INTERIOR SEAWAY IN MANITOBA, CANADA

**A. Knapp, G. Rangel, Z. Johanson, S. Giles, M. Friedman, A. Goswami.** HOW TO TUNA FISH: DRIVERS OF DIVERSITY IN PELAGIARIA (TUNAS, MACKERELS AND THEIR KIN)

**T.W. LaBarge, J.D. Gardner, C.L. Organ.** BAYESIAN REANALYSIS OF THE EVOLUTION OF PHORUSRHACIDAE (AVES, CARIAMIFORMES)

**J.K. McMinn, E. Saupe, A. Goswami.** HOW HAS THE BIOGEOGRAPHY OF GONDWANAN MAMMALIAN CLADES VARIED OVER DEEP TIME?

**J.G. Napoli.** THE MISSING DIVERSITY OF THE DINOSAUR FOSSIL RECORD

**M.I. Pardi, M. Greshko, A. Du, J. Louys, L. Yann, R.C. Hulbert, L. DeSantis.** LONG-TERM STABILITY OF INDIVIDUAL DIETARY SPECIALIZATION IN HERBIVOROUS MAMMALS

**L.E. Roberts, J. Head.** MORPHOMETRICS AND EVOLUTIONARY MODELING REVEAL THE COMPLEX EVOLUTIONARY HISTORY OF AXIAL SKELETAL REGIONALIZATION ACROSS ARCHOSAURIA

**L. Schnetz, R.J. Butler, M.I. Coates, I.J. Sansom.** QUANTIFYING THE COMPLETENESS OF THE PALEOZOIC CHONDRICHTHYAN FOSSIL RECORD

**T.M. Seerane, J.N. Choiniere, P. Viglietti, K.E. Chapelle.** DINOSAUR BODY SIZE EVOLUTION ACROSS THE TRIASSIC–JURASSIC BOUNDARY: INSIGHTS FROM SOUTH AFRICA'S ELLIOT FORMATION

**T.R. Simoes, S. Pierce.** DETECTING STRENGTH OF SELECTION AND MOSAIC EVOLUTION DURING THE RISE OF TETRAPODS

**R. Weppe, M. Orliac, G. Guinot, F. Condamine.** EVOLUTIONARY DRIVERS, MORPHOLOGICAL EVOLUTION AND DIVERSITY DYNAMICS OF A SURVIVING MAMMAL CLADE: CAINOTHERIOIDS AT THE EOCENE–OLIGOCENE TRANSITION

**C.H. Woolley, D.J. Bottjer, N. Smith.** THE COMPLETENESS OF THE FOSSIL RECORD OF LIZARDS AND SNAKES: QUANTIFYING THE EFFECTS OF BIAS ON GLOBAL SQUAMATE DIVERSITY THROUGH TIME



**B. Wynd, C. Griffin, S. Nesbitt.** TESTING THE PRESENCE OF ABIOTIC BIOGEOGRAPHIC DRIVERS USING ONLY PHYLOGENY: SUBTROPICAL ARIDITY AS A BARRIER FOR EARLY DINOSAUR DISPERSAL

**THURSDAY, NOVEMBER 4, 2021, 3:00PM EDT-3:30PM EDT  
TURTLES & MARINE REPTILE DIVERSITY & BIOLOGY NETWORKING SESSION**

**POSTERS**

**D. Larson, V.M. Arbour.** MESOZOIC TURTLES (TESTUDINES) FROM THE BOWSER BASIN OF BRITISH COLUMBIA, CANADA

**C.K. Mezak, S. Choi.** USING EBSD FOR THE IDENTIFICATION OF A FOSSILIZED EGG FOUND IN THE MIDDLE JURASSIC TIOURAREN FORMATION OF NIGER, AFRICA

**H.F. Smith, B. Adrian, C.R. Noto, A. Grossman.** A MARINE TURTLE (PROTOSTEGIDAE, CHELONIOIDEA) FROM THE ARLINGTON ARCHOSAUR SITE (CENOMANIAN), TEXAS

**T. Szczygielski.** OBSCURE BY NAME: THE TALE OF THE ENIGMATIC *CHELYTHERIUM OBSCURUM*, THE FIRST DESCRIBED TRIASSIC TURTLE

**TALKS**

**E.L. Bamforth, H.P. Street.** FIRST OCCURRENCE OF A SEA TURTLE (SUPERFAMILY CHELONIOIDEA) FROM THE CAMPANIAN DINOSAUR PARK FORMATION OF SASKATCHEWAN, CANADA

**P. Byrne, M. DeBlois, R. Motani, A. Tintori, O. Rieppel, F. Bernardini, D. Jiang.** A COPROLITE WITH THE FIRST 3D PRESERVED PECTORAL GIRDLE AND FORELIMB OF *KEICHOUSAURUS HUI* (PACHYPLEUROSAURIA; SAUROPTERYGIA) AND ITS IMPLICATIONS ON LOCOMOTION

**J. Chai, D. Jiang.** REVISION OF *NEOSINASAURUS* AND *WAYAOSAURUS*, AND THE CONSERVATIVE BODY DESIGN OF ASKEPTOSAUROIDEA

**R.O. Clark, F.R. O'Keefe.** AN EXCEPTIONALLY SMALL NEW POLYCOTYLID PLESIOSAUR (REPTILIA: SAUROPTERYGIA) WITH RAPTORIAL EYES FROM THE WESTERN INTERIOR SEAWAY OF NORTH AMERICA

**T. Dudgeon, M. Livius, J. Mallon.** A MORPHOMETRIC ANALYSIS OF THE TURTLE MANUS AND ITS IMPLICATIONS FOR THE PALAEOECOLOGY OF EXTINCT TURTLES

**P. Jiménez-Huidobro, K. Waskow, P. Sander.** LIFE HISTORY TRAITS OF TWO MOSASAUROID SPECIMENS REVEALED BY RIB HISTOLOGY

**R. Motani.** FIVE STEPS OF MARINE ADAPTATION IN NON-AVIAN MARINE TETRAPODS

**R.L. Schmeisser McKean, D.D. Gillette.** UNIQUE PALATE MORPHOLOGY IN A PARTIALLY COMPLETE POLYCOTYLID PLESIOSAUR FROM THE TROPIC SHALE (EARLY TURONIAN) OF SOUTHERN UTAH

**H.P. Street, M. Caldwell, J. MacLeran, R. Bennion, V. Fischer.** A EUROPEAN MOSASAURINE (SQUAMATA: MOSASAURIDAE) WITH AFFINITIES TO A CLADE FROM NEW ZEALAND

**T. Tran, J.F. Parham.** NEW FOSSIL SEA TURTLES FROM THE LATE MIOCENE (TORTONIAN) OF CALIFORNIA INFORM THE EVOLUTION OF FEEDING ECOMORPHOLOGIES

**L.M. Travis Taylor, R. Totten Minzoni, C. Suarez, L.A. Gonzalez, W. Lambert, D.J. Ehret, T. Harrell.** DID MOSASAURS DRINK FRESHWATER? OXYGEN ISOTOPES REVEAL MIGRATION AND CHANGING WATER HABITATS IN THE WESTERN INTERIOR SEAWAY, NORTH AMERICA

**A. Weil, M.W. Colbert, S.H. Weil.** NEW JURASSIC TURTLE FROM THE MORRISON FORMATION OF OKLAHOMA EXTENDS KNOWN MORPHOLOGY OF PLEUROSTERNIDAE

**THURSDAY, NOVEMBER 4, 2021, 3:30PM EDT-4:30PM EDT  
CROCODYLOMORPH & PTEROSAUR NETWORKING SESSION**

**POSTERS**

**L. Canejo, B. Holgado, E. Wilner, L. Weinschütz, A.W. Kellner.** A REASSESSMENT OF THE CRANIAL ANATOMY OF *CAIUAJARA DOBRUSKII* (PTEROSAURIA, PTERODACTYLOIDEA, TAPEJARIDAE) BASED ON NEW SPECIMENS

**B.S. Salem, H.M. Sallam, W.A. Thabet, S. El-Sayed, M.C. Lamanna.** THE FIRST PTEROSAUR FROM THE UPPER CRETACEOUS (LOWER CENOMANIAN) BAHARIYA FORMATION, BAHARIYA OASIS, WESTERN DESERT OF EGYPT

**K. Salih, M. AbdelGawad.** THE FIRST INVESTIGATION OF CROCODYLIAN REMAINS FROM THE UPPER PLEISTOCENE OF SUDAN

**H.N. Thomas.** THE PHYLOGENY OF AZHDARCHOIDEA (PTEROSAURIA) AND THE RISE OF TOOTHLESS PTEROSAURS

**TALKS**

**C.A. Brochu.** IF DR. SEUSS MADE AN ANIMAL WITH A WOODWIND INSTRUMENT COMING OUT OF ITS HEAD: THE SYSTEMATICS AND PALEOECOLOGICAL SIGNIFICANCE OF THE HYPER-TUBE-SNOURED OSTEOLAEMINE CROCODYLID *EUTHECODON* FROM THE LATE CENOZOIC OF AFRICA

**Y. Cho, C. Tsai.** THE HIDDEN DIVERSITY OF *TOYOTAMAPHIMEIA* (CROCODYLIFORMES, CROCODYLIA) FROM THE PLEISTOCENE OF TAIWAN

**A.J. Fitch, B. Bhullar, A.C. Pritchard, J. Bevitt, D.M. Lovelace, S. Nesbitt.** THE FORELIMB OF *ARCTICODACTYLUS CROMPTONELLUS* (PAN-AVES; PTEROSAURIA) AND THE ASSEMBLY OF THE PTEROSAUR WING

**D. Theda, A.H. Schwermann.** PTEROSAUR TRACKS FROM UPPER JURASSIC TIDAL FLAT DEPOSITS OF THE WIEHENGEBIRGE IN NORTHWESTERN GERMANY

**E. Wilberg, P.L. Godoy, E. Griffiths, A.H. Turner, R.B. Benson.** A NEW BASAL THALATTOSUCHIAN CROCODYLIFORM FROM THE EARLY JURASSIC (PLIENSCHACHIAN) OF DORSET, UK, AND IMPLICATIONS FOR THE ORIGIN AND EVOLUTION OF THE GROUP

**J. Yoshida, A. Hori, Y. Kobayashi, M.J. Ryan, Y. Takakuwa, Y. Hasegawa.** MORPHOLOGY AND ANATOMY OF THE HYOID APPARATUS IN CROCODYLIFORMS: THE ORIGIN OF THE GULAR VALVE IN NEOSUCHIA

**THURSDAY, NOVEMBER 4, 2021, 8:00PM EDT-9:00PM EDT  
HOLOCENE AND PLEISTOCENE MAMMALIAN FAUNAS NETWORKING SESSION**

**POSTERS**

**D. Davey, E. Mueller, L. DeSantis.** OVERSIZED KODIAK ISLAND BEARS: DIETARY BEHAVIOR AND BODY SIZE IN *URSUS ARCTOS* AS REVEALED BY DENTAL MICROWEAR TEXTURES

**M. Haji-Sheikh, M. Haji-Sheikh.** A BETTER BITE—THE THIRD DIMENSION IN *SMILODON FATALIS* MANDIBLE RECONSTRUCTION

**M.A. Khan, S.G. Abbas, M.K. Siddiq, M.A. Babar.** PLEISTOCENE PROBOSCIDEANS FROM THE SARDHOK PABBI HILLS, PAKISTAN

**B. Kraatz, O. Bedri, R. Bussert, A. Delagnes, A. Eisawi, I.A. Lazagabaster, M. Mohammednoor, J. Müller, K. Salih, S. Tsukamoto, F. Bibi.** NEW LATE PLEISTOCENE FOSSIL RODENT REMAINS FROM THE MIDDLE ATBARA, SUDAN

**R.L. Nava-Rodríguez, H.R. Sylva, J. Guzmán-Gutiérrez, I.E. Sánchez-Urbe, V.G. López-Díaz de León, C.A. López-Palma.** NEW LOCALITY OF PLEISTOCENE FOSSIL VERTEBRATES FROM THE MUNICIPALITY OF JULIMES, CHIHUAHUA, MEXICO

**I.A. Lazagabaster, T.E. Cerling, J. T. Faith.** A RARE FINDING OF A *HYLOCHOERUS* (MAMMALIA, SUIDAE) TOOTH FROM LATE PLEISTOCENE RUSINGA ISLAND, KENYA: PALEOECOLOGICAL AND PALEOENVIRONMENTAL IMPLICATIONS

**V.A. Perez-Crespo, V. Bravo-Cuevas, J. Arroyo-Cabrales.** DIETARY BEHAVIOR OF *EQUUS CONVERSIDENTS* AND *HARINGTONHIPPIUS FRANCISCI* FROM THE VALSEQUILLO BASIN, LATE PLEISTOCENE OF PUEBLA, MEXICO

**G.A. Rodríguez -Franco, V.A. Perez-Crespo, J. Rodríguez, A. Mateos, E. Cienfuegos-Alvarado.** ISOTOPIC BIOGEOCHEMISTRY OF CARBON, NITROGEN AND OXYGEN IN *URSUS SPELAEUS* FROM CUEVA DE GUANTES (SANTIBÁÑEZ DE LA PEÑA, PALENCIA, SPAIN)

**J. Schap, J. McGuire.** CHANGES IN THE RELATIVE ABUNDANCES OF THE MICROFAUNAL COMMUNITY AT NATURAL TRAP CAVE, WYOMING OVER THE LAST 20,000 YEARS

**TALKS**

**F. Bibi, R. Bussert, A. Delagnes, S. Tsukamoto, O. Bedri, B. Kraatz, I.A. Lazagabaster, M. Mohammednoor, J. Müller, K. Salih, A. Eisawi.** NEW MID TO LATE PLEISTOCENE FAUNA AND LITHICS FROM THE MIDDLE ATBARA, SUDAN

**M. Bushell, B. Schubert.** NEW DESCRIPTIONS OF *PANTHERA* REMAINS FROM ARKANSAS CAVE LOCALITIES

**C. Cortes, K. Smith, C. Monroe, N. Czaplewski, B. Postoak, L. Bement.** INVESTIGATING THE GENETIC AND ECOLOGICAL EFFECTS OF HISTORICAL SYMPATRY AMONG WOLF-LIKE CANIDS OF THE SOUTHERN GREAT PLAINS

**A. Kelly, J.H. Miller, L. DeSantis, M. Wooller, G. Zazula.** NICHE STABILITY THROUGH ENVIRONMENTAL CHANGE: A LATE PLEISTOCENE CHRONOLOGY OF *BISON PRISCUS* PALEOECOLOGY FROM YUKON TERRITORY, CANADA

**A. Lister, L. Dalen.** THE ORIGIN OF NEW WORLD MAMMOTHS: MORPHOLOGY MEETS DNA

**J.H. Miller, W. Wright, A. Kelly, B. Neale, M.Q. Gaetano, L. DeSantis, G. Zazula, M. Wooller.** CARNIVORES PREFERRED HORSE IN LATE PLEISTOCENE YUKON

**E. Mueller, M. Abdelmalak, L. DeSantis.** NICHE CONSERVATISM AND DIETARY ECOLOGY OF *DASYURUS* ACROSS SPACE AND TIME

**K. O'Brien, R.B. Irmis, J.B. Coltrain, D.M. Dalmas, T. Evans, E.S. Richards, F.M. Richards, J.T. Faith.** HIGH-ELEVATION CENSUS OF MONTANE ECOSYSTEMS: ECOLOGICAL IMPLICATIONS FOR QUATERNARY VERTEBRATES FROM BOOMERANG CAVE, UTAH, U.S.A.

**O. Oksanen.** PATTERNS OF RELATIVE ABUNDANCE AMONG LARGE CARNIVORANS IN WESTERN EURASIA DURING THE PLIO-PLEISTOCENE

**S. Olson, R.D. White, D.R. Prothero, D. Balassa, K.L. Marriot, V. Syverson.** ONTOGENETIC GROWTH IN THE PLEISTOCENE PRONGHORN *STOCKOCEROS* FROM SAN JOSECITO CAVE, MEXICO

**K.A. Prassack, L.C. Walkup.** NEW FINDINGS AND TEMPORAL-RANGE EXPANSION OF *FERINESTRIX VORAX* (MUSTELIDAE, MELINAE) AT HAGERMAN FOSSIL BEDS NATIONAL MONUMENT, NATIONAL PARK SERVICE

**FRIDAY, NOVEMBER 5, 2021, 10:00AM EDT-11:00AM EDT  
BIOMECHANICS & FUNCTIONAL MORPHOLOGY NETWORKING SESSION**

**POSTERS**

**S.H. Burch, J. Smith.** MUSCULATURE OF THE BIZARRE FORELIMB OF THE ALVAREZSAURID *MONONYKUS OLECRANUS* (DINOSAURIA: THEROPODA) AND ITS IMPLICATIONS FOR DIGGING

**M. Grohganz, H.G. Ferron, Z. Johanson, P. Donoghue.** TESTING HYPOTHESES ON HETEROSTRACAN FEEDING USING COMPUTATIONAL FLUID DYNAMICS

**E.D. Johnson-Ransom, E. Snively, D. Barta.** BIOMECHANICAL PERFORMANCE OF THE CRANIA OF TYRANNOSAUROIDS AND COMPARATIVE IMPLICATIONS FOR THEROPOD FEEDING

**A. Pérez Ramos, M. Burgos, J. Pastor, B. Figueirido.** A PRELIMINARY STUDY ON THE EFFICIENCY IN LARGE LIVING CATS USING COMPUTATIONAL FLUID DYNAMICS (CFD)

**J. Serrano, J. Garcia-Porta, A. Prieto-Márquez.** HINDLIMB EVOLUTION IN ORNITHOPOD DINOSAURS: A GEOMETRIC MORPHOMETRIC APPROACH

### **TALKS**

**P. Bishop, S. Pierce.** A NEW APPROACH TO MUSCULOSKELETAL MODELLING OF LIMB PERFORMANCE AND VERSATILITY IN EXTANT AND EXTINCT VERTEBRATES: A CASE STUDY OF THE SPRAWLING-TO-ERECT POSTURAL TRANSITION

**R.J. Brocklehurst, S. Pierce.** FUNCTIONAL PLASTICITY OF FORELIMB MUSCULATURE AND THE ORIGINS OF PARASAGITTAL POSTURE IN SYNAPSIDA

**D.C. D'Amore, M.B. Habib.** BIOMECHANICAL MODELING INDICATES TOOTH POSITION AND ROSTRUM SHAPE AS MAJOR INFLUENCES ON HETERODONTY IN THEROPODA

**H.G. Ferron, C. Martinez-Perez, I. Rahman, V. Selles de Lucas, H. Botella, P. Donoghue.** A FUNCTIONAL ASSESSMENT OF MORPHOLOGICAL HOMOPLASY IN STEM-GNATHOSTOMES

**J.D. Fortner, C. Holliday.** FUNCTIONAL MORPHOLOGY OF THE INTRAMANDIBULAR JOINT IN DINOSAURS AND OTHER REPTILES

**B.W. Griffin, E. Martin-Silverstone, O.E. Demuth, R. Pêgas, C. Palmer, E.J. Rayfield.** PECTORAL AND PELVIC RANGE OF MOTION: CONSTRAINTS ON ORNITHOCHEIRAEAN QUADRUPEDAL LAUNCH

**M.B. Habib, M. Pittman.** GOING UP OR COMING DOWN? *ARCHAEOPTERYX* AS THE EARLIEST KNOWN SECONDARILY FLIGHT-REDUCED VERTEBRATE

**A.R. Manafzadeh, S.M. Gatesy.** PALEOBIOLOGICAL RECONSTRUCTIONS OF ARTICULAR FUNCTION REQUIRE ALL SIX DEGREES OF FREEDOM

**S.K. Pevsner.** FUNCTIONAL TRADE-OFFS IN MULTITUBERCULATE THEORETICAL JAW MORPHOLOGY BETWEEN STRESS RESPONSE AND JAW SPEED

**M. Pittman, L.A. Barlow, T.G. Kaye, M.B. Habib.** PTEROSAURS IMPROVED FLIGHT PERFORMANCE BY EVOLVING ADVANCED AERODYNAMIC SMOOTHING OF THE WING-BODY JUNCTION AND SOPHISTICATED WING BASE CONTROL

**M. Pittman, T. Dececchi, A. Roy, T.G. Kaye, X. Xu, M.B. Habib, H. Larsson, X. Wang, X. Zheng.** AERODYNAMICS SHOW MEMBRANOUS-WINGED SCANSORIOPTERYGID THEROPODS WERE A POOR GLIDING FLIGHT EXPERIMENT

**H.L. Richards, P. Bishop, D. Hocking, J. Adams, A. Evans.** RECONSTRUCTION OF FORELIMB POSTURE AND FUNCTION IN A GIANT EXTINCT MARSUPIAL VIA COMPARATIVE RANGE OF MOTION MAPPING AND HELICAL AXIS ANALYSIS OF THE ELBOW JOINT

**A.J. Rowe, E.J. Rayfield, M.J. Benton, T. Williamson.** ASSESSING SKULL FUNCTION IN TYRANNOSAUROIDS USING 3D FINITE ELEMENT ANALYSIS

**K. Sellers, M.N. Nieto, F.J. Degrange, D. Pol, J.M. Clark, K.M. Middleton, C. Holliday.** THE EFFECTS OF SKULL FLATTENING ON SUCHIAN JAW MUSCLE EVOLUTION

**B. Shipps, K.D. Angielczyk, B.R. Pecoock.** THE TOPOGRAPHY OF DIET: USING MOLAR TO PREDICT FEEDING HABITS IN TURTLES

**D. Surmik, J. Slowiak, T. Szczygielski, D. Srodek, M. Wojtyniak, R. Pawlicki.** MULTI-SCALE STUDY OF OSSIFIED TENDONS OF LATE CRETACEOUS ORNITHISCHIANS

**F. Therrien, D. Zelenitsky, J.T. Voris, K. Tanaka.** TIMING OF ONTOGENETIC NICHE SHIFT IN *ALBERTOSAURUS SARCOPHAGUS* AND *GORGOSAURUS LIBRATUS* (TYRANNOSAURIDAE: ALBERTOSAURINAE) INDICATED BY MANDIBULAR BIOMECHANICAL PROPERTIES AND ONTOGENETIC CHANGES IN TOOTH MORPHOLOGY AND BITE FORCE

**H.P. Tsai.** THE DEVELOPMENT OF APPENDICULAR JOINT CARTILAGES IN *ALLIGATOR MISSISSIPPIENSIS*: EVOLUTIONARY AND BIOMECHANICAL IMPLICATIONS FOR ARCHOSAURIA

**P.A. van Bijlert, A. van Soest, K.T. Bates, A.S. Schulp.** EXPLORING WALKING AND RUNNING GAITS OF *TYRANNOSAURUS REX* USING MULTIBODY DYNAMIC SIMULATIONS

**K.K. Voegelé, S. Siegler, M. Bonnan, K. Lacovara.** RECONSTRUCTING ELBOW ARTICULAR CARTILAGE OF THE SAUROPOD DINOSAUR *DREADNOUGHTUS* USING MULTIBODY DYNAMICS AND THE EXTANT PHYLOGENETIC BRACKET

**FRIDAY, NOVEMBER 5, 2021, 1:00PM EDT-1:45PM EDT**

**TAPHONOMY, PALEOENVIRONMENTS, & STRATIGRAPHY NETWORKING SESSION**

## **POSTERS**

**M. AbdelGawad, G. Abu El-Kheir, W. Kassab.** THE VERTEBRATE BEARING HORIZONS IN THE LATE CRETACEOUS IN THE SOUTH WESTERN DESERT, EGYPT

**C.M. Brown.** POTENTIAL PRESERVATION OF KERATINOUS HORN TISSUE ASSOCIATED WITH THE FRILL ORNAMENTATION OF AN IMMATURE *CENTROSAURUS* (ORNITHISCHIA, CERATOPSIDAE)

**A.S. Brum, E.V. Araújo, G.A. Souza, A.C. Miceli, B. Bulak, L. Farias, M.B. Soares, J.M. Sayão, A.W. Kellner.** TAPHONOMIC ASPECTS OF VERTEBRATE FOSSIL OCCURRENCES FROM THE UPPER CRETACEOUS DEPOSITS OF THE JAMES ROSS BASIN (ANTARCTICA)

**S. Choi, N. Kim, H. Kim, J. Kweon, S. Lee, S. Zhang, D. Varricchio.** *IN SITU* PRESERVATION OF ARAGONITE IN A TURTLE EGG FROM THE JUDITH RIVER FORMATION (CAMPANIAN) OF MONTANA

**W.J. Freimuth, R.T. Tucker, L.E. Zanno.** INTEGRATED SEDIMENTOLOGY, VERTEBRATE FOSSILS, AND COPROLITES PROVIDE PALEOENVIRONMENTAL CONTEXT TO THE “LAST

CHANCE THEROPOD" LOCALITY, MUSSERTUCHIT MEMBER, CEDAR MOUNTAIN FORMATION, UTAH, USA

**S.J. Godfrey, A. Lowry.** MULTIPLE SHARK BITE-SHAKE TRACES ON A MIOCENE BALEEN WHALE RADIUS EVIDENCE SCAVENGING

**A.B. Heckert, I. Pugh, S. Ahmed, J. Crothers, J. Meyer, L. Rose, B. Lauer, R. Lauer, S. Nesbitt, M. Stocker.** PRELIMINARY TAPHONOMIC ASSESSMENT OF THE HOMESTEAD SITE, A NEW REVUELTIAN (UPPER TRIASSIC: MID-LATE NORIAN) MICROVERTEBRATE ASSEMBLAGE FROM EAST-CENTRAL NEW MEXICO: RECONSTRUCTING AN ASSEMBLAGE FROM INCOMPLETE DATA

**H. Maisch, M. Becker, V. Perez, K. Shimada.** ELASMOBRANCHS FROM THE PEACE RIVER AND TAMiami FORMATIONS (MIOCENE-PLIOCENE) ON THE SUBMERGED CONTINENTAL SHELF NEAR VENICE, FLORIDA, USA

**G. Panasci, D. Varricchio, R. Hirayama, S. Choi, J.P. Wilson, T. Dyman.** VERTEBRATE PALEONTOLOGICAL RECORD OF THE NON-MARINE CENOMANIAN-SANTONIAN FRONTIER FORMATION OF SOUTHWESTERN MONTANA

**B.M. Rothschild, L. Biehler-Gomez.** SKELETONS AND STONES: BIOLOGICAL CONCRETIONS IN THE FOSSIL RECORD

**A.B. Shaffer, L. Vietti.** DEPOSITIONAL ENVIRONMENT AND TAPHONOMIC INTERPRETATIONS OF AN EOCENE BRIDGER FORMATION SITE (WYOMING) CONTAINING CROCODYLOID AND *ECHMATEMYS* MATERIAL

**H.R. Sylva, R.M. Avila-Hernandez, A.M. Czaja.** VERTEBRATE PALEOFAUNA FROM A NEW LOCALITY OF THE CERRO DEL PUEBLO FORMATION (CAMPANIAN) IN COAHUILA, MEXICO

## **TALKS**

**C. Badgley, F. Hardy, K. Kravitz, B. Yanites.** IS MONTANE MAMMAL DIVERSITY CAPTURED IN THE FOSSIL RECORD?

**S.K. Drumheller, C.A. Brochu, G. Tekle, T. Getachew.** I LOVE LUCY, FOR DINNER: CROCODYLIAN BITE MARKS AND THE CHALLENGES OF EQUIFINALITY IN THE HOMININ-BEARING HADAR FORMATION OF ETHIOPIA

**M.Q. Gaetano, J.H. Miller, E.J. Wald, P. Druckenmiller.** A GNAWING QUESTION: EVALUATING TAXON-SPECIFIC BONE MODIFICATION IN AN ARCTIC ECOSYSTEM

**H.E. Smith.** TAPHONOMY AND SITE FORMATION HISTORY OF VERTEBRATE-BEARING BRECCIA IN THE CAVES OF SUMATRA

**J. Wiemann, D.E. Briggs.** MOLECULAR COMPOSITION DETERMINES BIASES IN THE FOSSIL RECORD OF VERTEBRATE SOFT TISSUES

**E. Wolff, I. Perea, J. Moore.** THE TAPHONOMY AND PATHOLOGY OF DEATH POSE IN ARCHOSAURS

**FRIDAY, NOVEMBER 5, 2021, 1:45PM EDT-2:30PM EDT  
QUANTITATIVE PALEONTOLOGICAL METHODS NETWORKING SESSION**

**POSTERS**

**E. Vollmer, B.R. Peacock, L. Tapanila, J. Pruitt.** 3D SURFACE SCANNING AND DIGITAL 3D RETRO DEFORMATION OF TIKTAALIK ROSEAEE FOR MUSEUM EXHIBITION

**TALKS**

**P.Z. Barrett, S.S. Hopkins.** SOPHISTICATED EVOLUTIONARY MODELS ON MORPHOLOGICAL DATA HAVE A HIGH IMPACT IN BAYESIAN PHYLOGENIES; A TEST CASE WITH THE FELIFORMIA (CARNIVORA)

**K.A. Beguesse, A. Canoville, E. Hyland, C. Walker, L.E. Zanno.** A NOVEL APPROACH FOR DISCRIMINATING MEDULLARY FROM PATHOLOGIC BONE IN EXTANT AND EXTINCT ARCHOSAURS

**M.M. Bradley-Cronkwright, A.D. Anaya, E. Fulwood, R. Ravier, J. Winchester, I. Daubechies, D.M. Boyer.** AN AUTOMATED APPROACH TO STUDYING THE EVOLUTION OF THE PARACONID CUSP IN A COMPREHENSIVE SAMPLE OF FOSSIL AND EXTANT EUARCHONTA

**T. Buskuskie, J. McHugh.** OH, THE MAP IS UPSIDE DOWN: IMPORTANCE OF STANDARDIZING AND COMMUNICATING MAPPING PROCEDURES FOR PALEONTOLOGY QUARRIES

**T.A. Gates, H. Cai, Y. Hu, X. Han, E. Griffith, L. Burgener, E. Hyland, L.E. Zanno.** MODEL-DISCRIMINATION INFERENCE IN THE BIOGEOGRAPHIC DISTRIBUTION OF EXTINCT BIOTAS

**A.S. Hall, J. Bevitt, U. Garbe, J.F. Hunter, R. Nelson, T. Williamson.** NEUTRON IMAGING FOR PALEONTOLOGY

**J. Hedge, L.E. Zanno.** QUANTITATIVE MEASURES OF EXTERNAL ORNAMENTATION IN AVIAN AND DINOSAURIAN EGG SHELL USING A NOVEL APPLICATION OF ORIENTATION PATCH COUNT ROTATED

**J. McHugh, S.K. Drumheller, M. Kane, A. Riedel.** SUBSAMPLING VERTEBRATE FOSSILS AS DIGITAL FRAGMENTS CAN ASSESS COLLECTIONS FOR BIASES AGAINST TAPHONOMIC DATA

**S.M. Van Ningen.** UTILIZING EXISTING MUSEUM COLLECTIONS AND GIS FOR PALEONTOLOGICAL SITE ASSESSMENT AND MANAGEMENT

**S. Wright, L. Vietti, M. Clementz.** AUTOMORPH: A SOFTWARE PACKAGE WITH POTENTIAL FOR AUTOMATED IDENTIFICATION OF FOSSIL MAMMAL TEETH



**FRIDAY, NOVEMBER 5, 2021, 3:00PM EDT-4:00PM EDT  
DINOSAUR SYSTEMATICS, DIVERSITY, & BIOLOGY NETWORKING SESSION**

**POSTERS**

**B. Curtice.** NEW DRY MESA DINOSAUR QUARRY *SUPERSAURUS VIVIANE* (JENSEN 1985) AXIAL ELEMENTS PROVIDE ADDITIONAL INSIGHT INTO ITS PHYLOGENETIC RELATIONSHIPS AND SIZE, SUGGESTING AN ANIMAL THAT EXCEEDED 39 METERS IN LENGTH

**J.E. D'Angelo.** A MAZE OF *OMEISAURUS*: OBSERVATIONS ON THE TAXONOMIC STATUS OF *OMEISAURUS JUNGHSIENSIS* (DINOSAURIA: SAUROPODA: MAMENCHISAURIDAE)

**A. Ghilardi, T. Aureliano, P. Buck, B. de Campos Pimenta e Marques Peixoto, M.A. Fernandes.** REASSESSMENT OF THE LOWER CRETACEOUS SOUSA MEGATRACKSITE IN THE BRAZILIAN OUTBACK

**E. Gorscak, P. O'Connor.** NEW TITANOSAURIAN SAUROPOD DINOSAUR FOSSILS FROM EASTERN AFRICA: EMERGING INSIGHTS FROM THE CRETACEOUS GALULA FORMATION OF TANZANIA AND REGIONAL FAUNAL PATTERNS ACROSS A CONTINENTAL SCALE

**M.N. Hudgins, P. Currie, R. Sissons, C. Sullivan.** POSTCRANIAL AUTAPOMORPHIES AND A NEW OCCURRENCE OF *PARKSOSAURUS WARRENI* (DINOSAURIA: ORNITHISCHIA) IN THE HORSESHOE CANYON FORMATION

**Y. Kobayashi, R. Takasaki, K. Kubota, A.R. Fiorillo.** A NEW BASAL HADROSAURID (DINOSAURIA: ORNITHISCHIA) FROM THE LATEST CRETACEOUS KITA-AMA FORMATION IN JAPAN ILLUMINATES THE ORIGIN OF HADROSAURIDS

**N.E. Morley, M.N. Hudgins, P. Currie, F. Han, C. Sullivan.** A MORPHOMETRIC ANALYSIS OF DENTAL VARIATION THROUGHOUT ONTOGENY IN *JEHOLOSAURUS SHANGYUANENSIS* (DINOSAURIA, ORNITHISCHIA) AND IDENTIFICATION OF TEETH FROM MICROSITES

**A. Prieto-Marquez, R. Gaete, J. Serrano Pérez, J.R. Wagner.** FIRST REMAINS OF THE CRANIAL CREST OF A LAMBEOSAURINE DINOSAUR FROM THE LATEST CRETACEOUS OF EUROPE, AND AN EVALUATION OF TSINTAOSAURINI

**M.J. Roloson, E.L. Bamforth, J. Scannella, J. Mallon.** *TRICERATOPS* FROM THE UPPERMOST MAASTRICHTIAN FRENCHMAN FORMATION OF SOUTHERN SASKATCHEWAN, AND IMPLICATIONS FOR THE ANAGENESIS HYPOTHESIS

**R. Takasaki, K. Chiba, A.R. Fiorillo, K. Brink, D. Evans, S. Ishigaki.** A NEW LAMBEOSAURINAE (DINOSAURIA, HADROSAURIDAE) SPECIMEN FROM THE UPPER CAMPANIAN JUDITH RIVER FORMATION WITH ITS BIOGEOGRAPHIC IMPLICATIONS

**N. Wakimizu, T. Tsuihiji.** COMPARATIVE STUDY ON THE ROSTRAL ENDOSKELETAL MORPHOLOGY OF THE TRIGEMINAL NERVOUS SYSTEM IN EXTANT ARCHOSAURS

**P.J. Wilson, L. King, M. Doughty.** A NEW LATE CRETACEOUS NODOSAURID (THYREOPHORA: ANKYLOSAURIA) FROM THE CAMPANIAN JUDITH RIVER FORMATION OF NORTHERN MONTANA

## TALKS

**L.W. Bradley.** DINOSAURS AND INDIANS: FOSSIL RESOURCE DISPOSSESSION OF SIOUX LANDS, 1846-1875

**A.A. Chiarenza, M. Fabbri, L. Consorti, M. Muscioni, D. Evans, F. Fanti.** UNFOLDING THE PALEODIVERSITY, AGE AND PALEOECOLOGY OF THE FIRST MULTI-INDIVIDUAL DINOSAUR-BEARING LOCALITY OF ITALY

**D.R. Dunfee, R.C. Ridgely, M.C. Lamanna, L. Witmer.** THE BRAINCASE OF A VERY YOUNG INDIVIDUAL OF THE EARLY-DIVERGING IGUANODONTIAN *DRYOSAURUS ELDERAE* (DINOSAURIA: ORNITHOPODA) FROM THE UPPER JURASSIC MORRISON FORMATION OF UTAH: ONTOGENETIC IMPLICATIONS

**J. Foster, M.J. Wedel, B. Engh, R.K. Hunt-Foster, Y. Haridy, J.I. Kirkland.** GEOLOGICALLY OLDEST SPECIMEN OF *BRACHIOSAURUS* (SAUROPODA) FROM THE SALT WASH MEMBER OF THE MORRISON FORMATION, SOUTHERN UTAH

**K. Melstrom, L. Chiappe, N. Smith.** EXCEPTIONALLY SIMPLE, RAPIDLY REPLACED TEETH IN SAUROPOD DINOSAURS DEMONSTRATE A NOVEL APPROACH TO HERBIVORY IN LATE JURASSIC ECOSYSTEMS

**J. Park, Y. Lee, Y. Kobayashi, L.L. Jacobs, R. Barsbold, H. Lee, N. Kim, K. Song, M.J. Polcyn.** A NEW SPECIMEN OF *TARCHIA GIGANTEUS* FROM THE UPPER CRETACEOUS NEMEGT FORMATION OF MONGOLIA, WITH EVIDENCE OF AGNOSTIC BEHAVIOR AND NICHE SHIFTS IN ARMORED DINOSAURS

**O. Regalado Fernandez, I. Werneburg.** EVALUATION OF THE MORPHOLOGICAL DIVERSITY OF '*PLATEOSAURUS*' FROM THE TROSSINGEN BEDS, GERMANY

**FRIDAY, NOVEMBER 5, 2021, 4:00PM EDT-4:45PM EDT  
EDUCATION & OUTREACH NETWORKING SESSION**

## POSTERS

**T. Aureliano, A. Ghilardi.** 'DINO HAZARD': A FRANCHISE TO UNITE ENTERTAINMENT, SCIENCE EDUCATION, AND SOCIAL IMPACT

**B.H. Breithaupt, N. Matthews, R.K. Hunt-Foster, H.G. McDonald, M.G. Lockley.** CHASING THEROPODS ACROSS AN EARLY JURASSIC SAND SEA: OPPORTUNITIES FOR YOUNG CITIZEN SCIENTISTS TO HELP DOCUMENT, INTERPRET, AND MANAGE AN ANCIENT TRACKSITE IN THE NAVAJO SANDSTONE

**B.B. Britt, N. Ortiz.** IMPACT OF EXPERIENTIAL VIRTUAL DINOSAUR EXCAVATION ASSIGNMENTS ON EXAM PERFORMANCE IN AN INTRODUCTORY, UNIVERSITY-LEVEL COURSE ON DINOSAURS

**S. Frigerio, L. Rolleri, J. Rassau, L. Speer, M. Haag, M. Fisk.** DINOSAURS ARE FOR EVERYONE: IMPLEMENTING ACCESSIBLE PREHISTORIC PROGRAMMING IN INFORMAL LEARNING INSTITUTIONS FOR DEAF AND HARD OF HEARING STUDENTS

**A. Ghilardi, T. Aureliano.** BROADCASTING PALEONTOLOGY: YOUTUBE AS A SCIENCE COMMUNICATION AND SOCIAL INTERACTION TOOL DURING PANDEMIC TIMES

**M.F. Guenther.** INCORPORATING VISION AND CHANGE CORE CONCEPTS AND COMPETENCIES INTO AN UPPER-LEVEL UNDERGRADUATE PALEONTOLOGY COURSE

**A.K. Hastings, C. Vargas-Vergara, S. Corbin, M. Ziegler.** TRACKING DINOSAUR FOOTPRINTS: USING 3D DIGITAL FOSSIL TRACKS IN STEM LESSONS

**T.J. Lepore, L. Hlusko.** INCLUSIVE DESIGN HELPS MORE STUDENTS FEEL INCLUDED IN ONLINE UNDERGRADUATE STEM AND PALEONTOLOGY COURSES

**T. Rodrigues, E. Nascimento, S. Lima, L. Souza, T. Nascimento, T. Souza, E. Holanda, A. Figueiredo, P. Dentzien-Dias, A. Hsiou.** DEMOGRAPHIC PROFILE OF BRAZILIAN VERTEBRATE PALEONTOLOGISTS

**T.M. Ruppert.** CAPTURING CURIOSITY: ADULT VISITOR ENGAGEMENT AT THE STERNBERG MUSEUM FOSSIL PREP LAB

**N. Smith, A. Celestian, a. gusick, A. Hendy, C. Thacker.** ACTIVATING COLLECTIONS FOR STUDENT RESEARCH AND EDUCATION: THREE YEARS OF RESULTS FROM THE NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY STUDENT COLLECTIONS STUDY AWARD

**A. Torices, A.I. Guzman Morales.** ILLUMINATING SCIENCE: WOMEN PALEONTOLOGISTS AND ILLUSTRATORS

### **TALKS**

**A.K. Behrensmeyer, M. Morgan, J. Csotonyi, C. Badgley, B. Jacobs, L. Flynn, J. Head.** SCIENCE-INFORMED ARTISTIC RECONSTRUCTIONS OF MIOCENE FAUNAS AND ECOSYSTEMS IN SOUTHERN ASIA

**A. Berta, S. Turner.** REBELS, SCHOLARS, EXPLORERS: WOMEN IN VERTEBRATE PALEONTOLOGY

## Paleohistology & Paleopathology

### TUSKS TELL ALL: INDIVIDUAL GROWTH AND SEASONAL CLIMATE INFERRED FROM THE TUSK OF AN EARLY TRIASSIC *LYSTROSAURUS* (THERAPSIDA, ANOMODONTIA) USING HISTOLOGY AND STABLE ISOTOPE GEOCHEMISTRY

Abbott, Caroline P.<sup>1</sup>, Angielczyk, Kenneth D.<sup>2</sup>

<sup>1</sup>Committee on Evolutionary Biology, The University of Chicago, Chicago, Illinois, United States, <sup>2</sup>Negaunee Integrative Research Center, Field Museum of Natural History, Chicago, Illinois, United States

The End-Permian Mass Extinction (EPME) was the largest mass extinction in Earth history. This event was caused by flood volcanism that drove global greenhouse conditions, and led to local climate instability during the Early Triassic. In the Karoo Basin, South Africa, geochemical and sedimentological data point to high climate variability, via wet-dry seasonality, which likely affected organism growth. *Lystrosaurus*, a medium-sized dicynodont, was the most geographically widespread and abundant tetrapod across the EPME, making it key to our understanding of life history evolution in the context of external environmental conditions during the event. *Lystrosaurus* possessed a pair of ever-growing tusks with incremental, hierarchically-organized dentine growth features. Recent work shows that *Lystrosaurus* tusks record normal growth and torpor, similar to patterns seen in rodent teeth. Likewise, geochemical research in the Karoo Basin indicates that Permo-Triassic bioapatite oxygen isotopic signals are diagenetically robust. Stable oxygen isotope ratios are particularly useful as they record meteoric water patterns in terrestrial environments. To date, there has been no work examining histological patterns of tusk growth in relation to inferred seasonal-scale climate from sequentially sampled oxygen isotopes. We examined histology and isotope values in a *Lystrosaurus declivis* tusk from the Katberg Formation in the Karoo Basin. We used light intensity profiles captured in ImageJ and visual inspection to measure growth and stress line thicknesses across transects in longitudinal sections of the tusk. For stable isotope geochemistry, we mounted half of the longitudinally sectioned tusk block on a glass slide, and used a scope-operated micro-mill to sample from second-order (~weekly) growth features. We analyzed  $\delta^{18}\text{O}$  from both phosphate and carbonate, and generated  $\delta^{18}\text{O}$  curves along the length of the tusk to analyze patterns of seasonality. Preliminary results indicate that the tusk preserves less than a Permo-Triassic

year's worth of growth, and a Mann-Kendall test shows there is a significant negative trend in growth feature thicknesses over time. Oxygen isotope values show evidence of cyclical variation across the time interval recorded in the tusk. Together these results suggest that dicynodont tusks can preserve a high resolution record of individual response to environmental variation during the EPME.

## Taphonomy, Paleoenvironments, & Stratigraphy

### THE VERTEBRATE BEARING HORIZONS IN THE LATE CRETACEOUS IN THE SOUTH WESTERN DESERT, EGYPT

AbdelGawad, Mohamed<sup>1</sup>, Abu El-Kheir, Gebely<sup>2</sup>, Kassab, Walid<sup>1</sup>

<sup>1</sup>Geology, Cairo University Faculty of Science, Giza, Egypt, <sup>2</sup>Geology, New Valley University, Faculty of Science, New Valley, Egypt

In North Africa, the Late Cretaceous is marked by 1) widespread marine cycles of transgression followed by regression, 2) tectonic events, materialized by syn-sedimentary deformations, local emergencies, clastic deposits, and rapid facies variations, and 3) deposition of black shales, related to high productivity model, associated with upwelling current, in Egypt, Tunisia, and Morocco. The Late Cretaceous is marked worldwide by those important geodynamic events which control the stratal pattern in all the basins worldwide and the distribution of marine vertebrates. In the Southwestern Desert basins, the Kharga -Dakhla- Farafra land stretch is considered as one of the most important areas containing Late Cretaceous vertebrates. The vertebrate fauna have been recorded mainly in three formations that are chronologically ordered from older to younger as follows; 1) Quseir Formation, which is composed of variegated claystones, siltstone, and sandstone intercalations enriched by benthic forams and plant remains which reflect deposition in shallow marine to swampy environments and are assigned a Campanian age. The Quseir Formation in Kharga Oasis is characterized by the presence of shark teeth, turtle shells, crocodile bones and dinosaurs which are concentrated in one horizon. 2) Duwi Formation is composed mainly of green shale intercalated by reddish siltstone and conglomeratic phosphate enriched by oyster banks deposited in protected inner shelf in a near-shore, oxic environment during the late

Campanian to early Maastrichtian age. Duwi Formation is characterized by the presence of various species of shark teeth and fish bone fragments which are reported in more than one horizon. 3) Dakhla Formation, which consists of thick shales intervened by thin beds of rippled sandstone and siltstone, marl, and marly limestone. The Dakhla facies is highly enriched by oysters and plant remains indicating deposition in inner neritic to lagoonal environments during Maastrichtian–Paleocene. The Dakhla Formation represents the thickest and most continuous outcrops along the scarp from south Kharga to Abu Minqar. The vertebrate fauna recorded in the Dakhla Formation are marine reptiles (plesiosaurs, mosasaurs, and turtles), crocodiles, fishes, and dinosaurs and occurred in five vertebrate horizons. All the vertebrate horizons in the three formations yield marine and freshwater vertebrate remains in addition to few terrestrial vertebrates remains.

**Funding Sources** This research is fully funded by the Science and Technology Development Fund, Egypt (STDF) under RS program, ID: 34811 Principal Investigator: Dr. Mohamed AbdelGawad.

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## Mesozoic & Paleogene Mammals

### THE CRANIUM OF *APTERODON* (HYAINAILOURIDAE, APTERODONTINAE) FROM ONE OF THE YOUNGEST VERTEBRATE- BEARING LOCALITIES (EARLY OLIGOCENE) IN THE FAYUM DEPRESSION, EGYPT

Al Ashqar, Shorouq F.<sup>1</sup>, Borths, Matthew<sup>2</sup>, Sileem, Afifi<sup>3</sup>,  
El-Sayed, Sanaa<sup>1</sup>, Seiffert, Erik<sup>4</sup>, Sallam, Hesham M.<sup>5</sup>

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<sup>2</sup>Division of Fossil Primates, Duke Lemur Center, Duke University, Durham, North Carolina, United States,

<sup>3</sup>Vertebrate Paleontology Section, Cairo Geological Museum, Cairo, Egypt, <sup>4</sup>Department of Integrative Anatomical Sciences, Keck School of Medicine of USC, University of Southern California, Los Angeles, California, United States, <sup>5</sup>American University in Cairo, Mansoura University, Cairo, Mansoura, Egypt

The Fayum Depression plays a vital role in enhancing our understanding of the evolutionary history, diversification and paleobiogeography of Paleogene terrestrial mammals on the Afro-Arabian continent. Hyaenodonta is the only group of carnivorous mammals known from the Fayum,

and this group shows a broad range of body size and dietary specialization. Apterodontinae is a peculiar group among Hyaenodonta, with fusiform crania and a highly modified dental morphology unknown in other carnassial-bearing mammals. Here, we report the most complete *Apterodon* cranium ever recovered from Quarry M (~29 Ma), one of the youngest terrestrial localities in the Jebel Qatrani Formation of the Fayum Depression. Based on craniodental morphology, the new cranium is very similar to *Apterodon macrognathus* from Quarry A (~33 Ma), also in the Jebel Qatrani Formation. The new skull preserves the complete upper left tooth row aside from I1 and P1 and right I2, P2-3 and M2. Like other apterodontines, the carnassial cutting blade is very reduced, reflecting a possible mesocarnivorous diet. The skull is anteroposteriorly elongate with a narrow, crushed rostrum. The nuchal crest and basicranium are well preserved with two large occipitals. The nuchal crest has a clover shape and does not reach the mastoid process. The neurocranium is complete and elongated. The zygomatic arches are dorsoventrally tall, broad and robust. The petrosal is preserved in the right side. The discovery of this cranium allows detailed craniodental comparisons with the better-known *A. macrognathus*, better documentation of the evolution of the distinct apterodontine bauplan, and closer examination of the transtethyan dispersal of *Apterodon* during the Paleogene.

**Funding Sources** Mansoura University, American University in Cairo Intramural grant, and U.S. National Science Foundation grants BCS-0819186 and BCS-1231288

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## Avialan Evolution & Biology

### SURVEY OF CORNIFIED TISSUE COVERINGS IN BIRD BILLS WITH IMPLICATIONS FOR HADROSAURID DINOSAUR RECONSTRUCTIONS

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Sexual selection acts on ornaments in modern animals, often incorporating soft tissue elements such as keratinous coverings. Soft tissues under sexual selection pressure are rarely preserved in fossils, so understanding the connection between bony and soft tissue is key to interpreting fossils with presumed sexually-selected bony

components. We sampled 225 species of extant birds from 67 families and recorded the extent of their cornified (heavily keratinized) bill tissue. Samples were selected to include at least one random species from each of the 41 bird orders, but samples were otherwise non-randomly selected to include all extant species with prominent bill ornaments. Of the sampled species, 109 had ornaments. Of the sampled families, 45 lacked any ornamented members. Out of those 109 ornamented species, 94 had cornified coverings over at least part of the ornament. The narial fenestra in most taxa was either covered in cornified tissue with a keratinous nostril rim, or covered in skin with a fleshy nostril. While ornamented taxa were more likely to have cornified tissue over the narial fenestra, the extent of keratinization was not exclusively linked to ornamentation. 99 species (representing 18 families) had cornified tissue extending over at least part of the frontal bones and associated region. Most birds with frontal cornification were ornamented (e.g. *Fulica*, *Musophaga*), though there were a few taxa which lacked ornaments but still had cornified tissue extending from the bill over the frontal region (e.g., *Geospiza*, *Mycteria americana*). These extant dinosaurs are useful to compare to extinct groups with keratinous bill coverings, such as hadrosaurid dinosaurs. Based on our results, we think that if their bills were similar to those of birds, most ornamented hadrosaurids likely had cornified coverings over at least the premaxillary and nasal bones. Some hadrosaurids (particularly lambeosaurines) likely had cornified tissue over the entire nasal region down to the nostril, and some (like *Gryposaurus*) may have had cornified tissue extending over at least the dorsoanterior region of the rostrum. Prior reconstructions of hadrosaurids have largely interpreted the post-oral region of the skull to be covered in skin, as opposed to a cornified rhamphotheca. Hardened structures such as we propose here could change our perspective on both the feeding ecology and sexually-selected ornamentation of these dinosaurs.

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## Fishes Evolution & Distribution

### RELATIVE ABUNDANCE BY TAXA IN A UNIQUE LATE CRETACEOUS BONEBED FROM WESTERN KANSAS, USA, LIKELY REVEALING A MORE ACCURATE REPRESENTATION OF THE 'NIOBRARA VERTEBRATE FAUNA'

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The Niobrara Chalk in western Kansas, USA, is a rock formation formed in the Late Cretaceous Western Interior Seaway of North America and is well known for diverse fossil marine vertebrates. FHSM VP-644 is a rock specimen collected from the Niobrara Chalk in Gove County, Kansas, housed in the Sternberg Museum of Natural History in Hays, Kansas. Whereas vertebrate remains in the Niobrara Chalk are generally sparse, FHSM VP-644 is unique because it is packed with numerous, small, disarticulated bones and teeth of fossil marine vertebrates that can be characterized as a bonebed. Its exact stratigraphic horizon within the formation is uncertain, but the general area where it was collected and the abundance of hesperornithiform bird teeth recovered from it suggest that it may be middle or late Santonian in age. The high density of fossil remains suggests that it could have formed during a period of regression concentrating vertebrate remains into a compact deposit, likely representing a time-averaged unit. Over 43,700 taxonomically identifiable specimens were collected from the bonebed; identified taxa consist of at least four chondrichthyans (e.g., anacoracids and *Rhinobatos*), 17 osteichthyans (e.g., pycnodonts, *Pachyrhizodus*, ichthyodectiforms, plethodids, *Cimolichthys*, *Enchodus*, and acanthomorphs), and two tetrapods (*Platecarpus* and *Hesperornithiformes*). However, it is noteworthy that the representations of specimens of these taxa from this bonebed are quite different from those represented in museum collections. For example, among the taxa represented in FHSM VP-644, the top two most abundant taxa in seven major Niobrara vertebrate museum collections combined are *Platecarpus* and Anacoracidae. In contrast, the two most abundant vertebrate taxa from the bonebed are both osteichthyan taxa, *Enchodus* and *Pachyrhizodus*. In fact, osteichthyan fishes are generally underrepresented in the museum collections, particularly compared to fossil tetrapods such as mosasaurs. Whereas museum collections may be collectively viewed as a time-averaged assemblage containing fossils collected from different horizons within the formation from a wide area in western Kansas, we argue that the relative abundance of different vertebrate taxa in the time-averaged bonebed likely represents a more accurate picture of the Niobrara vertebrate fauna compared to that in the museum collections that appear to show a strong bias towards tetrapods, such as mosasaurs and pterosaurs.

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## Fishes Evolution & Distribution

### A NEW DANIAN SQUIRRELFISH (ACANTHOMORPHA: HOLOCENTRIDAE) REVEALS EXTENSIVE SURVIVORSHIP ACROSS THE CRETACEOUS-PALEOGENE BOUNDARY

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Crown-group squirrelfishes (Holocentridae) are reef-dwelling, spiny-rayed fishes (Acanthomorpha) with a Cenozoic fossil record extending to the Eocene Bolca deposits of northern Italy. The crown-group can be split into two subclades: the shallower-dwelling Holocentrinae and deeper-dwelling Myripristinae. Nominal stem holocentrids are well-documented in Late Cretaceous deposits from the Cenomanian to the Campanian, but the relationships and timescale of diversification for fossil holocentrids is not well constrained. Here, we use  $\mu$ CT to describe the anatomy of an articulated, three-dimensionally preserved skull from the Danian Hornerstown Formation of New Jersey, USA. The specimen possesses several synapomorphies of crown-group squirrelfishes, notably an imperforate ceratohyal with strong ventral notching, and a parasphenoid that is laterally expansive posteriorly. However, the specimen displays a mosaic of traits found in both extant subclades, including an anterolaterally-expanded alveolar platform of the dentary, a notch ventral to the ascending process of the premaxilla, and a c-heterosulcoid sagittal otolith phenotype. The specimen possesses several notable apomorphies, including an unexpanded otic bulla and an unornamented lateral facet on the posteroventral margin of the maxilla. We included this and other well-known fossil holocentrids in a fossilized birth-death phylogenetic analysis. Previous hypotheses estimate the origin of crown holocentrids at approximately 61 Ma, and recover a single lineage crossing the Cretaceous–Paleogene boundary. Our analysis suggests that both the crown group and several now extinct lineages of holocentrids crossed the Cretaceous–Paleogene boundary.

**Funding Sources** The Rackham Merit Fellowship (Rackham Graduate School of the University of Michigan) and the Scott Turner Award (Dept. of Earth and Environmental Sciences, UofM)

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## Permo-Triassic Ecosystems

### THE MANDIBLE OF *COMPSODON HELMOEDI* (THERAPSIDA, ANOMODONTIA), WITH NEW RECORDS FOR THE RUHUHU BASIN, TANZANIA

Angielczyk, Kenneth D.<sup>1</sup>, Peacock, Brandon R.<sup>2</sup>, Smith, Roger M.<sup>3</sup>, Sidor, Christian A.<sup>4</sup>, Lungmus, Jacqueline K.<sup>5</sup>, Nesbitt, Sterling<sup>6</sup>, Olroyd, Savannah L.<sup>4</sup>, Steyer, Jean-Sebastien<sup>7</sup>, Stocker, Michelle<sup>6</sup>, Tolan, Steve<sup>8</sup>

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Correlations between Permian tetrapod assemblages in southern Africa rely on widespread dicynodonts, but uneven anatomical information available for different species complicates identification of potentially important but fragmentary specimens. The emydopoid *Compsodon helmoedi* was named from a single skull collected in putative *Daptocephalus* Assemblage Zone strata in the South African Karoo Basin. Description of recently collected specimens from the Luangwa Basin, Zambia, has improved knowledge of the species' cranial morphology and facilitated identification of other historically-collected Karoo specimens. Neither the holotype nor any of the Zambian specimens preserve a mandible. One Karoo specimen includes a mandible, but it is highly damaged and preserved in articulation with the skull, obscuring most details. We present a new Zambian specimen of *Compsodon* that includes an articulated skull and jaw, and use  $\mu$ CT to describe the mandible for the first time. The mandible has an upturned dentary symphysis; 'postcanine' teeth with coarse distal denticles; a shallow, elongate posterior dentary sulcus lateral to the tooth row; and a prominent lateral dentary shelf. Although the mandible is similar to those of *Emydops* and *Pristerodon*, it can be differentiated from *Emydops* by the less elongate symphysis and the absence of a rugose muscle scar on the lateral edge of the lateral dentary shelf.

It differs from *Pristerodon* in the absence of a dentary table rostral to the tooth row; the presence of a transverse ridge dividing the lateral dentary shelf into posterior and anterior sections; and the anterodorsal angulation of the lateral dentary shelf, with the anterior end of the shelf approaching the dorsal margin of the dentary. Three fragmentary specimens from the mid–upper Usili Formation (Ruhuhu Basin, Tanzania) display the same morphotype. Like the Luangwa specimen, the Ruhuhu specimens possess ‘postcanines’ and a posterior dentary sulcus, lack a dentary table, and have a lateral dentary shelf that approaches the dorsal margin of the mandible. If correctly identified, these specimens represent the first record of *Compsodon* from the Ruhuhu Basin. They provide a biostratigraphic correlation between the mid–upper Usili Formation and the *Daptocephalus* Assemblage Zone-like assemblage that has been recognized recently in the upper portion of the Upper Madumabisa Mudstone of the Luangwa Basin. *Compsodon* may appear earlier in South Africa than in Tanzania or Zambia.

**Funding Sources** National Science Foundation: EAR-1337291 (KDA, SJN), EAR-1337569 (CAS)  
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## Paleohistology & Paleopathology

### THE MICROSTRUCTURE AND SKELETOCHRONOLOGY OF *CAIUAJARA DOBRUSKII* (PTEROSAURIA, PTERODACTYLOIDEA, TAPEJARINAE)

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*Caiuajara dobruskii* is a tapejarine pterodactyloid pterosaur known so far by one of the very few pterosaur bone-beds from all over the world: the cemitério dos pterossauros (pterosaur graveyard), from Cruzeiro do Oeste (Paraná State, Southern Brazil). Hundreds of disarticulated bones with different sizes were found, establishing inferences of distinct ontogenetic stages of this flying reptile based on morphological comparisons. Here we performed microstructural and skeletochronological analyses to recognize and test how ontogenetic variation might be reflected in osteohistology. A sample of 13 appendicular bones of up to 12 different *Caiuajara* specimens were selected for this study. We also assessed the use of vascular and osteocyte lacunae densities. The sections present a thin fibrolamellar cortex, with vascular canals varying between reticular and plexiform patterns. LAGs and growth zones are absent in nine specimens and present in four others. Endosteal lamellae appear in two specimens, indicating that they have reached sexual maturity. However, these individuals do not attain their asymptotic growth, since EFS is absent. Resorption zones appear in only one specimen. Despite the fibrolamellar pattern of all samples, they are significantly different from each other, except for the high endosteal vascular density, present in all specimens. This feature indicates a fast deposition of bone matrix, reinforcing this common feature in pterosaurs. The comparison between bone elements allows us to establish two ontogenetic stages: juveniles, presenting open vascular canals in the periosteal region and absence of secondary bone tissue; and subadults, exhibiting endosteal lamellae, with growth marks and resorption zones. The data set indicates that sexual maturity is reached before the individual attained its full skeletal size. That also applies in other pterosaur species microstructures (i.e., *Pterodaustro* and *Rhamphorhynchus*), but in the latter the change in bone deposition from fibrolamellar to lamellar or parallel-fibered may indicate a possible change to powered flight. By contrast, *Caiuajara* does not seem to present sudden changes in growth rates, because these individuals present only fibrolamellar bone tissue. This could be due to several reasons; the appendicular bones of *Caiuajara* are highly pneumatized unlike *Pterodaustro* or *Rhamphorhynchus*, or it could be due to differences in sexual maturity and parental care between different pterosaur lineages.



**Funding Sources** Conselho Nacional de Desenvolvimento Científico e Tecnológico and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior. PPGZoo/MN-UFRJ

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### **Mammalian Skeletal Morphology**

#### **SKULLS, LATITUDE, AND 'RACE': HISTORICAL ATTEMPTS TO UNDERSTAND HUMAN CRANIAL VARIATION**

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The correlation of increasing latitude and size among animals has considerable empirical support across vertebrates, including humans. This pattern was first articulated in the mid-19th century, around the same time as data on human cranial variation began to be published. Yet the possibility of a latitude-skull morphology relationship among humans was not generally recognized for another century, and indeed its relevance remains less widely known compared to debates on racism and bias in data collection. A general decrease in skull size in Holocene compared to Pleistocene *Homo sapiens* may reflect external factors such as terminal-Pleistocene warming, and/or internal ones such as human self-domestication. Here, I test if recent and 19th century datasets show correlation of increased cranial volume with increasing latitudes. Recent datasets do, and at least using samples from the northern hemisphere, 19th century datasets do as well. Debates from previous centuries about 'intelligence' and other qualitative aspects of sociocultural worth have overshadowed other factors that might have helped to understand human evolution, such as latitude-related, anatomical variation due to temperature and seasonality. Disregard for such variation among humans persisted throughout the 20th century, for example in Gould's *The Mismeasure of Man*. By moving away from alleged social implications of human craniometric variation, we can better understand at least some of the relatively uncontroversial factors driving variation in human form, such as the relevance of climate and latitude.

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### **Marine Mammals**

#### **THE FIRST RECORD OF A COMPLETE SIRENIA FROM THE MIDDLE EOCENE FOSSILIFEROUS LIMESTONE IN THE EASTERN DESERT, EGYPT**

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A well-preserved, complete *Sirenia* skeleton has been reported from a highly fossiliferous dolomitic limestone from El Minya district. The fossiliferous limestone belongs to the middle Eocene epoch. This rock unit forms an extensive terrain of whitish to yellowish hard crystalline fossiliferous dolomitic limestone, which reaches a great thickness and is being quarried for its prized 'marbleized' qualities. The skull of a middle Eocene whale (marine mammal) was previously recovered within the El Minya district, contained within commercially prepared slabs from the Khasm El-Raqaba limestone quarry in the Eastern Desert of Egypt. The newly reported specimen was extracted from a quarry 100 km south of the Khasm El-Raqaba quarry. The preserved skeleton, which is embedded within limestone blocks, includes a skull and postcranial remains, such as ribs, limbs, and vertebrae. The reported specimen is split into two blocks of highly crystalline dolomitic limestone. The two blocks contain all of the skeleton, which is sectioned transversely. All the skeleton belongs to one *Sirenia* individual. The split blocks are 150 cm long and 120 cm wide, with the thickness of one being 20 cm and the other about 13 cm. The blocks containing the *Sirenia* skeleton are preserved at the Vertebrate Paleontology Laboratory (VPL) of the Geology Department, Faculty of Science, Cairo University. Preliminary results indicate that this specimen is completely different from all the specimens discovered previously from Egypt, and represents a new genus and species of *Sirenia*.

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### **Late Cenozoic Mammalian Evolution and Ecology**

#### **MIOTRAGOCERUS (ARTIODACTYLA, BOVIDAE) FROM CHINJI STRATA (MIDDLE MIOCENE) OF PAKISTAN**

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*Miotragocerus* is an extinct genus of the family Bovidae that has been recognized from the late Miocene of Europe and the middle-late Miocene of Siwaliks. It is one of the best represented bovids in the Chinji strata, northern Pakistan. Twenty-five new specimens of this genus including fairly complete skull, horn cores, maxillae, mandibles, isolated dentition and postcranials were recovered from the Chinji Formation (middle Miocene) sites of Rakh Wasnal, Bhilomar, Dhok Bar, Amir Khatoon, Lawa, Parrewala and Jand in Pakistan that allow identifying *Miotragocerus gluten*. Quantitatively, *Miotragocerus* is the most dominant taxa among the bovids of the middle Miocene. The new findings include deciduous premolars and rarely described postcranials of *Miotragocerus gluten*. The described materials add substantial knowledge to the anatomical and morphometric features of this extinct bovid. The current mesowear study shows that *Miotragocerus gluten* was a mixed feeder that preferably grazed on herbs and leaves and was dwelling in shrub land to light woodland. Because of its medium body size, *Miotragocerus* showed preference towards forested areas.

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## Non-avian Theropod Systematics, Biology, and Evolution

### ESTIMATING MASS PROPERTIES OF *ANZU WYLIEI*, WITH PARAMETERIZED RECONSTRUCTION OF THE RESPIRATORY SYSTEM

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The ability to rigorously estimate body mass of extinct taxa is vital for constraining the physiology and potentially even the behavior of long-dead animals. For this reason, paleontologists have experimented with many possible methods of estimating the body mass of extinct animals, with varying convergences of results. These methods can be divided into two main categories:

volumetric mass estimation, and extant scaling methods. Each has advantages and disadvantages, which is why, when possible, it is best to perform both, and compare the results to determine what is most likely while accounting for anatomy and phylogeny. Here we employ volumetric mass estimation (VME) for *Anzu wyliei* (Carnegie Museum of Natural History), founded on a digitally reconstructed skeleton (ZBrush 2020), combined with extant scaling methods to circumscribe reliable mass estimate for this taxon. Towards the VME we present the first digital life restoration and convex hull model (Meshlab) of *Anzu wyliei* used for mass estimation purposes. The life model includes a fully parameterized reconstruction of the respiratory system, to determine the effects that inferred configurations of air sacs might have on the body mass and center of mass of the animal. The volumetric mass estimation using the full anatomical model was 216–270 kg, consistent with the range predicted by extant scaling techniques. By contrast, mass estimates (159–199 kg) using minimum convex hulls falls below the predicted range. The volumetric estimate for *Anzu wyliei* affirms the broad predictive utility of extant-based scaling. However, volumetric mass estimates are likely more precise because the models are based on comprehensive specimen anatomy rather than regressions of a phylogenetically comprehensive but disparate sample.

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## Education & Outreach

### 'DINO HAZARD': A FRANCHISE TO UNITE ENTERTAINMENT, SCIENCE EDUCATION, AND SOCIAL IMPACT

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Not every audience actively consumes formal science communication products such as documentaries, books, and social media channels. These are the most vulnerable people to misinformation and misleading disclosures of the Post-Truth Era. Entertainment is a well-known venue to discuss such themes with people not usually interested in science. Worried about that, we created a science-fiction franchise to reach a broader audience and capture the attention of the public. Our main focus is raising

awareness of the paleontological patrimony of Brazil, engaging people with knowledge about its local heritage while also promoting diversity and inclusion of minorities. We planned this approach both to supply an internal need for science communication in this country, but also to export our science to foreign cultures. We also aim to revert bad foreign stereotypes regarding South Americans and reinforce women's empowerment with a strong female protagonist. We first published a book in 2016 ('Hidden Reality') that gained unprecedented niche popularity in our country. The book was translated into different languages in the following years. Other colleagues joined us and raised funds to expand the franchise and reach a broader public. We started producing toys and collectible miniatures of our national dinosaurs, and a comics series as well. Then, we decided to explore another niche: gaming. This area has usually been hostile to female players, misrepresenting this group as either hypersexualized or dumb, and rarely as protagonists. This fact contrasts with data indicating that nearly 50% of players are women. We decided to release a sequel to the book as a turn-based RPG game and embraced the challenge of having a group of seven main characters, and none is a caucasian man (60% are women and 50% are AfroBrazilian). The software contains a map to explore and discover more than 250 extinct taxa. Each type one discovers a new organism, a new slot appears in the encyclopedia menu with an educational text and image. The game beta version is currently available for testing on Steam and we had an even greater engagement. We received positive feedback from players in 37 countries and with a very strong women presence. Live streamings on the internet show that players are effectively learning paleontological terms. Therefore, we conclude that responsible science fiction multimedia can be a very powerful tool for science communication and should be encouraged.

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### **Paleohistology & Paleopathology**

#### **AIR SACS ATTACHMENT OR TENDON SCARS? DISTINCTION BETWEEN SOFT TISSUE TRACES IN A TITANOSAUR VERTEBRA**

Aureliano, Tito<sup>3</sup>, Ghilardi, Aline Marcele<sup>1</sup>, Fernandes, Marcelo A.<sup>2</sup>, Sander, P. Martin<sup>4</sup>, Ricardi-Branco, Fresia<sup>3</sup>

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There is an effort in paleontology to expand paleohistological sampling in order to improve our understanding of the evolution of avian-like air sacs in archosaurs. This work expands the occurrence of pneumosteal bone tissue in dinosaurs to the lithostrotian titanosaur '*Aeolosaurus*' *maximus* from the Upper Cretaceous of Brazil. CT scans of a posterior dorsal vertebral neural arch revealed a complex arrangement between fossae and laminae associated with pulmonary diverticula. Here we brought characters from optical mineralogy to differentiate those biomineralized tissue types. Pneumosteum is distinguished from the lamellar bone tissue making up regular bone trabeculae by constituting an array of tiny asbestiform densely packed fibers (usually shorter than 60 µm). These fibers depicted a low optical relief in every rotation angle and exhibited undulose extinction. Our study also indicated that despite the absence of any camellate structure in the preserved laminae, pneumosteal bone was present. This observation corroborates the hypothesis that diverticula would be attached to their surrounding fossae. Furthermore, it may be quite challenging to distinguish pneumosteal bone fibers from the ones resulted from muscle and tendon insertions (Sharpey's fibers). We established a solid base for histological comparison between these tissues. All Sharpey's fibers found in this approach are in accordance with previous observations from other taxa. They exhibit a high relief, undulose extinction, and insertion angles of approximately 60° relative to the cortical surface. These fibers are considerably longer (>200 µm) and thicker (<60 µm) than the pneumosteum ones. Another difference is that the former shows an organized parallel pattern in contrast to the chaotic asbestiform organization of the latter. Finally, we conclude that the localized nonexistence (or absent preservation) of camellae is not definitive evidence to discard the pneumatization of bone. We hope this will assist colleagues to collect more data for the expansion of the knowledge on the evolution of the respiratory system in archosaurs.

**Funding Sources** CNPq, CAPES, FAPESP, Bone Collectors Studio and their investors, and IGE-Unicamp postgraduate department

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### **Taphonomy, Paleoenvironments, & Stratigraphy**

## VERTEBRATE PALEOFAUNA FROM A NEW LOCALITY OF THE CERRO DEL PUEBLO FORMATION (CAMPANIAN) IN COAHUILA, MEXICO

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The municipality of General Cepeda has produced the largest number of paleontological sites in the State of Coahuila, in northern Mexico. The most important outcrops belong to the Cerro del Pueblo Formation, with an age between 73 and 72 Ma, from the late Campanian (Upper Cretaceous). The fossil outcrops in this formation appear discontinuously in the field, making it difficult to predict the location of additional deposits. The study area of the present work was recently discovered and produced an important diversity of vertebrate fossils. The fossil specimens were surface collected in a semi-desert area located on the slopes of a hill, where the sediments have been greatly eroded. The material was taken to the Museo del Desierto (MUDE) in Saltillo, Coahuila, for preparation and study. To date, we have been able to identify nine sauropsid families using skeletal elements consisting of teeth, vertebrae, fragments of carapace and plastron, squamosals and parietals, phalanges and manual unguals, which we have determined as belonging to the turtle families Trionychidae, Chelydridae, Dermatemydidae, Adocidae; the saurischian families Tyrannosauridae and Dromaeosauridae; and to the ornithischian families Hadrosauridae, Parksosauridae and Ceratopsidae. A paleoecological study of the locality will eventually be carried out.

**Funding Sources** The financial and material resources to carry out the field work during 2019 were covered by the Museo del Desierto and the Universidad Juarez del Estado de Durango.

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### Colbert Poster Prize

## A COMPARISON OF BAYESIAN AND PARSIMONY OPTIMALITY CRITERIA FOR THE ANALYSIS OF NEORNITHISCHIAN PHYLOGENIES

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Phylogenetic topologies are foundational to understanding the evolutionary process. Analyses requiring a phylogeny depend on the accuracy, precision, and resolution of a given topology. Currently, phylogenies hypothesizing relationships among early diverging ornithischians do not meet these requirements because of insufficient character resolution, incomplete taxonomic sampling, different interpretations of characters and states, inclusion of ontogenetically sensitive characters, and only a single analytical model (i.e., parsimony). Compared to parsimony, Bayesian phylogenetic methods improve accuracy and precision in matrices with 50–200 taxa, 100–500 characters, high amounts of missing data, and high levels of homoplasy. Another benefit of Bayesian analysis is the ability to apply prior knowledge (such as stratigraphic data) to help achieve resolution when character data is lacking, as well as model-testing statistics to determine the overall effect of adding priors. We performed a series of Bayesian analyses on the phylogeny presented in the recent *Burianosaurus* description using the software Beast2 to document topological differences from the original published parsimony results and identify beneficial parameters for increasing resolution. Bayes factor (BF) tests were performed on nested clock and tree building models to identify if a single rate or multiple rates, and simple or complex tree building models produced better results. Consistent BF values of ~1 indicate no significant difference between Strict and Relaxed Clock models. The same ambiguous results were received with a simple Yule tree model versus a complex array of Fossilized-Birth-Death plus tip-dating, meaning that the addition of prior information does not improve our current understanding of ornithischian phylogeny. The topology of the Strict Clock tree differed from the parsimony result, recovering Iguanodontia as a sister clade to all other ornithischians with strong node support (0.84 posterior probability). In all analyses, Orodrominae and Thescelosaurinae were recovered as sister taxa composed of the same OTUs. Uncertainty in resulting tree architecture highlights the need for expanded morphological characterization, open access data sharing, annotated character lists, and collaborative efforts to more consistently discretize and score character data widely across the global distribution of early diverging ornithischians.

**Funding Sources** Jurassic Foundation, The Paleontological Society, Harkema Fund, and National Science Foundation Grant No. 1925973

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### **Paleohistology & Paleopathology**

#### **BONE HISTOLOGY ON *KOREACERATOPS HWASEONGENSIS* FROM KOREA**

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*Koreaceratops hwaseongensis* is a basal ceratopsian dinosaur found in the Lower Cretaceous Sihwa Formation (Albian), Hwaseong City, Gyeonggi Province, South Korea. It was found only with the lower part of the body, including an articulated 36 caudal vertebrae associated with partial hind limbs and ischia. To study its bone histology, we sampled the right tibia and fibula in hopes of uncovering the phylogeny, environment, and mechanics. The result shows that both bones exhibit poor histological preservation due to microbial degradation. They are characterized with signs of extensive tunneling by micro-organisms, which rendered the bone cortex into an amalgam of microscopical globules and foci. Consequently, informative histological features like lacunae, canaliculi, and lamellar have been erased. However, a few remaining traces of histological features like the vasculature and growth marks enabled us to determine that the growth pattern of *Koreaceratops hwaseongensis* is very similar to that of a sub-adult *Protoceratops andrewsi*. Both species exhibit zonation with a bit of bone remodeling in their tibiae and lines of arrested growth with an extensive bone remodeling in their fibulae. We also noticed that the only histological similarity between *Koreaceratops hwaseongensis* and the more basal ceratopsians *Psittacosaurus mongoliensis* and *P. lujiatunensis* is the longitudinal and reticular vasculature in their fibulae. These suggest that *Koreaceratops* is much closer to *Protoceratops* than *Psittacosaurus* in terms of phylogeny. The fibula of *Koreaceratops* shows a constant osseous drift that initially drifted toward the medial axis but abruptly changed to the anterior axis in the final growth interval. In addition, the right tibia's final growth exhibiting an anteromedial osseous drift suggests that *Koreaceratops* experienced a change in its right hindlimb's biomechanics before death. The number of

growth zones in the tibia indicates that *Koreaceratops* was approximately eight years old when it died. The predominantly longitudinal vasculature suggests a relatively moderate growth tempo. The absence of external fundamental systems or narrowing growth intervals indicates this individual was not physically or sexually mature. Unfortunately, the heavy microbial erosion prevents us from getting further histological information, implying it was buried in a semi-arid climate regime that was favorable for microbial bone decomposition.

**Funding Sources** National Research Foundation of Korea (Grant Number 2019R1A2B5B02070240)

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### **Late Cenozoic Mammalian Evolution and Ecology**

#### **ANTHRACOTHERIIDS (ARTIODACTYLA) FROM MIDDLE SIWALIK SUBGROUP, PAKISTAN**

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Anthracotheriids, members of the family Anthracotheriidae of the order Artiodactyla, are unique mammals that show dental, osteological and physical character between the family Suidae and Hippopotamidae. All the anthracotheriid species are now extinct and were largely confined to Asia. In the Siwalik Group, this family is represented by two genera, a small one, *Microbunodon*, and a large one, which progressively attained the large body size, *Merycopotamus*. *Microbunodon* is represented by two species in the Siwaliks and *Merycopotamus* is represented by three species, which are time transgressive. Remains of both genera are not found frequently, especially the cranial remains, which are extremely rare. Here, I am reporting the remains of both these genera from the Nagri and Dhok Pathan formations of the Middle Siwaliks subgroup including a partly complete skull from the Nagri outcrops of the Lawa village, Chakwal, Punjab, Pakistan.

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### **Taphonomy, Paleoenvironments, & Stratigraphy**

## IS MONTANE MAMMAL DIVERSITY CAPTURED IN THE FOSSIL RECORD?

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Mountainous regions today support disproportionately high numbers of species for the area they occupy. Steep environmental gradients, opportunities for isolated as well as connected populations, and numerous microhabitats all support high biodiversity of terrestrial vertebrates. But the vertebrate fossil record occurs primarily in sedimentary basins at low elevation, with the exception of caves, lakes, and plateaus at high elevation. Using the mammals of Colorado as a test case, we investigated the overlap between the geographic ranges of species residing primarily in montane environments and the current distribution of active depositional environments. Colorado is home to 128 species of native mammals with well documented elevational ranges. About one fifth of these species have geographic ranges that lie above 1800 m, the elevation separating foothills and high mountains from the plains and river valleys. Active depositional environments include alluvial and aeolian sediments, distributed east of the Front Range of the Rocky Mountains and in restricted valleys within the montane region. We determined the overlap of geographic ranges of high-elevation species with four categories of alluvial and aeolian sediments. The majority of high-elevation species exhibit some overlap with active depositional environments. However, this overlap involves less than 5% of the geographic range for most of these high-elevation species. The amount of overlap is greater for alluvial than for aeolian sediments. Rodents show greater amounts of overlap than do other mammal species. The main signature of montane species diversity occurs in the foothills where mammal diversity is high and overlap with alluvial depositional environments is moderate. These results imply that basin-margin sediments are the most likely source of fossils representing the montane mammal diversity of the past.

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## Holocene & Pleistocene Mammalian Faunas

### DID PRONGHORNS BECOME SMALLER AFTER THE ICE AGES?

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According to Adams and colleagues in 1999, Holocene pronghorns (*Antilocapra americana*) reduced in size at the end of the last Ice Age. This conclusion was based on very small samples from the late Pleistocene Natural Trap Cave in Wyoming (17,000–20,000 years BP), the early Holocene (early Plains Archaic culture, about 7000 years BP) Trappers Point site in Wyoming, the Protohistoric (less than 500 years old) Ecker-Fallon site in Wyoming, and modern samples. We re-examined this claim, adding to the sample the pronghorns from the late Pleistocene deposits at Rancho La Brea tar pits in Los Angeles, mostly from Pit 3 and dated around 18,000 years BP, as well as additional modern pronghorns. We measured the same bones that Adams and colleagues reported, as well as other dimensions of the common limb bones. We employed the Kruskal-Wallis test for significance of difference in single variable between non-parametric samples, and Hotelling's T<sup>2</sup> test for significance of differences in bivariate data. There is no statistically significant difference between late Pleistocene pronghorns from either La Brea or Natural Trap Cave compared to each other, or to modern samples. Only the early Holocene Trappers Point samples are slightly larger (about 8% larger) than all the remaining samples, and this is not statistically significant. Thus, if pronghorns changed size at all in the last 20,000 years, they increased slightly in the early Holocene, but have reverted to their late Pleistocene size since then.

## Turtle & Marine Reptile Diversity & Biology

### FIRST OCCURRENCE OF A SEA TURTLE (SUPERFAMILY CHELONIOIDEA) FROM THE CAMPANIAN DINOSAUR PARK FORMATION OF SASKATCHEWAN, CANADA

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Sea turtles (chelonoids) are an intriguing component of western Canada's marine faunas. Studies of sea turtle diversity patterns in the Late Cretaceous suggest that these animals favored southern portions of the Western Interior Sea, meaning they are much rarer in Canada than in the United States. Accordingly, there is very little diagnostic chelonoid material known from Saskatchewan's Late Cretaceous marine deposits. Herein is described the first occurrence of a sea turtle from a marine unit of the Campanian Dinosaur Park Formation of Saskatchewan. RSKM P3197.198 is a left costal plate of the carapace, with a maximal length of 150 mm, maximal width of 90 mm in width, and maximal thickness of 16 mm. Although broken along its medial margin, the lateral peripheral edge is reasonably well preserved. The costal plate is broad and slightly convex dorsally, with no noticeable suturing or orientation. The specimen was collected in 2016 from a marine bonebed near Herschel, Saskatchewan, within a marine interval of the Dinosaur Park Formation that represented a shallow-marine barrier-island basin environment. In Alberta, the province to the west, two of the three known Campanian chelonoid taxa are from a similar, though not necessarily coeval, nearshore marine unit in the Dinosaur Park Formation known as the Lethbridge Coal Zone. (A third taxon is known from open marine Bearpaw Formation of Alberta). Unfortunately, due to the lack of post-cranial material for the Lethbridge Coal Zone genera, *Lophochelys* and *Kimurachelys*, there is as of yet insufficient data to assign RSKM P3197.198 to either of these. Regardless, the Saskatchewan specimen does represent another chelonoid specimen from a nearshore marine environment in western Canada. RSKM P3197.198 corroborates the theory that northern chelonoids may have been brackish-water or even freshwater tolerant and, although the sample size is small, suggests chelonoid diversity may have been higher in nearshore, shallow-marine or estuarine environments. RSM P3197.198 represents the largest and most diagnostic chelonoid in Saskatchewan. Future work on this specimen may reveal important information on the diversity and paleoecology of marine turtles in western Canada.

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#### Quantitative Paleontological Methods

#### SOPHISTICATED EVOLUTIONARY MODELS ON MORPHOLOGICAL DATA HAVE A HIGH

#### IMPACT IN BAYESIAN PHYLOGENIES; A TEST CASE WITH THE FELIFORMIA (CARNIVORA)

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Phylogenetic analyses have become increasingly sophisticated over the past two decades with the advent of Bayesian total-evidence methods. However, treatment of molecular and morphological data has received disparate attention. Molecular analyses feature standard assessment of partitioning strategies and evolutionary models, often in an automated format such as PartitionFinder. Comparatively, morphological data are only typically explored via *a priori* schemes of anatomical partitions, such as cranial/post-cranial or other anatomical modules thought to evolve at similar rates and in a coordinated manner. Surprisingly, little attention has been given to evolutionary models of morphological data beyond the sequential ordering of characters first seen in parsimony analyses. I assessed the impact of partitioning and custom evolutionary models on a phylogenetic analysis of the Feliformia (129 taxa) in BEAST2. I assessed character partitions by cranial/post-cranial association, number of states a character possesses (n-states), or a combination of the two. I further explored ordered, multipath and irreversible (Dollo) evolutionary models. These models were assessed via stepping-stone analysis and Bayes Factor (BF) support. The best supported models combined n-states partitioning and complex evolutionary models, with the latter conferring an approximate 200 BF boost in support compared to models featuring only an n-states scheme. This analysis demonstrates the need to standardize assessment of character partitioning and evolutionary models for morphological data in Bayesian analyses and explore the effects of complex evolutionary models in future work.

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#### Late Cenozoic Mammalian Evolution and Ecology

#### CANIS FEROX REVISITED WITH DIETARY INFERENCE ON EUCYON SPECIES

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The late Miocene was a period of great radiation for the subfamily Caninae in North America. During this time of rapid flourishing, the two tribes that compose this subfamily, Vulpini and Canini, arose. Among them, *Eucyon* and *Canis* are two of the most important elements of the latest Miocene–Pliocene Canidae guild of both North America and Eurasia. The earliest member of the latter genus, *Canis ferox*, has been reported from late Hemphillian (4.95–4.80 Ma) deposits. There is a certain degree of uncertainty and debate on the taxonomy of these Miocene–Pliocene Caninae. One of the most debated issues concerns a number of species referred to *Eucyon* and *Eucyon*-like taxa. Furthermore, no one has ever analyzed the dietary habits of fossil Caninae, such as *Eucyon* or closely related taxa. In this study we revise the type and paratype specimens of *C. ferox*. Numerous cranial and dentognathic features of this late Miocene canid do not fit with the diagnostic characteristics of the genus *Canis* and are more consistent with those of *Eucyon*. Although reopening the question of the origin of *Canis*, the reassessment of *E. ferox* reveals a previously underestimated ecomorphological variability of *Eucyon*. Some dentognathic features of *E. ferox* (depth of the mandible, stoutness of the carnassials, the development of buccal cusps/cuspids relative to the lingual ones, reduced crushing area) are suggestive of a hypercarnivorous diet. To test this hypothesis, we selected well-established morphometric ratios and applied different analyses on a sample of *Eucyon* species. Our results indicate that *Eucyon* and closely related taxa had mesocarnivorous diets (50–70% vertebrate diet), with the exception of the large-sized *E. ferox*. Although it remains difficult to assess if it preyed on small animals or on prey larger than itself, our analyses clearly confirm a highly carnivorous diet for this species.

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## Quantitative Paleontological Methods

### A NOVEL APPROACH FOR DISCRIMINATING MEDULLARY FROM PATHOLOGIC BONE IN EXTANT AND EXTINCT ARCHOSAURS

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Comparative studies of the (paleo)pathology of extant and extinct species can provide valuable information about the evolution of disease and associated physiological responses across macroevolutionary timescales. Data derived from these studies are critical to testing macroevolutionary models of bone disease, trauma, and repair. Analyses of fossil bone pathologies employing standard methods (gross, histologic, diagnostic imaging) can be confounded by taphonomic processes that distort, obscure or even prevent identification and differentiation of pathologic (PB) and normal (NB) bone. Additionally, some endosteal PB can exhibit microstructural features that resemble medullary bone (MB), a type of reproductive bone deposited by living female birds during the egg-laying cycle. MB has tentatively been identified in extinct taxa spanning over 150 million years of evolutionary time including pterosaurs, non-avian dinosaurs, and extinct birds. To date, no definitive techniques have been successfully identified to differentiate MB from endosteal PB. The current inability to differentiate endosteal PB from MB across such a broad gamut of life is highly problematic for conducting macroevolutionary studies. Hence, there exists a need for verified techniques that can confidently discriminate PB from MB and NB.

Clumped isotope analysis is one approach to evaluate the potential for differential temperature development of NB, MB, and PB, and possibly discriminate these tissues in fossil and osteological collections. Clumped isotope signature is solely dependent on precipitation temperature of the carbonate mineral thus allowing for direct measurement of formational temperature within an accuracy of  $\pm 2^\circ\text{C}$ . However, potential effects of low-heat diagenesis during fossilization and/or standard treatments commonly used in natural history museums and veterinary diagnostic labs on bones have not yet been tested.

We performed stable and clumped  $^{13}\text{C}$ - $^{18}\text{O}$  isotope analyses on extant avian material subjected to a variety of standard treatments (freezing, boiling, formalin, hydrogen peroxide) to test potential diagenetic and common treatment effects that might limit the utility of this technique. Results demonstrate  $\delta^{13}\text{C}$  (-8 to -14‰),  $\delta^{18}\text{O}$  (+14 to +18‰), and  $\Delta_{47}$  (0.630 to 0.700‰) values within environmental ranges and show no evidence for bias based on treatment style, indicating osteological



collections and fossil materials can reliably be used for these analyses in future studies.

**Funding Sources** Work supported by the Triangle Center for Evolutionary Medicine (TriCEM)

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## Education & Outreach

### SCIENCE-INFORMED ARTISTIC RECONSTRUCTIONS OF MIOCENE FAUNAS AND ECOSYSTEMS IN SOUTHERN ASIA

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Collaborations between scientists and artists create realistic visualizations of extinct communities that convey important messages about ecosystem structure and how it changed over time. Using multiple lines of evidence, we developed three reconstructions of vertebrate faunas and habitats on the sub-Himalayan alluvial plain of southern Asia. Individual scenes represent abandoned-channel and proximal-channel paleoenvironments. The taphonomy of the fossil assemblages indicates that accumulations of skeletal remains resulted from attritional deaths with limited transport by fluvial processes and represent time-averaged faunal samples of  $\sim 10^3$  kyrs. Key species of small, large and mega-mammals, birds, non-avian reptiles and fishes were identified for each reconstruction. These were selected from fauna preserved at three taxonomically rich fossil localities in the Siwalik Series of the Potwar Plateau, Pakistan, dated at 12.4 (Y496), 9.2 (Y182) and 7.2 (Y581) Ma. We included a representative diversity of mammal species that co-occurred at each locality, adding a few taxa from similar-aged localities (e.g., carnivorans, porcupine). Each scene includes 20 to 30 Siwalik species, and all major Siwalik mammalian and many other vertebrate groups are visible in at least one of

the three scenes. In the absence of preserved plant remains, we used present-day south Asian plant taxa and fossil plants from the Nepalese Miocene to reconstruct the vegetation, along with stable isotopes and biomarkers indicating the proportion of C3 versus C4 vegetation, seasonality, and the presence of fire. Reconstructions also include arthropods, fungi, and other organisms expected in analogous modern habitats. JC created perspectives from different arboreal and ground-level views to show both small and large plants and animals at specific places, times of day, and seasons. Realistic associations of animals with different substrates and interactions among focal species shaped the composition of each reconstruction. Intensive team discussion of successive drafts by JC allowed us to integrate evidence from the Siwalik record with inferences based on modern South Asian ecosystems. The temporal sequence of the three reconstructions captures the profound change in Siwalik ecosystems through the C3–C4 transition (woodland and forest to subtropical grassland) in south Asia and the accompanying decline in vertebrate biodiversity.

**Funding Sources** Smithsonian Institution, American School of Prehistoric Research, Peabody Museum, Harvard University, University of Michigan

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## Macroecology & Macroevolution

### COMPARISON OF THE THRESHOLD MODEL AND PHYLOGENETIC GENERALIZED LEAST SQUARES IN CORRELATION ANALYSES OF DISCRETE TRAITS

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The scarcity of fossil data is the greatest limitation to drawing evolutionary inferences from the fossil record. Nearly all soft tissue traits are lost and fossil remains are frequently fragmentary, meaning many continuously measured physical traits are reduced to simple discrete states. The threshold model has been an analytical tool since 1934, yet it is infrequently applied in paleontology, despite the profusion of discrete traits in fossil data. Application of the threshold model involves transforming a discrete trait into a continuous ‘liability’ value using a particular model of evolution where transitions between discrete states occur by crossing a ‘threshold’ of the continuous liability. Continuous liabilities are then tested

for correlation with either another continuous liability or to a measured continuous trait.

We tested the efficacy of the threshold model compared to phylogenetic generalized least squares regression (PGLS) when identifying correlation between discrete and continuous traits. Sixty-three hundred timescaled trees were simulated containing between 25 and 1000 tips (150 at each size). Each tree was rescaled using Pagel's delta to replicate the effects of variable evolutionary rates. Continuous and discrete traits with known correlation values were then generated using both the constant-rate and variable-rate simulated trees. Threshold and PGLS model correlation analyses were performed using *threshBayes* in the R package *phytools*.

In constant-rate trees with < 350 tips and variable-rate trees with < 200 tips, the threshold model generated fewer total errors than PGLS, but produced relatively more Type 1 errors. Both methods underestimate the strength of correlation, especially as correlation value increases, but the threshold model consistently predicted correlation values closer to actual values whereas PGLS more severely underestimates strong correlations. The threshold model produced significantly more errors in variable-rate trees than in constant-rate trees, but its accuracy was not significantly correlated with the magnitude of rate acceleration.

Despite this model's vulnerability to distortion by variable evolutionary rates, it remains more effective than PGLS in trees with a small number of tips such as those often used in vertebrate paleontology. We recommend application of the threshold model as an alternative to PGLS due to its demonstrated increased sensitivity to correlations between discrete and continuous traits.

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## Avialan Evolution & Biology

### 40 NEW SPECIMENS OF *ICHTHYORNIS* PROVIDE UNPRECEDENTED INSIGHT INTO THE POSTCRANIAL MORPHOLOGY OF CROWNWARD STEM GROUP BIRDS

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*Ichthyornis* has long been recognized as one of the crownward-most non-neornithine avialans, and as such its postcranial morphology may be more representative of the ancestral crown bird skeleton than that of any other known Mesozoic taxon. However, since the initial descriptions of partial *Ichthyornis* skeletons in the 19<sup>th</sup> century, little significant new postcranial material has been brought to light.

Here, we present new information on the postcranial morphology of *Ichthyornis* based on 40 previously undescribed specimens, providing the most detailed morphological assessment of *Ichthyornis* to date. The new material includes four partially complete skeletons and multiple isolated elements preserved in exceptional condition, allowing inferences into their three-dimensional morphology and preserving clear muscle attachments not previously described for Mesozoic euornithes. Among the elements that were previously unknown or poorly represented for *Ichthyornis*, the new specimens preserve an almost-complete axial series, as well as a hypocleideum-bearing furcula, radial carpal bones, and fibulae. Three specimens include sterna, preserving for the first time the caudal portion of the sternum and representing one of the first-known nearly complete three-dimensional sterna from a Mesozoic avialan. The new specimens include the first complete *Ichthyornis* tarsometatarsus, including a rudimentary hypotarsus that was previously unknown. Several pedal phalanges are preserved, revealing a remarkably enlarged pes presumably related to foot-propelled swimming. Although diagnosable as *Ichthyornis*, the new specimens exhibit a substantial degree of morphological variation. Notably, the four preserved synsacra vary in the number of ankylosed vertebrae and may plausibly represent different ontogenetic stages. Phylogenetic analyses incorporating our new data and employing two distinct morphological datasets recover *Ichthyornis* stemward of Hesperornithes and *Iaceornis marshi*, in line with recent hypotheses regarding the topology of the crownward-most portion of the avian stem group. These new data from the postcranial skeleton of *Ichthyornis* will improve our understanding of morphological evolution among the crownward-most non-neornithine avialans, immediately preceding the origin of crown group birds.

**Funding Sources** This research was funded by UKRI Future Leaders Fellowship MR/S032177/1, Royal Society Research Grant RGS/R2/192390, and the Palaeontographical Society Richard Owen Fund.

## Paleohistology & Paleopathology

### EVIDENCE OF INTRASPECIFIC FACE-BITING IN GORGONOPSIA (SYNAPSIDA, THERAPSIDA)?

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Despite the extensive fossil record of paleopathologies in vertebrates and its relevance for palaeobiological reconstructions, certified healed bite marks have never been reported in non-mammalian therapsids. We here report the occurrence of a tooth embedded in the snout of a middle Permian gorgonopsian for the first time. The bone around the tooth shows signs of healing (presence of a callus) that demonstrates the bite did not happen post-mortem. Though attempted predation cannot be ruled out, intraspecific face-biting (or head-biting) would better account for the position of the tooth, its size and morphology, and the fact that the attack was not lethal (an expected outcome of intraspecific agonistic behavior). The practice of social biting and the use of saber-like canine for social signaling have long been hypothesized in non-mammalian therapsids, but evidence was lacking. This fossil thus fills an important gap in our knowledge of the onset of this social behavior in the lineage that eventually gave birth to mammals.

**Funding Sources** DST-NRF Centre of Excellence in Palaeosciences

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## Education & Outreach

### REBELS, SCHOLARS, EXPLORERS: WOMEN IN VERTEBRATE PALEONTOLOGY

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In our book project (*Rebels, Scholars, Explorers: Women in Vertebrate Paleontology*), we celebrate the 200+ year history of women vertebrate paleontologists (VPs) around the world including researchers, educators, curators, preparators, artists, and collection managers. We examine women in VP chronologically, providing profiles of major

contributors to the field against a historical backdrop of political, social, and cultural change. Women have worked from the poles to the tropics and made amazing discoveries such as the earliest fish mothers, feathered dinosaurs, the origin of the tetrapod limbs, and earliest mammals, as well as led new subdisciplines such as paleoneurology and taphonomy.

We report anonymized data (nationality, research topic, and employment) for more than 1,200 women in VP (amateurs and professionals) in four time periods (18<sup>th</sup>–19<sup>th</sup> century, late 19<sup>th</sup>–early 20<sup>th</sup> century, mid 20<sup>th</sup> century and late 20<sup>th</sup> century–present). We also analyzed, with permission, records published or provided by SVP in terms of membership (awards and leadership) and scholarship (publications, meeting presentations, and grant success). Comparison of our dataset with those published by other societies and meetings (e.g. CAVEPS, EAVP, NAPC, PA, PS, and SVPCA) revealed similar significant gender gaps in most instances. Although initially not represented in leadership positions in SVP, from 2006–2010 women achieved their highest representation to date, comprising nearly 50% of the Executive Committee. Although SVP female student awardees have held steady at 34% since 2007, in its 80-year history, women have received just 16% of senior awards. Women encompassed only 10% of the membership until 1964, increasing to nearly 25% in 1975 and expanding to 36% in 2017. Women making presentations (talks, posters) at SVP annual meetings has increased from less than 10% from 1940–1971 to 29% in 2017. Women first-authored only 7% of JVP papers from 1981–1985, increasing to 26–32% from 2010–2017. The reasons for the underrepresentation of women, challenges such as racial and gender equality, ageism, mentoring difficulties, family issues and sexual harassment, were revealed through historical research, videotaped, and written interviews with selected VPs. Finally, we identified successful strategies and provide recommendations to ensure diversity and inclusiveness for paleontology and science in the future.

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## Paleohistology & Paleopathology

### BONE HISTOLOGY AND LIFE HISTORY OF FOSSILISED ANGULATE TORTOISES (TESTUDINES: TESTUDINIDAE) FROM SOUTH AFRICA

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The growth dynamics and lifestyle habits of fossilized tortoise remains are poorly understood. The current study examines the bone microstructure of both modern and fossil tortoises, including *Chersina angulata*, in order to track variability in histology and growth among animals recovered from late Miocene–early Pliocene to Pleistocene deposits as compared to modern forms. The study focused on analysis of the tibia because it retains the best track record of growth. The cross-sections of all the bones revealed highly vascularized, uninterrupted, fibrolamellar bone tissue in the perimedullary regions, suggesting that early growth was relatively fast. However, later in ontogeny, growth was slow and even ceased periodically as indicated by slowly formed parallel-fibered bone tissue and several growth marks in the outer cortex. Because the environment is thought to have been mostly cooler and drier with seasonal fluctuations during the late Miocene–early Pliocene, it is possible that *Chersina* was sensitive to such environmental fluctuations. Some intra-skeletal histovariability was noted, where the number and prominence of growth rings vary among different skeletal elements, and the spacing between growth marks corroborates the earlier findings, that *Chersina* might attain sexual maturity much before than previously thought. In addition, limb bone cross-sectional geometry revealed a relatively thick bone wall and supports earlier proposals that the species was fossorial in behaviour. Based on the comparisons with modern angulate tortoises, it appears that fossilised tortoises recovered from the late Miocene-early Pliocene had slower growth rates, suggesting less optimal environmental conditions for growth prevailed at the time.

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## Holocene & Pleistocene Mammalian Faunas

### NEW MID TO LATE PLEISTOCENE FAUNA AND LITHICS FROM THE MIDDLE ATBARA, SUDAN

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Fieldwork in eastern Sudan since 2018 has resulted in the recovery of a diverse vertebrate fauna from the middle stretches of the Atbara River, the last major tributary of the Nile before it reaches the Mediterranean. Previous work had characterized the geology and identified fossil and Paleolithic remains, but a detailed understanding of the fauna and geochronology remained lacking. New high-density OSL and <sup>14</sup>C dating indicate a chronology spanning ~200 to ~15 ka. One new site appears to be ~450 ka in age, which could make it the oldest dated vertebrate fossil site from the entire Cenozoic of Sudan. The new fossil collection comprises over 500 specimens representing ~30 species. These are mostly extant taxa, providing an opportunity to examine sub-specific (morphocline) variations between North African and East African populations and to reconcile the fossil record with extant molecular phylogeography. Extinct forms include *Palaeoloxodon* (“*Elephas*”) *jolensis*, *Kolpochoerus majus*, *Syncerus antiquus*, and a hipparionine equid. Hominins are represented by robust postcranial remains likely attributable to *Homo sapiens*. Excavation of a new Paleolithic site dated to ~150 ka reveals the late persistence of Acheulean technology in eastern Sudan at a time when it had been replaced by the Middle Stone Age in many other parts of the continent. Paleosol carbonates indicate diverse grassland-woodland habitats, and sedimentary analyses indicate a complex fluvial history influenced by Pleistocene climate and regional tectonics. The Middle Atbara project is opening up a new regional window onto African Pleistocene biogeographic regionalization and the emergence of modern African ecosystems.

**Funding Sources** National Geographic Explorer's Grant to F.B.

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## Biomechanics & Functional Morphology

### A NEW APPROACH TO MUSCULOSKELETAL MODELLING OF LIMB PERFORMANCE AND VERSATILITY IN EXTANT AND EXTINCT VERTEBRATES: A CASE STUDY OF THE SPRAWLING-TO-ERECT POSTURAL TRANSITION

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The application of musculoskeletal modelling to the study of vertebrate anatomy and function is gaining popularity for investigating large-scale macroevolutionary questions. Studies applying this approach to the appendicular skeleton typically quantify moment arms or maximal muscle moments to estimate leverage at a given limb joint (e.g., hip). However, such analyses fail to capture how multiple joints act in concert simultaneously, or the impact of muscle biarticularity, co-contraction and redundancy, thus obscuring inferences of whole-limb function and performance. Here we introduce a new modelling approach for analyzing vertebrate limb function that explicitly accounts for these issues and apply it to the sprawling-to-erect postural transition, a key event in amniote locomotor evolution. For a given limb pose, our method computes the totality of results produced by all potential combinations of limb muscle activity, using a rapid optimization procedure (~5 minutes per pose). This circumscribes the maximum magnitude of force able to be produced at a limb endpoint (foot) in a given direction, for all possible directions, directly relating whole-limb anatomy to function. We used our method to explore how hindlimb performance and functional versatility co-vary with posture in several extant representative species that span the sprawling (e.g., lizard) to erect (e.g., opossum) continuum. High-fidelity musculoskeletal models of each species were put into a set of standardized poses that capture variation in limb adduction (sprawled-to-erect) and extension (crouched-to-upright). From our simulation results, we computed metrics of limb performance (i.e., capacity to produce large forces) and versatility (i.e., ability to produce useful force over a range of directions and postures). Performance and versatility showed strong variance across the range of postures tested for each species, highlighting a posture-mediated tradeoff between different aspects of limb function. Importantly, metrics of

overall performance and versatility were found to be maximal or near-maximal in the *in vivo* postures used by each species during locomotion. Not only do these results signal a new way of reconstructing whole-limb posture and function in extinct tetrapod vertebrates, but they also reveal novel insight into functional tradeoffs that would need to have been accommodated during evolutionary postural transitions.

**Funding Sources** Harvard University and The William F. Milton Fund (to S. Pierce).

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## Colbert Poster Prize

### THE LATEST RECORDS OF *MELISSIODON DOMINANS* FROM THE EARLY MIOCENE OF MOKRÁ-QUARRY (MORAVIA, CZECH REPUBLIC)—PRELIMINARY RESULTS

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The genus *Melissiodon*, known from the early Oligocene to the early Miocene of Europe, is a rare fossil cricetid whose remains have only been recovered from a few European localities. Currently, two species are recognized from the early Miocene: *Melissiodon schlosseri*, known from a few teeth from MN2 localities of Central Europe; and *Melissiodon dominans*, reported from several European localities from the early Miocene. In the few localities where *Melissiodon* remains are found, its remains are usually scarce as well. Four fissures from Mokrý-Quarry (i.e., 1/2001 and 2/2003 from the Western Quarry and 3/2005 from the Central one) are among the best documented early Miocene (MN4) sites from which *Melissiodon dominans* remains have been recovered. Overall, these fissures have yielded more than 35 teeth, including fragmented mandibles, 26 of which were recovered from MWQ2/2003. Some of the latest early Miocene *Melissiodon dominans* specimens, such as those from Rembach, Fortshart (both MN4 German localities) and Vieux-Collonges (MN4, France), are smaller in size than the type population of the genus (Wintershof-West, MN3), which led to the idea that there was a trend

towards decreasing body size for this species in the final stages before its extinction. However, the remains from all of the Mokr-Quarry fissures fall within the size range of *M. dominans* from the type locality, and are larger than those from Rembach and Fortshart. In addition to size, there are some clear morphological differences between *Melissiodon dominans* from Mokr-Quarry and the other MN4 localities, such as a posterior spur of the lingual anterocone on M1, a well-marked anterocone on M2 and the presence of a labial anteroconid on m1. Some of these morphological characters are shared with other *Melissiodon dominans* populations from MN4 Czech sites. The preliminary results presented here suggest the existence of different morphotypes of the species right before its extinction at the end of the early Miocene.

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## Late Cenozoic Mammalian Evolution and Ecology

### **ALIVERIA SP. NOV. AMONG OTHER SCIURID REMAINS (MAMMALIA, RODENTIA) FROM THE EARLY MIOCENE OF MOKR-QUARRY (MORAVIA, CZECH REPUBLIC) AND ITS LOCOMOTOR ADAPTATIONS**

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Mokr-Quarry is an open-cast limestone mine located on the Mokr Plateau, 12 km ENE of Brno, Czech Republic. The micromammal assemblage comes from several karst fissures from the Western Quarry (1/2001 Turtle Joint, 2/2003 Reptile Joint and 4/2018), and from the Central Quarry (3/2005). Several sciurid remains (dentognathic and postcranial) have been recovered from the early Miocene of Mokr-Quarry sites: *Palaeosciurus*, belonging to the subfamily Sciurinae (ground and tree squirrels); and *Miopetaurista*, *Blackia* and *Aliveria* of the subfamily Pteromyinae (flying squirrels). Sciuridae found

in the different fissures range from one (MWQ4/2018) to four different genera (MCQ3/2005). *Aliveria* nov. sp., has been identified in all four fissures, being especially abundant in MCQ3/2005. The postcranial remains consist of several isolated calcanei and astragali. However, the calcanei attributed to cf. *Palaeosciurus* show clear morphological features belonging to ground squirrels (i.e., cruciform-shaped and a short and round sustentacular process). The rest of the calcanei and astragali have been identified as Sciuridae gen. et spec. indet 1 and 2. The former one shows clearly different characters from ground squirrels (i.e., the more distal sustentacular process and the slightly curved calcaneal tuber); however, it does not show clear diagnostic elements of Sciurinae or Pteromyinae, making it difficult to assign to tree or flying squirrels. The latter, although sciurid-like in morphology, shows the peroneal process located more anteriorly than the sustentacular facet. Preliminary results of a PCA analysis show arboreal behaviour affinities for Sciuridae gen. et spec. 1, and more generalist terrestrial conduct for Sciuridae gen. et spec. 2. In addition, the results of the calcanei assigned to cf. *Palaeosciurus* support a terrestrial behaviour like other extant sciurids. The presence of both ground and/or tree squirrels in the different fissures is in concordance with an open landscape with patches of woodland previously proposed for Mokr-Quarry sites.

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## Paleohistology & Paleopathology

### **OSTEOHISTOLOGY OF SOUTH AFRICAN SAUROPODIFORMS PROVIDES INFORMATION ABOUT THE TRANSITION TO SAUROPODAN GROWTH STRATEGIES**

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Sauropodomorph fossils from South Africa's Elliot Formation provide critical information about the anatomical and locomotory transitions within the clade. However, little is known about the growth strategies of early branching South African sauropodiforms, exemplified by *Sefapanosaurus* and *Aardonyx*. Here we present results of an osteohistological study of multi-element, multi-specimen samples of these genera, which are key to examining the transitional growth from sauropodomorphs to eusauropods. Both genera have highly vascularized parallel-fibered bone with mostly laminar but also plexiform and reticular arrangements. Fibrolamellar bone is found in patches to varying degrees depending on the element. *Aardonyx* contains more longitudinally oriented vascular canals. Numerous Lines of Arrested Growth (LAGs) are present, and are fairly regularly spaced throughout the cortex, indicating annual interruptions in growth. The absence of any decrease in spacing between the LAGs towards the outer cortex indicates that the individuals were subadults, actively growing at the time of death. These growth patterns differ from those of later-branching eusauropods, which exhibit either sustained growth during early to mid-ontogeny (lacking LAGs) or sporadic, widely-spaced annuli. Although the innermost LAGs have been destroyed by secondary remodeling, the inner and mid-cortex of *Aardonyx* and *Sefapanosaurus* elements reveals the presence of LAGs even from mid-ontogeny. This suggests a relatively slower growth rate compared to the closely related Argentinian *Mussaurus*, which only exhibits growth marks during late ontogeny or other basal sauropodomorphs such as the Argentinian *Adeopapposaurus*, *Leyesaurus*, *Colaradisaurus* or *Riojasaurus*, which exhibit widely spaced growth marks during early and mid-ontogeny, indicating greater tissue deposition during the favourable growing season. The growth patterns are most similar to some specimens of the European plateosaurid *Plateosaurus* and South African massospondylid *Massospondylus* in exhibiting relatively closely spaced growth marks from mid-ontogeny. However, these taxa lack the extreme developmental plasticity seen in *Plateosaurus* and *Massospondylus*, which also display periods of rapid bone expansion. Early branching taxa were capable of developmental plasticity, but this was lost in the *Sefapanosaurus-Aardonyx* clade, and may signify a gradual decrease in erratic growth to the more sustained growth seen in the more derived sauropods.

**Funding Sources** National Research Foundation, Centre of Excellence in Palaeosciences, and the Palaeontological Scientific Trust

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## Stem Tetrapod, Squamate, & Amphibian Diversity & Biology

### A NEW RHINEURID (SQUAMATA: AMPHISBAENIA) FROM THE OLIGOCENE (WHITNEYAN) BRULE FORMATION OF NORTH DAKOTA

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Our current knowledge of Eocene and Oligocene rhineurids results mostly from chance discovery of surface collected crania and/or mandibles. Given their small size, it is unsurprising that most of these taxa are known from either one or only a few specimens, and it is likely that the full diversity and paleogeographic distribution of this clade remains undersampled. Ongoing screen washing of rocks from throughout the Brule Formation at the Fitterer Ranch locality in southwestern North Dakota has produced hundreds of squamate fossils. Among those specimens rhineurid fossils are common, despite the fact that amphisbaenians are unreported from the Northern Great Plains region during the Oligocene. Although these disarticulated specimens vary in size, likely owing to ontogeny, tooth counts and morphologies are consistent between all specimens, suggesting the presence of a single taxon throughout the sampled range of the Brule Formation at Fitterer Ranch. The dentaries (7 teeth) and maxillae (6 teeth with a diastema between positions 3 and 4) are morphologically consistent with *Rhineura* spp.; however, the premaxillae (1 tooth) do not conform with any described species of rhineurid. The anterior margin of the premaxilla is slightly swollen and broadly rounded in lateral view ('V-shaped' in *Rhineura*) and anterior to the alveolar plate the ventral margin is deeply dorsally concave (flattened in *Rhineura*). The ventral rostral foramina are situated anterodorsal to the alveolar plate, posterior to the constriction between the external nares (anterior to the constriction in all other rhineurids). The narial process is elongate, mediolaterally narrow, and is exposed on the dorsal surface of the cranium along its entire length, with articulation facets on the ventral surface for contact with the nasals. This unique combination of features indicates that the Fitterer rhineurid represents a new taxon, a conclusion supported by phylogenetic analysis. This work further supports the

concept that basing studies of the diversity and paleogeographic distribution of small-bodied vertebrate taxa on data derived largely from chance discovery of surface collected specimens is problematic. Increasing the use of screen washing to recover microvertebrate fossils, even in rocks that are highly fossiliferous and generally considered well-sampled by surface collecting, is key to improving both our knowledge of these taxa and the accuracy of broader studies of past faunas and environments.

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### **Dinosaur Systematics, Diversity, & Biology**

#### **DINOSAURS AND INDIANS: FOSSIL RESOURCE DISPOSSESSION OF SIOUX LANDS, 1846-1875**

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Since the middle of the nineteenth century, vertebrate paleontological resources have been yet another natural resource dispossessed from the indigenous populations of the Great Plains. Geographic locations in the North American continental interior, including many Indian reservations, have been known to yield fossiliferous stratigraphic sequences. The founding fathers of American paleontology exploited the abundance of vertebrate fossils located in Indian country so that their respective careers, museums, and universities could progress. Such dispossession of vertebrate fossils from Native American treaty land has continued to the present day. In order to understand the present situation of fossil resource management practices on Native American reservations, we must study the past history of interaction between early American paleontologists and the various tribes.

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### **Quantitative Paleontological Methods**

#### **AN AUTOMATED APPROACH TO STUDYING THE EVOLUTION OF THE PARACONID CUSP IN A COMPREHENSIVE SAMPLE OF FOSSIL AND EXTANT EUARCHONTA**

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Mammalian tooth morphology must balance the functional demands of efficient food breakdown and structural integrity while constrained by evolutionary history. A nuanced understanding of the interplay between function and constraint relies on detailing how specific regions of the tooth vary across a phylogeny. Dental morphology has historically been quantified through categorical ranking (presence/absence) of traits (cusps) or, more recently, through the topography of whole teeth. However, these approaches lack consideration of continuous variation within specific regions. In this study, we aim to better trace the evolutionary patterns of specific dental features using the hecate algorithm which automatically identifies a user-designated number of corresponding segments of the occlusal surface based on local shape similarity. Hecate extracted 10 segments across a sample of 500 surfaces of second mandibular molars of 104 extant and fossil species within primates and euarchontan outgroups. We calculated Dirichlet Normal Energy (DNE) as a metric of the curvature of the mesial-most segment, which we validated against traditional discrete characterizations where intermediate to high DNE is associated with the presence of a paraconid. Then, we conducted a maximum-likelihood ancestral state reconstruction (ASR) of the DNE of this segment.

The most recent common ancestor (MRCA) of euarchonta is reconstructed with intermediate DNE. The DNE at the MRCA of primates is lower than that of the euarchonta MRCA, indicative of a reduced or absent paraconid at this node. The MRCAs of crown anthropoids and crown strepsirrhines are each reconstructed with intermediate DNE, indicating that lineages leading to catarrhines, platyrrhines, lorisiforms and lemuriforms each independently lost paraconids, and within lemurids and platyrrhines some folivorous taxa subsequently evolved morphology with high DNE along the mesial edge of the second molar.

By assessing cusp morphology as continuous regional curvature, we were able to study paraconid evolution without subjective categorization. Our results suggest high curvature within the mesial region of the second



molar has evolved multiple times within the euarchonta (in scandentia, dermoptera, some plesiadapiform taxa, some early anthropoids, and tarsiers), which supports the notion that paraconid cusp morphology experiences strong selection as a consequence of functional demands in spite of phylogenetic constraint.

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## Marine Mammals

### TACKLING THE MYSTICETE MYSTERY: COMBINING DISPARATE MATRICES TO EXAMINE THE EVOLUTION OF FEEDING MODES IN EARLY BALEEN WHALES

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The timing of the evolution of baleen in mysticetes remains unresolved, despite an abundance of early mysticete fossils. The preservation of baleen in the fossil record is rare, and the basal-most mysticetes possess teeth, making inference of baleen among stem mysticetes difficult. Recent studies have suggested that tooth loss and the evolution of baleen are not necessarily correlated events, and a variety of disparate feeding modes have been proposed for stem mysticetes, including: interdental filtration, suction feeding, and baleen assisted filter feeding. The description of many new taxa in rapid succession has served to muddy the waters regarding the relationships among the stemward mysticetes, in part because of the use of several different matrices which contain different taxa and codings for many characters. The combination of these matrices into a single matrix serves as an ideal starting point for assessing the phylogenetic relationships of newly published basal mysticetes. To that end, the most recently published versions of two prominent fossil mysticete data matrices were combined. The first matrix contains 106 taxa and 275 characters, while the second contains 87 taxa and 363 characters. Crown Mysticeti were coded as a limited set of operational taxonomic units, as an abundance of crown taxa were not likely to be informative of the phylogenetic relationships of stem taxa. Cetotheriids remain separate taxa as their relationships to *Caperea* are still an area of active interest. Duplicate characters are condensed.

Characters unique to one matrix are retained, and taxa exclusive to just one matrix were coded for the other matrix's characters as thoroughly as allowed by their published descriptions. To address a lack of overlap of preserved material in basal mysticetes, new characters were added to the combined matrix to improve resolution within and between clades. Phylogenetic analysis of the resulting matrix was performed in PAUP. A heuristic search with random stepwise addition over 10,000 replicates was performed. Initial results suggest a monophyletic Cetotheriidae exclusive of *Caperea*, with *Caperea* + *Miocaperea* as sister to Balaenidae. A monophyletic Balaenopteroidea + monophyletic Cetotheriidae group is recovered as sister to the *Caperea* + *Miocaperea* + Balaenidae clade. The Eomysticetidae are retained as monophyletic and basal to Crown Mysticeti. *Aetiocetus* is recovered as paraphyletic, while Aetiocetidae is retained as monophyletic.

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## Education & Outreach

### CHASING THEROPODS ACROSS AN EARLY JURASSIC SAND SEA: OPPORTUNITIES FOR YOUNG CITIZEN SCIENTISTS TO HELP DOCUMENT, INTERPRET, AND MANAGE AN ANCIENT TRACKSITE IN THE NAVAJO SANDSTONE

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Southeastern Utah contains a myriad of unique paleontological resources within its spectacular geology. Newly discovered dinosaur footprints add to an already impressive array of ichnological sites known from the area. Discovered in 2015, the Mail Station Dinosaur Tracksite (MSDT) has been managed primarily for educational and research purposes by the Bureau of Land

Management. The MSDT is one of largest and best-preserved Lower Jurassic dinosaur tracksites in the western United States. Numerous tracks and trackways (*Eubrontes*) of large theropods at this Navajo Sandstone locality provide an excellent outdoor classroom for teaching scientific methods, resource management, and site stewardship. Over the course of three years, middle-school students were involved in STEM-based "Paleocamps," allowing them to become active researchers at the tracksite. These citizen scientists are provided instruction and tracking kits, so they can engage in actual dinosaur footprint discovery, documentation, and interpretation. Students learn traditional ichnological measuring and mapping techniques, as well as state-of-the-art photogrammetric documentation. Because the MSDT occurs in an active arroyo, the tracks are seasonally buried by sediments, creating a different experience for each year's class of students to do both paleoichnological and neoichnological studies. While uncovering footprints, students use their observational skills and collect data to make calculations and interpretations about the dinosaurs, as well as discuss how the site should be managed and protected. This information has been incorporated along with the scientific data of researchers to understand the significance of this tracksite. Currently, approximately 100 tracks and 24 trackways have been documented. Trackways with highly variable orientations indicate multiple track-making events by numerous theropods crossing a small playa in the Early Jurassic. At least four trackways represent animals running at speeds of up of ~49 km/hour, the fastest speed known for any Jurassic theropod.

Unique opportunities such as this "Paleocamp" allow for increased scientific literacy and a better understanding of the importance of paleontological resources and their value as parts of America's natural heritage. Hopefully, this new generation of citizen scientist will be more aware of the significance of the resources in the West and will make additional new discoveries to benefit science and the American public.

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### **Non-avian Theropod Systematics, Biology, and Evolution**

#### **A NEW DEINONYCHOSAURIAN THEROPOD FROM THE MID-CRETACEOUS (ALBIAN) MUSSENTUCHIT MEMBER OF THE CEDAR MOUNTAIN FORMATION IN DINOSAUR**

#### **NATIONAL MONUMENT, NORTHEASTERN UTAH, USA**

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The Mussentuchit Member of the Cedar Mountain Formation has produced an extremely rich and diverse terrestrial and aquatic, macro and micro vertebrate fauna. Theropod dinosaurs are represented by at least five families, of which three are large bodied forms. Smaller bodied forms are only known from teeth. Thus, the specimen reported here is the most complete small theropod from the Mussentuchit. The material is limited (posterior dorsal vertebra, rib fragments, hindlimb with astragalocalcaneum and partial pes). Salient characters include 1) camellate pneumatization of posterior dorsal vertebrae, 2) extremely high, parallel sided astragalar ascending process, 3) diminutive calcaneum fused to the astragalus, and 4) adaptations for extreme retraction and flexion in pedal Digit II. This suite of characters suggests affinities with the Troodontidae. This was a moderate sized individual, with an estimated length of 3 m, about the size of *Deinonychus*. Histology shows four preserved, widely spaced LAGs with no EFS, indicating the individual was a subadult and growing rapidly at time of death.

The Cedar Mountain Formation elsewhere in Utah contains a rich and diverse fossil record, especially of dinosaurs. However, while exposures in northeastern Utah are extensive and have been closely examined in some areas, fossil vertebrates remain rare. Our specimen is only the second reported mid-Cretaceous dinosaur from this area, the other being the brachiosaurid sauropod *Abydosaurus mcintoshi*. Both are preserved near the base of the same paleochannel complex but at different sites. The channels are characterized by heterolithic, trough cross-stratified to planar bedded clay-rich sandstones deposited in a distributive fluvial setting flowing into the southward encroaching Cretaceous seaway. The paleochannel (maximum depositional age between 100 and 104 Ma based on detrital zircons) rests on the LK2 sequence boundary. The terrestrial sequence package here is comprised of the sandstone-dominated Naturita Formation at the top and the Mussentuchit Member of the

Cedar Mountain Formation at the bottom, filling a paleovalley deeply incised into the Ruby Ranch Member of the Cedar Mountain Formation.

**Funding Sources** BYU College of Physical and Mathematical Sciences

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## Crocodylomorphs & Pterosaurs

### **IF DR. SEUSS MADE AN ANIMAL WITH A WOODWIND INSTRUMENT COMING OUT OF ITS HEAD: THE SYSTEMATICS AND PALEOECOLOGICAL SIGNIFICANCE OF THE HYPER-TUBE-SNOURED OSTEOLAEMINE CROCODYLID *EUTHECODON* FROM THE LATE CENOZOIC OF AFRICA**

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*Euthecodon* was established in 1920 for crocodylian material from the Pliocene of Egypt and has subsequently been applied to specimens of early Miocene through Pleistocene age throughout North and East Africa, with the best-known material coming from the early Miocene of Libya (*E. arambourgi*) and the Plio-Pleistocene of the Turkana Basin of Kenya and Ethiopia (*E. brumpti*). It is characterized by a long, tubular snout; indeed, derived forms have the most elongate tubular snout of any known crocodylian. The snout is also characterized by deep concavities between maxillary and dentary alveoli that are set on tubular projections, making it look as though a flute has been grafted onto the orbital region of a crocodile skull. Moreover, the snout was dorsally concave, which would have allowed the animal to keep all but its eyes and nostrils submerged. But in spite of its gharial-like snout, the occipital region and quadrate rami are anteroposteriorly short and dorsoventrally deep, more closely resembling those of extant blunt-snouted crocodylians such as the African dwarf crocodiles (*Osteolaemus*) to which, based on phylogenetic analyses, *Euthecodon* is closely related.

A review of *Euthecodon* in the East African Rift Valley System reveals several unnamed late Miocene through Pliocene species related to Pleistocene *E. brumpti*. Reports of early Miocene *Euthecodon* from the Rift Valley System are based on fragments that could be derived from gharials, and collecting locality names may have been confused. One new species is based on a 147

cm long skull—one of the longest known for any crocodyliiform. Phylogenetic analyses combining morphological and molecular data, using maximum parsimony and Bayesian inference, support a close relationship between *Euthecodon* and early to middle Miocene *Brochuchus*; these were part of an osteolaemine radiation that dominated East Africa during the early and middle Miocene, with only *Euthecodon* persisting into and beyond the late Miocene.

In the eastern branch of the African Rift Valley System, *Euthecodon* is known from the late Miocene only in the Lake Turkana Basin. It is absent from coeval deposits further north in Ethiopia (Afar region) or further south in Tanzania and Malawi. Some of these sites represent deposition in smaller rivers and lakes than at Turkana, which might have limited the size and diversity of crocodylians, but the reason for the absence of *Euthecodon* in other ancient rift lake systems is unclear.

**Funding Sources** US National Science Foundation, Leakey Foundation

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## Biomechanics & Functional Morphology

### **FUNCTIONAL PLASTICITY OF FORELIMB MUSCULATURE AND THE ORIGINS OF PARASAGITTAL POSTURE IN SYNAPSIDA**

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Extant therian mammals (marsupials and placentals) can be distinguished from other land-living quadrupeds by their derived parasagittal postures and gait. This contrasts with the sprawling postures of the earliest ancestors of mammals among the non-mammalian synapsids. This 'sprawling-to-parasagittal' postural shift was a major transition during mammalian evolution and is considered key to their ecological diversity. While the anatomical changes underpinning this transition can be traced through the fossil record, how these relate to functional changes, and the acquisition of parasagittal posture, remains poorly understood. Here, we performed three-dimensional musculoskeletal modelling of sprawling versus parasagittal extant species to better understand the biomechanical differences between limb postures. We calculated forelimb joint range of motion to determine a 3D pose space and estimated muscle moment arms across

pose space for all muscles crossing the shoulder joint. Results indicate that several muscles function differently in extant sprawlers versus parasagittal therians. Of particular interest is the m. pectoralis. The m. pectoralis acts as an anti-gravity muscle in sprawlers, depressing the humerus and resisting ground reaction forces; however, in therians this same muscle elevates the humerus, flexing it in the dorsoventral plane and thus contributing to forward propulsion. We found that irrespective of habitual posture, the m. pectoralis changes function—from depression to elevation—as the forelimb becomes more retracted in the horizontal plane. However, the m. pectoralis in parasagittal therians acts as an elevator across a wider range of joint retraction angles and has relatively greater elevation moment arms compared to sprawlers. Preliminary data comparing m. pectoralis moment arms in fossil non-mammalian synapsids shows an evolutionary increase in elevation moment arms towards the origin of mammals. We propose that although muscles such as the m. pectoralis have become specialized for new roles to support therian locomotor behaviors, pre-existing plasticity in muscle function may have facilitated postural evolution and the 'sprawled-to-parasagittal' transition.

**Funding Sources** NSF DEB-1757749 (S.E.P)

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## **Fishes Evolution & Distribution**

### **NEW RECORDS OF LATE DEVONIAN ISCHNACANTHIFORM ACANTHODIANS FROM THE CATSKILL FORMATION OF NORTH-CENTRAL PENNSYLVANIA, USA**

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Fluvial strata of the Late Devonian Catskill Formation contain diverse faunal assemblages. Recent work at Catskill Formation exposures that lie just above the marine Lock Haven Formation has revealed several new fossil sites in Tioga, Lycoming, and Bradford counties in

north-central Pennsylvania. Invertebrate taxa recovered from some of these sites include *Lingula* brachiopods and *Archanodon* bivalves. Vertebrate taxa include “placoderms” (*Bothriolepis*, *Phyllolepis*, and dinicthyid arthrodiros), sarcopterygians (lungfish, *Holoptychius*, and *Langlieria*), and paleoniscid actinopterygians. Also recovered from these Catskill Formation exposures are several isolated dentigerous jaw bones of ischnacanthiform acanthodians. Ischnacanthiforms more commonly occur in Lower–Middle Devonian marine strata at many sites globally but are less common in Upper Devonian strata; no younger taxa are known. Frasnian-age ischnacanthid taxa include those from marine deposits of North America, Europe, Spitsbergen, Russia, and Iran, while Famennian ischnacanthid taxa are represented by only two genera from marine deposits of Iran and non-marine deposits of Australia. The recently-collected upper Famennian-age Catskill Formation specimens are the first ischnacanthids identified from the Catskill Formation. These are the youngest records of ischnacanthid acanthodians in North America and are among the youngest ischnacanthids globally. All records of ischnacanthids in the Late Devonian are from localities that were in the subtropics and tropics at that time. The discovery of upper Famennian-age specimens from North America show that ischnacanthiform acanthodians occurred synchronously at similar paleolatitudes in Laurussia and Gondwana for > 20 million years spanning Frasnian to upper Famennian time.

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## **Taphonomy, Paleoenvironments, & Stratigraphy**

### **POTENTIAL PRESERVATION OF KERATINOUS HORN TISSUE ASSOCIATED WITH THE FRILL ORNAMENTATION OF AN IMMATURE *CENTROSAURUS* (ORNITHISCHIA, CERATOPSIDAE)**

Brown, Caleb M.

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Keratinized epidermal structures in dinosaurs are becoming increasingly recognized. Ceratopsidae possess several cranial features likely to have had robust keratinized tissues, rhamphothecae (rostral & prementary) and keratinous sheaths (nasal, postorbital, frill, and jugal horns). Despite their abundant fossil record, and high potential for keratinous tissue, direct evidence of preservation is rare to absent. Preparation of a small

*Centrosaurus* parietal (Dinosaur Park Fm., Alberta) revealed several flat, semi-circular to crescentic structures associated with, but not articulated to, the parietal. Shape and association led to an initial identification as unfused frill epiossifications (i.e., epiparietals), however they are entirely ironstone. The eight structures preserve convex margins with rounded, beveled edge, and flat/concave 'basal' margin often showing a concave facet. One specimen shows a bi-lobed facet similar to the epiossification across the parietosquamosal suture. They vary in size: basal width=30–80 mm, basal-apical height=21–41 mm, and thickness=6–11 mm. The surface texture is distinctive, bearing parallel ridges and grooves (~1 mm wide) forming a distinctive ropey appearance along the periphery of the rounded margins. The parietal preserves the midline, posterior, and right lateral bar, missing the left side. P1 loci (medial-most horns) are preserved on both left and right sides, with a gap in the right P2 (and P3?) area, followed by four right lateral loci (P3–P6 or P4–P7) to the squamosal suture, with all loci thin, subtle scallops. The parietal is 391 mm long (sagittal) and 317 mm wide (right half width), one of the smallest known for the taxon. Size, shape, ornamentation, and mottled texture are consistent with an early subadult stage. Centrosaurine parietals of similar age do not have epiossifications, with these appearing in larger/older specimens, first associated then fused. The thickness and bevel of the periphery of the parietal correlates well with the thickness and concave facets on the structures. These structures are tentatively identified as fossils preserving the shape of keratinous sheaths of the parietal horns. If this interpretation is correct, it indicates that keratinous horns may precede the development of the epiossification at parietal loci. Further, the size of these keratinous horns is larger than expected for a specimen at this ontogenetic stage. Alternate identifications of these structures are welcome.

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#### Preparators'

#### ON THE RISK OF USING CAST REPLICAS AS EVIDENCE OF THE FOSSIL RECORD

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Paleontologists have made cast duplicates of fossils since the early days of the science, and they serve a number of useful purposes in research and education. As exhibition and teaching models, casts may stand in as proxies for fragile fossils, enabling handling and display in environments where specimens could be damaged or destroyed. As research tools, they can supplement direct observation of fossil material in the same manner as photographs, CT data, and illustrations. Often referred to as "research casts" there exist methods of producing cast replicas made from techniques and materials that minimize data loss or distortion. However, in recent debates over scientific publication of privately held, destructively sampled, or lost specimens, conflicting arguments have been made in the literature and through press releases, social media posts, and court filings related to the fidelity and accuracy of cast specimens. Some have gone so far as to suggest that casts can replace fossils as scientific objects.

A case study of composite casts of a new species of the Late Cretaceous azhdarchid pterosaur *Quetzalcoatlus* examines previous arguments that casts are unreliable or misleading in the absence of the original fossil material. In this instance, a composite vertebra was created by skillfully joining casts of the anterior half of a fifth cervical vertebra with the posterior half of a sixth cervical vertebra in order to approximate a complete fifth cervical for (presumably) exhibition purposes. Discovered in a drawer without labels or other identifying information, this mystery element was not identifiable as a composite except by direct comparison to the real fossils elsewhere in collections. The amount of sculpted reconstruction present on the hybrid cast did not exceed the amount of reconstruction present on natural bones in the collection, and thus did not immediately draw attention to its composite nature. The fabrication was only established by careful comparative research with original specimens, supporting prior studies that demonstrate the fraught status of casts as unreliable scientific vouchers, and underscoring the vital importance of detailed record-keeping in the laboratory and collections.

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#### Non-avian Theropod Systematics, Biology, and Evolution

#### DIMINUTIVE THEROPODS FROM APPALACHIA AND THE EARLY EVOLUTION OF THE AVIAN BRAINCASE

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The stepwise evolution of birds from theropod dinosaurs has received much attention since the first descriptions of bird-like dinosaurs from Europe. The diversity of small-bodied bird-like forms is particularly well-represented in Mesozoic biotas from China but lacking elsewhere. Unfortunately, the crushed nature of Chinese theropod fossils has precluded examination of large portions of their anatomy. Here, we use computed tomography (CT) scans to describe material of diminutive (<1 m) theropods from the Ellisdale site, a microvertebrate assemblage from the Cretaceous Atlantic coast. These include a small dentary with associated teeth and a partial braincase preserving much of the internal osseous labyrinth. Preliminary phylogenetic and morphometric tests suggests that the Ellisdale bones belong to small members of the Dromaeosauridae, a globally distributed predatory paravian clade. A few features of the dentary might also indicate an affinity to the gliding microraptoran dromaeosaurids, although further analysis will be needed to confirm this. The new material provides rare information about the internal braincase anatomy of small theropods near the base of Aves and the diversity of small-bodied dinosaurs outside Asia.

**Funding Sources** Richard Gilder Graduate School Student Fellowship (J. Napoli)  
Yale Graduate Fellowship (Alex Ruebenstahl)

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## **Taphonomy, Paleoenvironments, & Stratigraphy**

### **TAPHONOMIC ASPECTS OF VERTEBRATE FOSSIL OCCURRENCES FROM THE UPPER CRETACEOUS DEPOSITS OF THE JAMES ROSS BASIN (ANTARCTICA)**

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The James Ross Basin yields most of the Antarctic fossils, particularly from Cretaceous deposits. Here we analyze the literature to access taphonomic data of fossil vertebrates from the Snow Hill Island (SHI; late Campanian-early Maastrichtian) and López de Bertodano (LB; Maastrichtian) formations. SHI is a deltaic-estuarine depositional system, whereas LB represents a shallow sea. The specimens recovered in our survey comprise 36 plesiosaurs, 24 mosasaurs, 7 non-avian dinosaurs, 6 avians, 1 pterosaur, 28 osteichthyans, and 78 chondrichthyans. Four taphonomic classes were identified: I: associated skull elements; II: incomplete articulated postcranium; III: associated postcranial elements; IV: isolated bones. No nearly complete specimen with skull and postcranium has been recorded so far. Due to the small sample size, we performed chi-square tests (goodness-of-fit and test of independence) considering  $p < 0.25$ , and Cramer's V. The sample size effect in all analyses is moderate. LB shows 57 tetrapods, 16 osteichthyans, and 57 chondrichthyans, whereas SHI shows 17, 12, and 21, respectively. Our approach indicates that Plesiosauria and Chondrichthyes are regularly reported in the literature from 1984 to 2021, being the most representative vertebrates. Mosasaurs and plesiosaurs are represented mainly by vertebrae, pelvic and pectoral girdles, and propodials+epipodials (long bones). The reports from LB are predominantly from classes III and IV, especially the last. The SHI exhibits class II as predominant, but the small number of reports in SHI could bias it. Mosasaur specimens are markedly from class IV, while plesiosaurs represent mainly class III, followed by classes II and IV. Terrestrial tetrapods chiefly comprise Dinosauria and Aves of classes II and III, with propodials as the predominant bones. The fish record—almost entirely restricted to teeth—mostly comprises the pelagic Lamniformes chondrichthyans and Ichthyodectiformes osteichthyans. The occurrence of these two groups is dependent on the formations SHI and LB, with SHI biasing the general pattern of occurrence. Our results suggest that the disarticulation of elasmosaurids was not prolonged after sinking and could

be more related to water-sediment interactions. Mosasaurs with class IV and skull bone reports point out a distinct disarticulation pattern. The depositional system of LB enabled the preservation of more complete specimens, as well as the coastal depositional system of SHI.

**Funding Sources** Programa Antártico Brasileiro through the Conselho Nacional de Desenvolvimento Científico e Tecnológico and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior

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## Marine Mammals

### FUNCTIONAL AND ONTOGENETIC IMPLICATIONS OF STERNAL STRUCTURE IN MYSTICETE CETACEANS

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The mammalian sternum is an understudied element located at the intersection of the head, forelimb, and thorax that functions in support, protection, locomotion, and ventilation. In contrast to terrestrial mammals, mysticete sterna lack sternebrae, have no diaphragmic attachment site, and articulate with a single rib (Rib 1). Their small and variable shape has led to questions of their functional and taxonomic value. The anterior (pre-costal) mysticete sternum retains attachment sites for muscles that act indirectly on the tongue (sternohyoid, sternothyroid), on the skull (sternomastoid) and on the mandible (sternomandibularis). These muscles function primarily in feeding, which occurs in several highly specialized modes (skim, suction, lunge). This project explores the hypothesis that the variability of mysticete sterna is functional, and reflects taxonomic and ontogenetic differences in feeding style. A database of >100 mysticete sterna was assembled from museum collections, mounted museum exhibits, and the primary literature, recording sternal size, body size, and collection data as available. Relative sternal length was evaluated for each species by regression on total body length. Sternal length is accurately predicted by, but falls just short of isometry with, body length, allowing assembly of an approximate ontogenetic sequence based on size. 2D geometric morphometrics (Geomorph, R) was used to evaluate sternal shape. Balaenid sterna are shield-shaped and have a defined lateral facet for the articulation of Rib 1. Balaenopterid sterna are trefoil-shaped and have a

subtle, two-point articulation for Rib 1 posterior to the lateral wings. The relationship between sternal shape and feeding style is highly significant (Procrustes ANOVA,  $p < 0.001$ ). Sternal shape varies little with size or taxon in balaenids, but differs markedly with both factors in balaenopterids. Individuals that are small and/or from taxa with multiple feeding styles have anterior sterna dominated by origin sites for the infrahyoid muscles; larger animals and those from taxa with more dependence on lunge feeding have progressively more differentiated and exaggerated lateral sternal wings. These differences are tentatively tied to an enlarged lateral area for the origin of the sternomandibularis in animals that emphasize lunge feeding and to the transition from suction to lunge feeding at weaning. Sternum shape is a potential tool for predicting the feeding style of extinct taxa.

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## Colbert Poster Prize

### BIOMECHANICS BEYOND BONES: INFERENCES ABOUT THE SOFT TISSUE OF THE PTEROSAUR NECK

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Although several papers discuss the biomechanics of the pterosaur necks, their soft tissues have never been reconstructed. Here, we reconstruct them according to osteological correlates present in their cervical vertebrae and the Extant Phylogenetic Bracket method. We obtained micro-CT scans of the cervical series of *Anhanguera piscator* (NSM-PV 19892), *Azhdarcho lancicollis* (ZIN PH, several specimens) and *Rhamphorhynchus muensteri* (MGUH 1891.738), which have almost all vertebrae three-dimensionally preserved. We also dissected a *Caiman latirostris* individual and specimens representing 16 species of Aequorlitornithes and Inopinaves. Rough surfaces in the joints and a discreet fovea in the condyles indicate the presence of synovial cartilage between the cervical vertebrae of pterosaurs. The partial overlap of the zygapophyses in a neutral pose shows that the thickness of the intervertebral cartilage would be greater between the more caudal cervicals. The joint between the more cranial vertebrae probably had a slightly ascending angle, and caudally to the fifth vertebra there is a downward slope, until the

cervicals align with the trunk, suggesting slightly sinuous necks. The tubercles surrounded by small muscle scars and developed epiphyses, hypapophyses and neural spines support the inference of 13 muscles associated with the pterosaur neck. The well-developed tubercles and scars in the fifth vertebra indicate that the muscles responsible for cranial movement extended to the middle of the neck, supporting the hypothesis of an extremely mobile skull. The reduced neural spine in *Azhdarcho lancicollis* suggests less robust *transversospinales* muscles, indicating lower neck retraction forces than in other pterosaurs. Although absent in birds, depressions in the paraoccipitals of *Anhanguera piscator* and the slightly developed transverse processes in the caudal cervical vertebrae of the pterosaurs showed that the *m. longissimus capitis superficialis* was present, allowing a high degree of lateral mobility in the most caudal portion of the neck. Intervertebral synovial cartilage has not been incorporated in previous reconstructions of pterosaurs, which can lead to errors in inferring the neutral pose. The inclusion of articular tissues increases the length and elevate the curvature of the neck in neutral pose, besides having the potential to solve inconsistencies on the mobility of the pterosaur neck.

**Funding Sources** CAPES - finance Code 001, CNPq - processes 421412/2018-6 and 309666/2019-8

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## Holocene & Pleistocene Mammalian Faunas

### NEW DESCRIPTIONS OF *PANTHERA* REMAINS FROM ARKANSAS CAVE LOCALITIES

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Presented in this study are new descriptions of material assigned to the genus *Panthera* from two caves in Newton County, Arkansas. The first of the material are associated postcrania of a single felid found within Wind Tunnel Cave. These remains are assigned to jaguar (*Panthera onca*) based on measurements of North American fossil specimens as well as morphological characteristics. The remains are average size for an adult late Pleistocene *P. onca*. The other material comes from Chilly Bowl Cave and is primarily distal limb elements as well as tracks that may be associated. Much of the bones from this locality are fragmentary but identifiable elements mostly consist of metapodials, phalanges, and carpals. The metapodials

are incomplete but are still noticeably large. Proximal width measurements for these metapodials are generally consistent with that of the largest fossil *P. onca* while the length measurements of more complete metapodials appear to exceed lengths known for *P. onca*. Despite lying on the high end of the range, the width measurements are fairly standard for *P. onca* and are not within the range of measurements for any other large Pleistocene felids, including *Panthera atrox*, *Smilodon*, *Homotherium*, or *Miracinonyx*. For this reason, these remains are being tentatively assigned to *P. onca*.

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## Quantitative Paleontological Methods

### OH, THE MAP IS UPSIDE DOWN: IMPORTANCE OF STANDARDIZING AND COMMUNICATING MAPPING PROCEDURES FOR PALEONTOLOGY QUARRIES

Buskuskie, Thomas, McHugh, Julia

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Paleontology collections and exhibits represent a significant aspect of natural history museums. As one of the most popular attractions for many museums, collections and exhibits further the public education mission in addition to being important repositories for fossil resources and the data associated with them. Therefore, it is important that data collection and storage be as detailed and intuitive as possible. The Museums of Western Colorado Dinosaur Journey museum is an unique case that shows not only the importance of a collection for research purposes, but also how that importance can be demonstrated for the general public. Visitors are taken out for day long excavations at the Mygatt-Moore Quarry (MMQ), an overbank deposit in the Late Jurassic Brushy Basin Member of the Morrison Formation that has been excavated at for over 30 years. Visitors are shown general fieldwork techniques, including mapping of specimens. Due to the long period of excavation at the site, the mapping procedures have lacked continuity between field seasons. Also, storage and organization of the quarry maps has likewise been subject to individual idiosyncrasies. Here, we detail the process of determining past years' mapping procedures, organization and cataloguing of the produced quarry maps, and standardizing and communicating a mapping procedure for future MMQ volunteer and visitor digs.



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## Preparators<sup>1</sup>

### MOVING AN OVERSIZE COLLECTION DURING A PANDEMIC

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For historic museums like the Harvard Museum of Comparative Zoology (MCZ), certain building repairs and maintenance are expected. In January 2021, an inspection and replacement of the fire suppression sprinkler heads was expected; a failure of ceiling plaster was not, specifically the failure of a portion of plaster which fell onto oversize vertebrate fossils. Due to Harvard University's pandemic policy, assessing the scene and developing a plan to resolve the damage required communication, quick thinking, and flexible re-deployment of person-power.

In response to the pandemic policy, MCZ staff adopted a work-from-home model that transitioned to a hybrid model, where the VP collection manager worked at the museum one day per week and the curatorial assistants worked there one day per month, with no scheduled overlap. Building and room access was restricted and tracked by two university systems. All staff were required to comply with pandemic policy procedures including mask-wearing, virus testing, social distancing, and sanitation of surfaces.

Quick relay of the damage to the MCZs Director of Collections Operations (CO) and the Collections Manager (CM) of Vertebrate Paleontology (VP) allowed the two departments to formulate and execute a safe plan to evacuate the fossils. To assess the scene, the CM obtained emergency permission to enter the MCZ building, assess the condition of the room, and document the damage. The CM decided that the upcoming sprinkler maintenance and the ceiling repair validated the temporary removal of all exposed fossils to mitigate risk of further damage. Given the size of the affected fossils, the collection manager and CO staff member estimated three people may be able to complete the move in one day.

For the move, we obtained permissions for all staff, determined the equipment needed to move the fossils, and

created tags to track and inventory each specimen. The specimen removal team learned valuable lessons that improved the success of the specimen return team. First, a three-person team was not sufficient for moving the specimens in one day. Second, different equipment and methods improved the ease of moving certain fossils. We learned that a team of four people working in teams of two can complete the move in one day by increasing efficiency and reducing the workload for all. Communication and trust between the CO and VP staff allowed us to care for the fossils while preventing further damage.

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## Turtle & Marine Reptile Diversity & Biology

### A COPROLITE WITH THE FIRST 3D PRESERVED PECTORAL GIRDLE AND FORELIMB OF *KEICHOSAURUS HUI* (PACHYPLEUROSAURIA; SAUROPTERYGIA) AND ITS IMPLICATIONS ON LOCOMOTION

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The role of the forelimb in the locomotion of stem sauropterygians has been controversial, partly because specimens preserving a complete limb in 3D are rare. For example, specimens of the pachypleurosaur sauropterygian, *Keichousaurus hui*, are typically flattened on a bedding plane of mudstones or marls, with the original morphology deformed through geologic compaction, obscuring the true forelimb morphology. We describe the first, three-dimensionally preserved pectoral girdle and proximal forelimb of *Keichousaurus hui*; recovered inside a nodular coprolite from the Middle Triassic of Guizhou Province, China. We reconstructed the limb elements as 3D computer models, revealing more

clearly the anatomy of the shoulder and elbow. This allows a test of forelimb mobility in pachypleurosaurs based on undistorted bones of a single individual for the first time. For instance, the dorsal process of the scapula is notably longer than in taphonomically flattened specimens, which may facilitate easier humeral elevation during locomotion. Although a restricted elbow joint, as implied by taphonomy, could be indicative of advanced swimming specialization like in plesiosaurs, the 3D articulated elbow joint excludes this possibility. When compared with the pectoral girdle and forelimbs of Galápagos Marine Iguanas, varanids, and basal to derived sauropterygians, the elbow joint of *Keichousaurus hui* still largely retained the typical reptilian design, in which zeugopodials form a plane at an angle with the distal expansion of the humerus. When trying to reconstruct an alternative model in which the zeugopodials were aligned end-to-end, as seen in flattened specimens where the elbow joint is restricted, the zeugopodials and articular facets of the humerus did not articulate correctly. The articulation angle indicated that the forelimbs are better suited to paddling locomotion, as seen in freshwater turtles, in line with a previously proposed swimming mode for nothosaurids. Our data provides a valuable insight into the early stages of morphological change that occur across the land-sea transition in basal-most sauropterygians by allowing us to better understand the mobility of the forelimb. This also supports the idea that the unique style of underwater flight in plesiosaurs was not exhibited in basal sauropterygians. Rather, the elbow joint was more flexible, but not as flexible as what is seen in terrestrial squamates.

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## Macroecology & Macroevolution

### A DATABASE OF RODENT BODY MASS FOR THE END OLIGOCENE THROUGH PLIOCENE

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Recent investigations of the association between biodiversity and climatic, topographic, or environmental changes have focused on small mammals, particularly rodents, due to their short breeding cycles, limited ranges, and high taxonomic and ecological diversity. Over the

past fifteen years, several taxonomic and occurrence databases for mammals and rodents have been compiled to facilitate this work. This work has been complemented by analyses of categorical hypsodonty and locomotion variables. Here, we present a new database of rodent body mass, a continuous trait, which will enable further analyses of mammal paleoecology over 29 million years. We updated the records of Miomap and other databases with the primary literature to develop a compilation of all 661 valid rodent species present in the continental United States for the Arikarean through Blancan North American land mammal ages. For the 627 species for which it was possible (~95% of species), we compiled body mass proxies from the literature and directly from specimens (toothrow length, skull length, lower first molar area [m1A], and lower fourth premolar length [p4L]). We used these proxies to estimate species-level body mass means. We reanalyzed published data on the relationship between m1A or p4L and body mass to develop family-specific regressions.

We also investigated patterns of change in body mass through time in Rodentia, as well as in select clades that were abundant on the landscape or represented large proportions of late Cenozoic rodent diversity. Our results show that mean and median rodent body mass remain stable from ~30 to 1 Ma, particularly after the mid-Miocene climatic optimum (MMCO) from 18 to 14 Ma. In contrast, disparity is low prior to the MMCO and high afterwards. Increased disparity is associated with an increase in maximum body mass. At the family level, increased body mass through time is recovered for Castoridae and Mylagaulidae. Other clades, including Dipodidae, Geomyidae, Heteromyidae, and Sciuridae, do not show significant changes in body mass through time. Cricetids show an opposite pattern with smaller mean and median masses through time, particularly post-MMCO, and increasing body mass disparity through the mid and late Miocene and the Pliocene. Analyses of fossil Rodentia as a whole will enable us to assess body-size evolutionary trends through time in relation to dynamic landscape and climate, as well as changes in faunal composition, diversity and turnover.

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## Crocodylomorphs & Pterosaurs

**A REASSESSMENT OF THE CRANIAL ANATOMY OF *CAIUAJARA DOBRUSKII* (PTEROSAURIA, PTERODACTYLOIDEA, TAPEJARIDAE) BASED ON NEW SPECIMENS**

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*Caiuajara dobruskii* is a tapejarid pterosaur from the Cretaceous of the pterosaur graveyard site, at the locality of Cruzeiro do Oeste (Paraná, southern Brazil). This site is one of the unique pterosaur bonebeds known so far, which bears hundreds of mostly disarticulated but associated specimens relative to this species. *Caiuajara* was originally characterized by several cranial features, such as a ventrally deflected anterior end of the premaxilla relative to the ventral margin of the rostrum; a marked lateral depression on the maxilla ventral to the anterior portion of the nasoantorbital fenestra; a rounded ventral margin of the orbit; and an elongated groove on the anterolateral margin of the quadrate. Here we reassess the cranial anatomy of *Caiuajara dobruskii* through the comparison and description of a total of seven new specimens. The most striking feature is the slope of the anterior end of the rostrum, which is straight and sharply oriented downwards in all small specimens, and is lower and dorsally confluent with the premaxillary sagittal crest in larger individuals. In two large specimens the premaxillary sagittal crest has a thickened posterodorsal margin with a dorsal projection and an enlarged concave posterior margin of the premaxillomaxilla over the nasoantorbital fenestra. This feature is recognized in lateral view as a gently rounded oval margin, being absent in the other specimens with preserved premaxillary crest. Another specimen with the posterior portion of the skull preserved displays a thin lacrimal process of the jugal subvertically orientated, similar to that of *Tupandactylus imperator*, with a central rod extending laterally. The lacrimal is roughly triangular and highly fenestrated, with a concave ventral margin, differing from other tapejarines. The frontal is located above the highly fenestrated orbit, similar to that of *Tapejara*. The occipital condyle is well-developed and the parietal crest is extended, narrowing posteriorly in a similar condition to that of *Tupandactylus imperator*. This high variability on cranial features between different *Caiuajara* specimens may be due to diverse causes as ontogeny—as the slope in

the anterior end of the rostrum differing between small and large individuals—or sexual dimorphism—as the gently rounded oval margin of the premaxillary crest of some specimens. In any case, these new specimens shed light on the complexity and variability of the cranial morphology of *Caiuajara dobruskii*.

**Funding Sources** CNPq (#313461/2018-0), (#132765/2020-9) FAPERJ (#E-26/202.905/2018), and PPGZoo of the Museu Nacional (UFRJ).

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**Paleohistology & Paleopathology**

**REEVALUATING PURPORTED MEDULLARY BONE IN SELECT NON-AVIAN DINOSAURS**

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Unambiguous sex indicators are scarce in the fossil record of dinosaurs. Thus far, the identification of medullary bone (MB), a sex specific tissue produced by females within extant dinosaurs (modern birds), is the most promising avenue for sex discrimination in non-avian dinosaurs. Based on the finding of vascularized woven endosteal tissues, an increasing number of fossil specimens are being described as containing MB and therefore hypothesized to be gravid females. However, these reports are contentious because MB shares microstructural and chemical characteristics with some endosteal bone pathologies. Here we reassess unusual endosteal tissues reported in some theropod and ornithomimid dinosaurs based on new data from several research teams on the microstructural diversity and skeletal/phylogenetic distribution of avian medullary bone, with an eye toward discriminating these tissues from pathological tissues in the fossil record. Our resampling effort includes new ground sections from the femur of ornithomimid ZIN PH 1400/16 (a complete cortical section) and the tibia of *Dysalotosaurus lettowvorbecki* SMNS T3; we also reexamined existing sections of the tibia of *Allosaurus fragilis* UUV 5300. The ornithomimid exhibits abnormally asymmetrical expansion of the medullary cavity, a layer of reactive bone lining most of the periosteal surface, and a region of

heavy remodeling and resorption cavities within the cortical bone superficial to the endosteal tissue in question. Similarly, the *Allosaurus* tibia presents not only a radial organization of its endosteal bone tissue, which is unlike avian MB, but also exhibits a reactive periosteal bone layer that contrasts microstructurally with the underlying primary cortex; a statement already made by previous authors. In the *Dysalotosaurus* tibia, the restricted deposit of woven endosteal tissue coincides with a change in vascular orientation in the superjacent cortex, as well as two localized concentrations of Haversian tissue. In all cases considered, the unusual endosteal tissue is also restricted to a small subset of the medullary cavity, in contrast with avian MB, which typically lines the entire medullary cavity and is more evenly resorbed. Taken together with evidence of periosteal reactive bone and/or abnormal cortical remodeling localized to the region of endosteal deposition, these specimens present a set of histological features in favor of a pathological origin and inconsistent with a reproductive causation.

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## Fishes Evolution & Distribution

### FOSSILS REVEAL LONG-DISTANCE MARINE DISPERSALS AND MAJOR ENVIRONMENTAL TRANSITIONS IN THE BIOGEOGRAPHIC HISTORY OF BONYTONGUE FISHES (OSTEOGLOSSOMORPHA)

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The fossil record provides a unique window to natural history beyond the limited snapshot of the present. However, how fossils affect inference of major evolutionary patterns and processes for extant groups of organisms remains poorly understood. Bonytongue fishes (Osteoglossomorpha) represent an ideal system to investigate the impact of fossils on biogeographic reconstructions, due to a widespread modern geographic distribution and a fossil record extending back to the mid Mesozoic. More importantly, while extant bonytongues live exclusively in freshwater environments, several extinct forms are known from early Paleogene marine deposits worldwide, hinting at marine dispersal as an important ‘hidden’ mechanism behind their current

distribution. Using a newly generated set of phylogenetic hypotheses based on combined molecular and morphological data and including every extant genus and over 35 fossil taxa, we estimated ancestral geographic areas and environmental preferences under several time-stratified biogeographic models in a likelihood framework. Even with considerable uncertainty in the placement of many fossil taxa, we consistently recover some extant bonytongues, including the South American *Arapaima* and its close relative *Heterotis* from Africa, as descendants of marine ancestors that reinvaded freshwater settings multiple times independently. Removing fossil taxa from the analysis significantly alters the reconstruction of ancestral areas and ignores evidence in favor of marine dispersal as a key process in shaping the biogeography of Osteoglossomorpha, highlighting the importance of adding fossil data, when available, in this type of analysis. Overall, inclusion of the bonytongue fossil record dramatically changes the most likely scenario for the biogeographic history of this fish group, and reveals several long-distance dispersals and major environmental transitions that would not be apparent by examining living species only.

**Funding Sources** Rackham Predoctoral Fellowship, University of Michigan

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## Colbert Poster Prize

### THE ORIGIN OF PLACENTAL MAMMALS ACCORDING TO THE FOSSIL RECORD

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Recent molecular clock analyses have suggested that placental mammals originated in the mid to late Cretaceous, before the Cretaceous–Paleogene (K–Pg) mass extinction. However, there are no unequivocal fossils of placental mammals from the Cretaceous to support this. Definitive fossils of placental mammals only appear after the K–Pg boundary, at which point they rapidly radiate leading into the ‘Age of Mammals’. Here we use the Bayesian Brownian Bridge model to estimate the age of origin of placental mammals based on the fossil record. The model uses fossil diversity through time to inform a random walk from the clade’s present day diversity back to the estimated origin of the clade within a

Bayesian framework. This model works well with clades that have poor fossil records, such as the early placental mammals, and does not require a phylogeny, thereby mitigating the lingering uncertainty over the branching pattern at the root of the placental tree of life. Our results support a Cretaceous origin for placental mammals, in agreement with the molecular data, and demonstrate that the group was already present before the K–Pg mass extinction and experienced a radiation during the Paleogene. The Bayesian Brownian Bridge model can therefore help to reconcile paleontological data with molecular data when estimating the origin of clades.

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## Fishes Evolution & Distribution

### REVISITING *TRAWDENIA PLANTI*: ENDOSKELETAL DATA AND A FRESH LOOK AT ACTINOPTERYGIAN ROOTS

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The actinopterygian crown group is thought to have diverged close to the Devonian–Carboniferous boundary, but a persistent failure to find Paleozoic taxa to populate the stems of extant clades obstructs understanding the origin of modern biodiversity. Here we present new data on the endoskeletal anatomy of *Trawdenia planti* from the Early Pennsylvanian of Lancashire, UK. This species has already revealed exquisitely preserved details of the hyoid arch, pectoral, axial, and dermal skeletons via microcomputed tomography ( $\mu$ CT), coupled with a partly exposed cranial endocast. The neurocranium and gill skeleton are now revealed as similarly well preserved, and the newly-exposed morphologies demand revision of existing phylogenetic hypotheses. Unexpectedly, the *Trawdenia* braincase is reminiscent of the Devonian *Moythomasia*, but sports a paddlefish-like gill skeleton and a host of other morphological characters that beg the question: are these symplesiomorphies or might *Trawdenia* be a stem chondrosteian? In pursuit of answers, we built a dataset comprising broadly-applicable characters from the neurocranium, hyoid and gill arches, and parasphenoid. Preliminary analysis recovered a topology with an ‘ancient fish clade’ (in this instance Polypteriformes plus Chondrostei) branching from the base of the tree and Paleozoic taxa branching from the

neopterygian stem, thereby conflicting both with accepted molecular phylogenetics as well as current paleontological consensus. To mitigate the influence of convergence, we then excluded characters contingent upon determinate growth, for example regarding the persistence of fissures and fontanelles, and repeated the analysis. This approach generated intriguing results including a populated chondrosteian stem – a radical departure from alternative tree topologies that have dominated since the 1980s. We recover *Trawdenia* as a stem-actinopteran, polarizing downstream character state changes and shedding new light on the evolutionary trajectory of endoskeletal systems across Actinopteri. By employing modern  $\mu$ CT methods on excellently preserved specimens such as *Trawdenia* and applying discriminate character choice, we might be finally uncovering the deep Paleozoic roots of the major extant actinopterygian divisions.

Funding Sources NSF DEB-1541491

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## Dinosaur Systematics, Diversity, & Biology

### THE PHYLOGENETIC PLACEMENT OF TWO NEW SPECIES OF CERATOPSID DINOSAUR FROM THE CAMPANIAN WAHWEAP FORMATION ALLOW FOR NEW INSIGHT ON CERATOPSID EVOLUTION

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Two new species of centrosaurine ceratopsid dinosaurs have been recovered from the Campanian-aged Wahweap Formation of southern Utah. UMNH VP 20600 was recovered from the lower member of the Wahweap Formation and represents the oldest known ceratopsid from Utah. Stratigraphic work has placed it as older than 80.6 Ma. It shares with *Machairosteops cronusi* a single epiparietal on each side of its frill. UMNH VP 9549 was recovered from the very top of the upper member of the Wahweap Formation and has been dated to older than 77 Ma. It has a unique dorsal ridge on the perimeter of the dorsal surface of the frill that corresponds to a groove on the ventral surface. Together these two

new species extend the range of known centrosaurs from the bottom to the top of the Wahweap Formation. Their stratigraphic positions make these species useful reference taxa when seeking to understand evolutionary development amongst ceratopsids. The morphological traits of both new species have been analyzed and used to perform a phylogenetic analysis. Using over 620 morphological characters scored across 102 taxa, we were able to test the relationships of a large number of ceratopsian families in a unique, comprehensive analysis. UMNH VP 20600 is recovered as the sister taxon to *Machairoceratops cronusi*, which form a clade with the basal centrosaur *Diabloceratops eatoni* of the middle Wahweap Formation. UMNH VP 9549 is recovered in a clade with other centrosaurs with round frills including: *Avaceratops lammersi* from the Judith River Formation in Montana, *Nasutoceratops titusi* from the upper Kaiparowits Formation of Grand Staircase-Escalante National Monument in southern Utah. This novel analysis provides a novel context of the placement of basal centrosaurs within Ceratopsia and reveals patterns of the radiation of centrosaurs across Laramidia.

**Funding Sources** University of Utah Undergraduate Research Opportunities Program

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### Colbert Poster Prize

#### ASSESSING THE DISTRIBUTION OF CRANIAL KINESIS AMONG MOSASAUROIDS (SQUAMATA)

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For much of the history of mosasaur paleontology, researchers have concluded that mosasaurs possessed at least partially kinetic skulls similar to living squamates. However, numerous studies from the past two decades have reanalyzed key elements and articulations critical to cranial kinesis and revealed that numerous mosasaurs instead possessed rigid and akinetic skulls. This akinesis is considered an adaptation to feeding in an aqueous environment and is shared by many of the more derived mosasauroids. This study investigates the distribution of various cranial kinesis regimes across mosasauroid phylogeny. The specific types of cranial kinesis that are

broadly evaluated in this study through literature review and direct observation of specimens include: mesokinesis, metakinesis, and streptostyly. An additional facet of this study seeks to evaluate the range of possible motion in the intramandibular joint of three well sampled mosasaur genera from the Niobrara Chalks of Kansas: *Tylosaurus*, *Clidastes*, and *Platecarpus*. This was accomplished by noting the shape of the splenial and angular articulations and manual manipulation of disarticulated anterior and posterior mandibular units for the given taxa. When data regarding the presence or absence of various types of cranial kinesis is mapped on a mosasaur phylogeny, no obvious patterns emerge. Typically, the majority of a given mosasaur subfamily either uniformly possesses or lacks one kind of kinesis or another with plioplatecarpines serving as a distinct exception. This suggests that cranial kinesis may be more closely linked to ecological function than phylogenetic relationships among mosasauroids. Looking specifically at Niobrara taxa, there appears to be a noticeable trend of either lateral or vertical motion in the intramandibular joints of *Platecarpus* and *Clidastes* respectively. Though it should be noted that the intramandibular joints of these taxa are not as mobile as many extant snakes. Conversely, *Tylosaurus* possesses a more braced and akinetic intramandibular joint. These distinct arrangements were likely widespread throughout mosasauroids and may have been ecologically significant. Future studies evaluating intramandibular kinesis and additional potentially kinetic components such as the pterygoids in other mosasauroid taxa will further the collective understanding of the functional units of the mosasaur skull.

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### Non-avian Theropod Systematics, Biology, and Evolution

#### TYRANNOSAURUS REX: AN ENDANGERED SPECIES

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Instead of museum collections, many fossils of *Tyrannosaurus rex* are in the stockrooms of commercial dealers, in the private collections of wealthy collectors, or are privately owned but on display in museums and touring exhibits. Arguably, the commercial trade has depleted the scientific record of *T. rex* because vertebrate

fossils that are outside of public trusts are not available for scientific study. This ethical principle and practice protects the integrity of vertebrate paleontology as a science by ensuring replicability and testability of observations.

The goal of this study was to quantify the effect of the fossil trade upon the sample size of *T. rex*. The sources of data come from the primary literature, museum collection records, articles from the mainstream media, and anecdotal accounts. The specimens range from diagnostic individual bones to nearly complete specimens. The results found that there are 58 *T. rex* fossils in public trusts, whereas there are 47 commercially- and privately held specimens.

The commercial exploitation of *T. rex* fossils began in 1990, with the discovery of FMNH PR2081 (“Sue”). The current rate of discovery of *T. rex* fossils made by commercial companies is higher (mean: 2/annum) than of museums (mean: 1.7/annum). Commercial collection of *T. rex* occurs in the Northern Rocky Mountain region, where the heaviest exploitation is in Montana (15 specimens) and South Dakota (14 specimens). Of particular scientific concern is the private ownership of juvenile and subadult specimens, the part of the growth series that has the fewest specimens in public trusts. Approximately 18% of commercially- and privately held *T. rex* fossils are from those undersampled growth stages. Complete *T. rex* skeletons command top dollar, and the price ranges from \$5 million to \$31.8 million USD. These prices prevent most museums from acquiring the fossils; only 17% of commercially collected *T. rex* fossils are accessioned into public trusts. A related issue is whether public trusts should purchase fossils from companies that also sell fossils into private collections.

In conclusion, the sample size of *T. rex* would be doubled (from 58 to 105 specimens) if it weren’t for the intervention of profit-driven commercial and private interests. Thankfully, the situation isn’t entirely hopeless: for example, several Canadian provinces, Mongolia, and Italy, among others, provide models for legislation that successfully protect dinosaur fossils from the open market.

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#### Preparators'

#### EVALUATION ON THE PROCEDURES FOR THE REMOVAL OF ADHESIVES USED FOR FOSSIL SPECIMENS FROM THE 19<sup>TH</sup> CENTURY

#### EXHIBITIONS AT THE NATIONAL MUSEUMS OF SCOTLAND

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The oldest registered fossil specimen (1812.1.9902, ‘petrified vermes’) in the palaeontological collection of the National Museum of Scotland (NMS) dates back to 1812. The collection contains thousands of specimens with adhesives used in the 1800s. Today these adhesives have aged badly, having changed color and become brittle leading to some parts of the fossils falling apart, which makes their removal urgently needed. Unfortunately, little information is available on the origin or types of materials used during previous conservation treatments. To shed more light on these adhesives, testing with water, IMS (de-ionised alcohol), acetone, and peroxide were conducted on small areas to identify the best removal technique without damaging the specimens. Adhesives were softened by brushing the area with room-temperature water and then removed mechanically with a scalpel. In parallel, a set of micro-samples (~1 mg) from several types of adhesives were removed for molecular analysis using Fourier-Transformed Infra-Red Spectroscopy (FT-IR). Samples of adhesive were selected based on their color, physical properties, and how they reacted during removal with water (as several samples displayed effervescence in contact with water). FT-IR analysis confirmed that the main consolidant used was animal glue, although gum, shellac, cellulose nitrate, and natural resin were found too. Former conservation (both materials and methods used) should be respected. By studying the materials used, it can help us to understand how they were applied and used in the past. Animal glue was used in the eighties for a reason: reversibility, adhesion to a variety of substances, stress resistant, different colors, easily obtained, flexible and elastic, and safety (as soluble in water). Research has proven that animal glue is lacking other important properties needed in conservation: not archival and it will deteriorate with time. We should be conscious and responsible for our actions as conservators. Future analysis might involve proteomic analysis. This work allows us to better understand how these types of collections were preserved in the past. The combination of conservation work and analytical techniques is particularly useful in identifying degraded organic materials. From the test results, it was observed that water was the most effective removal treatment. In general, the adhesive or consolidant used

could be removed with water without damaging the specimens.

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## Mesozoic & Paleogene Mammals

### A NEW LATE OLIGOCENE PYGMY POSSUM (BURRAMYIDAE) FROM THE LAKE EYRE BASIN, SOUTH AUSTRALIA

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Pygmy possums of the Family Burramyidae have an unusual history. First, there are only two known genera either extinct or extant. The genus *Burramys*, was originally described as a fossil first in 1895 and then a living species, *Burramys parvus*, the mountain pygmy possum, was found in 1966. There are now three fossil *Burramys* species ranging in age from the Ngama local fauna at 25 to 24.7 Ma to the Hamilton local fauna at 4.5 Ma. The other genus is *Cercartetus*, pygmy possums, with four extant species and a fossil record that only goes back to the late Pleistocene.

The new specimens, discussed here, are clearly not a representative of any of the previously known species of *Burramys* or *Cercartetus*. It comes from the Kutjamarpu local fauna of the Wipajiri Fm. with an assigned age of 23.8 Ma.

This new species differs from the four species of *Burramys* by: (1) a lack of a plagiolauroid p3, the new species has an enlarged bicuspid sectorial p3, which lacks denticles on the blade and ridges on buccal and lingual surfaces; (2) a mental foramen that is below m1 whereas in *Burramys* it is below p2; (3) a ventral margin of the mandible that is concave and not linear; (4) a p3 that is equal in length to m1 versus *Burramys* where  $p3 > m1$ ; and (5) an m1 that retains paralophid shear, which is lost in *Burramys*.

This new species differs from the four species of *Cercartetus* by: (1) a mental foramen that is below m1 whereas in *Cercartetus* it is below p3; (2) a ventral margin of the mandible that is concave and not linear; (3) a p3 that equals m1 in length versus  $p3 < m1$  in length as in most species of *Cercartetus*; (4) an entoconid on the m1 that is not at the lingual corner, as in *Cercartetus*, but anterior to it as in *Burramys*; and (5) a styler shelf on the M1 that is less reduced buccally compared to the species of *Cercartetus*.

Phylogenetic analyses place the new species with *Cercartetus* rather than with *Burramys* as the new species lacks the signature plagiolauroid p3 of *Burramys*. However, the placement in the *Cercartetus* lineage is not supported by bootstrap analysis, although the new species is well supported within the Burramyidae. Molecular data on the extant taxa indicate that the burramyids originated in the middle Eocene, while the two genera *Burramys* and *Cercartetus* diverged in the latest Eocene. *Burramys* has a fossil record back to the late Oligocene, but the *Cercartetus* fossil record only goes back to the late Pleistocene. This new taxon may be the first pre-Pleistocene fossil in the *Cercartetus* half of the family.

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## Preparators'

### YET ANOTHER TECHNIQUE FOR CURATING MICROMAMMAL FOSSILS THAT EMPHASIZES COST, VISIBILITY, TIME AND STORAGE EFFICIENCY, SPECIMEN AND DATA PROTECTION

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Several techniques have been designed and used to curate and store micromammal teeth in fossil collections. Since at least the 1960s this was done with corked glass vials containing specimens glued to pinheads, with the pin sticking into the cork. Problems with this include that the glue used was often not archival, and more importantly that users often complain that it is too easy to break or lose the specimen as it is being pulled out of the vial for study. More recently developed techniques include storage in gel capsules and in centrifuge cuvettes with a foam lining. Each technique has its advantages, limitations and shortcomings. A new method described here does not claim to be the end-all curation solution for these small fossils, but simply another way to balance the pros and cons. Things to consider when choosing a curation system include but are not limited to costs, physical and visual specimen availability, specimen protection, storage efficiency, time efficiency and avoiding loss of data, and use of archival materials. This system involves mounting the specimens on trimmed



bamboo toothpicks, which are then mounted on a simple foam core board. The specimens are adhered to the toothpick using polyethylene glycol 3350, (PEG), which is water soluble and, arguably, leaves little residue. A water-soluble glue like Aquazol 50 could be used as well; the advantage of PEG is its almost instantaneous set time at this scale. The specimen numbers can be written directly on the toothpick preventing the number and the specimen from getting separated. Multiple toothpicks can be mounted onto a small square of foam core and the specimen number written on this as well. The foam core and specimens are inserted into a small lidded polystyrene box. The PEG is the weak point; if the specimen and support bamboo are stressed, the PEG will fail before the specimen.

The fact that there are 16 specimens in a box may invite confusion, especially if the PEG should fail for whatever reason. To lessen the risk of loss of data, each specimen is photographed in the unlikely case there is a mass failure of PEG and specimens need to be re-mounted.

There are advantages and disadvantages to this system. Advantages of this system include easy visibility and access, time efficiency when mounting and studying, cost, storage efficiency, specimen protection, avoiding loss of data. The big disadvantage: is it archival?

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## Turtle & Marine Reptile Diversity & Biology

### REVISION OF *NEOSINASAURUS* AND *WAYAOSAURUS*, AND THE CONSERVATIVE BODY DESIGN OF ASKEPTOSAUROIDEA

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*Neosinasaurus hoangi* and *Wayasaurus bellus* were firstly named and described by Yin et al. (2000). They were discovered in Guanling, Guizhou Province, southwestern China and initially classified as Sauropterygia. Reidentification shows that *Neosinasaurus* and *Wayasaurus* are definitely members of Thalattosauriformes rather than Sauropterygia, because they fit well in the diagnostic characters of Thalattosauriformes, including T-shaped interclavicle, no pectoral fenestra, straight and robust humerus without posterior curvature, L-shaped ilium and hooked fifth metatarsal. They can be classified to Askeptosauroida

based on the fusion of pterygoid, the absent of palatine dentition, and 7 ossified carpals. However, the holotypes are not well prepared, and the detailed characters on the skull still remain ambiguous. The postcranial characters show that both *Neosinasaurus* and *Wayasaurus* have 13 cervical vertebrae, humerus with a broad shaft, and ischium with blunt posterior process, which are similar to *Miodentosaurus brevis*. The skull in the holotype of *Neosinasaurus* is preserved in lateral view, and the currently prepared parts shows that it has a short snout (nearly equal to the post snout region), teeth only present on premaxilla and the anterior most part of the dentary, angular suddenly broaden at the posterior one third. These characters fit well to the diagnosis of *Miodentosaurus*. The short snout of *Wayasaurus* is also similar to that of *Miodentosaurus*. Because other bones are not diagnostic and are partially covered, further preparation is needed for definite conclusions. The postcranial characters within Askeptosauroida are convergent, making it difficult to distinguish different species from each other. Also, this similar body design is not a high-pelagic-adapted type. A PCA analysis is in progress to establish a morphospace, take the ones found in southwestern China as an example (including *Miodentosaurus*, *Neosinasaurus*, *Wayasaurus* and *Anshunsaurus*). Additionally, we noticed that the orientation of the orbit is anterolateral, suggesting that Askeptosauroida may have lived near the sea surface. This low adaptation to marine life could be one of the reasons that this taxon went extinct at the end of the Triassic, because the sea level had been rising since Middle Triassic globally.

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## Permo-Triassic Ecosystems

### TRICKY TRIASSIC TRILOPHOSAURS: WERE THE REPTILES *TRICUSPISAURUS THOMASI* AND *VARIODENS INOPINATUS* REPRESENTATIVES OF TRILOPHOSAURIDAE IN EUROPE?

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Trilophosaurs were a group of lizard-like archosauromorph herbivorous reptiles known for their transversely broadened multi-cuspid teeth. Until now, the group has been known exclusively from the Late Triassic of North America. Potential European members of the group were noted in the 1950s, *Tricuspisaurus thomasi* and *Variodens inopinatus*, but they were commonly identified as procolophonids. Here, we re-study these taxa using new CT scan data, confirm they were trilophosaurs, and for the first time include them in a phylogenetic analysis. Our investigation and results conclude that the two European taxa do belong to Trilophosauridae, and that they may represent the youngest known trilophosaurs in the fossil record before the group's extinction at the end of the Triassic.

**Funding Sources** Tratman Scholarship (SCT)

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## **Non-avian Theropod Systematics, Biology, and Evolution**

### **A CT-BASED REVISED DESCRIPTION AND PHYLOGENETIC ANALYSIS OF THE SKULL OF THE BASAL MANIRAPTORAN *ORNITHOLESTES HERMANNI* OSBORN 1903**

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*Ornitholestes hermanni* was one of the first small-bodied theropods named in the 1900s. It is known from a single specimen discovered during the American Museum Expedition of 1900, at the Jurassic Morrison Formation site known as Bone Cabin Quarry, in Wyoming. It has long been a critical taxon in understanding the evolution of the Coelurosauria, the clade that includes tyrannosauroids, living birds, and their common

ancestors. The holotype specimen comprises a nearly complete skull and most of a postcranial skeleton. Despite this abundant material, its precise phylogenetic relationships have been difficult to determine. This is in part due to the intense mediolateral crushing of the skull and the relatively generalized postcranial anatomy. Here we present the results of a micro-computed tomography-based investigation of the cranial anatomy and subsequent incorporation of these data into a phylogenetic data matrix designed to test coelurosaurian interrelationships. We find robust evidence across different optimality criteria that *Ornitholestes* is the earliest-branching oviraptorosaurian species. Using parsimony as an optimality criterion, this phylogenetic position is supported by 14 unambiguous synapomorphies, including: a short frontal process of the postorbital; short, deep, and pendant paroccipital processes; a large mandibular foramen; an anterodorsally oriented dentary symphysis; a surangular that is longer than the dentary; short maxillary and dentary tooth rows; and procumbent dentary and premaxillary teeth. Using Bayesian fossilized birth-death models, we find high posterior probabilities (>.99) that *Ornitholestes* is the earliest-branching oviraptorosaurian species. We additionally find strong support in both analyses that the superficially bat-like and possibly arboreal scansoriopterygids are an early branching lineage within Oviraptorosauria. This new phylogenetic position fills in a persistent ghost lineage in Oviraptorosauria and confirms that scansoriopterygids are basally branching oviraptorosaurians that represent an independent origin of aerial habits, separate from those of dromaeosaurs and avialans.

**Funding Sources** Kalbfleisch Fellowship, Richard Gilder Graduate School, AMNH; DSI-NRF Centre of Excellence in Palaeosciences; Palaeontological Scientific Trust

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## **Avialan Evolution & Biology**

### **CONTROLS ON THE CAMPANIAN DISTRIBUTION OF *HESPERORNIS* (AVES: HESPERORNITHIFORMES) IN THE WESTERN INTERIOR SEAWAY**

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The epicontinental Western Interior Seaway (WIS) divided North America during the Late Cretaceous and

created a unique habitat for marine life. Endemic vertebrate life included fish, marine reptiles, and the foot-propelled diving seabird *Hesperornis*. While several predator–prey relationships between *Hesperornis* and other WIS animals have been hypothesized based on gut contents, bite marks, and coprolites/colonites, nothing has been quantitatively tested. Species distribution models (SDMs) describe species distributions using environmental and biological factors. Paleontological SDMs have focused on non-marine taxa and marine invertebrates, but only two studies included marine vertebrates. Here, two SDM methods tested how local vertebrate faunas, sedimentary rock type, and paleogeography influenced the *Hesperornis* distribution: generalized linear models (GLMs) and occupancy models. Modeling results indicate a decreased probability of *Hesperornis* presence at elasmosaur-occupied sites; an increased probability of *Hesperornis* presence was found at mosasaur-occupied sites or higher paleolatitudes. The low probability of elasmosaurs and *Hesperornis* being found together likely reflects competition for food resources, restricting biogeographic overlap. Mosasaurs increased the probability of *Hesperornis* presence which may indicate that *Hesperornis* took advantage of mosasaur feeding activities, but the relationship is equivocal. The positive influence of paleolatitude may reflect seasonal migration patterns that drive *Hesperornis* breeding or feeding congregations. This study represents the first application of occupancy modeling and GLMs to extinct marine vertebrates. These models provide novel hypotheses that may be tested or modified in future studies on *Hesperornis* or other extinct marine vertebrates.

**Funding Sources** Fort Hays State University Graduate Scholarly Experience Grants

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## Fishes Evolution & Distribution

### FROM ALLOMETRY TO LIFE-HISTORY – ONTOGENETIC SALTATORY PATTERNS IN THE LATE DEVONIAN JAWED STEM- GNATHOSTOME *BOTHRIOLEPIS CANADENSIS*

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Saltatory ontogeny is the transition between periods of rapid development; the thresholds, and slower development; the steps. This ontogenetic pattern is hypothesized to be a general gnathostome character. The Late Devonian placoderm *Bothriolepis canadensis* from the Escuminac Formation (Miguasha, Quebec, Canada) is considered as a reference taxon for antiarchs and holds the most extensive ontogenetic series known for antiarchs, with dermal armour (head + thoracic shields) ranging from ca. 5 mm to 220 mm. With hundreds of specimens, morphological and morphometric ontogenetic changes can be examined in detail, notably to identify the presence of saltatory ontogenetic patterns. The objective of this study was to combine morphological and morphometric changes during the ontogeny of *B. canadensis* to validate the presence of ontogenetic saltatory patterns in this phylogenetically basal gnathostome. Logistic binomial regressions were used to identify the size at which characters of immature individuals were lost during growth. Segmented regressions were also estimated on different bivariate relationships to identify the presence of a breakpoint (a significant slope change) in the ontogenetic trajectory of *Bothriolepis*. In extant fishes, the congruence of a loss/gain of a morphological character and a significant allometric variation in a bivariate relationship suggests the presence of a developmental threshold and thus saltatory ontogeny. Our analyses show that: (1) a shared breakpoint in bivariate relationships is present on the plates of the head shield surrounding the orbital fenestra (premedian, lateral, nuchal, postpineal), (2) this breakpoint is congruent with the loss of immature features such as the external ridge system of the dermal armor, among others. Some features preceding the ontogenetic threshold are similar to plesiomorphic conditions in antiarch phylogeny, while features following the threshold correspond to apomorphic condition. Ontogenetic thresholds are interesting since they represent periods within which new life-histories and novelties could evolve.

**Funding Sources** This project was funded by the parc national de Miguasha - SEPAQ (FC) and the Natural Sciences and Engineering Research Council of Canada (RC).

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## Avialan Evolution & Biology

## TOWARDS A COMPREHENSIVE ANATOMICAL MATRIX FOR CROWN BIRDS: PHYLOGENETIC INSIGHTS FROM THE PECTORAL GIRDLE AND FORELIMB SKELETON

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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, 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.

In this study 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 190 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 62 extant avian taxa and incorporated into phylogenetic analyses. Preliminary results suggest that increased taxon sampling improves congruence with recent molecular analyses, and implementation of molecular scaffolds allows identification of diagnostic character combinations for several clades previously only recognized through molecular data. Future work will assess optimized synapomorphies against the observed morphology of putative stem members of major lineages known from the fossil record, as well as investigate the effects of different analytical parameters on morphological tree topology.

**Funding Sources** UKRI Future Leaders Fellowship, Royal Society Research Grant, and Paleontological Society Student Research Award.

## Dinosaur Systematics, Diversity, & Biology

### UNFOLDING THE PALEODIVERSITY, AGE AND PALEOECOLOGY OF THE FIRST MULTI-INDIVIDUAL DINOSAUR-BEARING LOCALITY OF ITALY

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The paleobiogeography and geodynamic history of the latest Cretaceous Adriatic Carbonate Platform (AdCP) system in the paleo-Mediterranean area, stand as one of the most complex and debated topics related to the evolution of land vertebrates in the area surrounding the Tethys Sea. This biogeographic realm, bracketed by Laurasian and Gondwanan continental remnants of Pangea, represents a long-lasting challenge for paleontologists focusing on dispersal events across the Tethys and the consequent adaptive response to environmental changes that affected several lineages of land-dwelling vertebrates from this setting. Italy holds the sole Late Cretaceous dinosaur-dominated site of the AdCP system, namely the Villaggio del Pescatore locality (VdP). The VdP site was discovered thirty years ago in the Late Cretaceous–Paleogene beds exposed near Duino Aurisina, northeastern Italy, and produced, among fish, crustaceans and plant remains, an exquisitely preserved skeleton of the hadrosauroid *Tethyshadros insularis*. Ever since, prospecting activities combined with the collection of new specimens, confirmed the presence of seven sub-complete skeletons at the VdP site accounting for possibly eleven individuals of *T. insularis*, making this site the first, multi-individual Italian dinosaur lagerstätte and a stand-alone case in the AdCP. A pilot project we started in 2019 generated compelling biostratigraphic data to finally constrain the largely disputed age of the VdP, thus inferring the paleogeographic role of the site and its fauna in the latest Cretaceous. We provide the description of several partial but articulated skeletons of *T. insularis*, and focus on a new sub-complete skeleton (SC 57247):

given the larger size of this individual in comparison to the holotype (SC 57021), we tested the hypothesis of their relative ontogenetic stages using osteohistology as a proxy of maturity. Consequently, we revise the former description of the holotype, documenting the morphological variation in this taxon, and highlighting the ontogenetically variable characters in our sample. Finally, we investigated the phylogenetic position of *Tethyshadros* using a phylogenetic comparative framework, which combine ancestral state reconstruction and multiple regime Ornstein–Uhlenbeck models to evaluate whether the evolution of body-size was following a significant and accelerated trend of reduction in this clade, to further test the interpretation of this taxon as an aberrant, insular dwarf.

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### Paleohistology & Paleopathology

#### **A PATHOLOGICAL METATARSAL OF A LARGE-BODIED ORNITHOMIMID (DINOSAURIA: THEROPODA) DINOSAUR FROM THE UPPER CRETACEOUS EUTAW FORMATION (UPPER SANTONIAN) OF MISSISSIPPI, U.S.A.**

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Paleopathological diagnoses provide important insight into the macroevolutionary origin of disease as well as species-specific behavioral and physiological inferences which are usually inaccessible via direct observation. Here we present gross morphology and microstructural data derived from CT imaging and histology from a pathologic right second metatarsal (MMNS VP-6332; Length: ~434 mm) of a large-bodied ornithomimid (~480 kg) from the Upper Cretaceous Eutaw Formation, Mississippi. Referral to Ornithomimosauria is based on features identified via reconstruction of the original cortical outline via CT imaging, and include an elongate shaft, lack of a buttress on the ventrolateral surface, and a suboval cross-section.

In gross inspection, a large mass of reactive periosteal bone pierced by multiple foramina extends approximately two-thirds of the shaft, originating just proximal to the

distal condyles, and entirely circumnavigating the transverse plane (it is thickest craniomedially). The metatarsus exhibits an enlarged medullary cavity (15.78 mm) and thin cortical bone (7.64 mm). Microstructurally, the periosteal cortex transitions from a woven/reticular to a parallel-fibered/plexiform matrix/vascularization complex periosteally with limited secondary remodelling concentrated in the endosteal region of the lateral cortex, and throughout the cortical section in the ventromedial region. We recognize seven growth marks (LAGs and annuli), three of which are closely spaced near the periosteal surface but do not represent an EFS. There is no endosteal lamellar bone visible. The pathologic periosteal bone is composed of perpendicularly deposited, interconnecting trabeculae with a woven matrix bearing a high density of plump, disorganized osteocyte lacunae. The transition zone is predominantly characterized by a sharp line of demarcation of abrupt change from normal cortical bone transitioning to the pathological periosteal bone. In some areas, the transition zone is obscured by active pathologic bone growth. Pathological bone growth infills multiple longitudinal cortical bone fractures and is also present endosteally.

It is presently unclear if the cortical fracturing was primary or secondary to the disease process. No evidence of lysis is visible in the thin-section; however, it may be evident in more distal regions via CT imaging. Overall, the bulk of evidence is consistent with infectious as opposed to neoplastic processes or fracture as the primary etiology

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### Crocodylomorphs & Pterosaurs

#### **THE HIDDEN DIVERSITY OF TOYOTAMAPHIMEIA (CROCODYLIFORMES, CROCODYLIA) FROM THE PLEISTOCENE OF TAIWAN**

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*Toyotamaphimeia* (Tomistominae) is a monotypic crocodile genus represented only by *T. machikanensis* from the Pleistocene of Japan. The first record outside Japan was recently reported based on an almost-century-old and fragmentary fossil from the Pleistocene of Taiwan. The incomplete nature of the historical specimen

restricts our understanding of the *Toyotamaphimeia* lineage outside Japan or along the eastern margin of Eurasia. Here, we describe the presence of possibly two new species of *Toyotamaphimeia* from the Pleistocene of Taiwan. The first taxon was previously known as *Tomistoma taiwanicus* from the Middle Pleistocene of Tainan (southern Taiwan). We reexamined the holotype and found its morphological affinity to *Toyotamaphimeia*, such as the circular and flat margins of the orbit. Additionally, it differs from *T. machikanensis* in having medial occlusal pits on the anterior maxilla. The second species is a newly-discovered specimen dredged from the sea bottom between Penghu Islands and Taiwan; its geological horizon is uncertain but likely to be Middle–Late Pleistocene based on previous studies. This sea-bottom specimen preserves the posterior portion of the skull, showing the *Toyotamaphimeia* traits: quadrate and expanded medial hemicondyle, exoccipital ventral process robust and participating in occipital tubera, and basisphenoid anteroposteriorly long and exposed ventrally. Similarly, it differs from *T. machikanensis* in having a skull table surface sloping ventrally and the opening of the lateral carotid foramen dorsal to basisphenoid lateral exposure. Our results strongly indicate the occurrence of *Toyotamaphimeia* in the southern margin of the Far-East (Taiwan) and also reveals the hidden diversity of the *Toyotamaphimeia* lineage. Moreover, our discovery of possibly two new *Toyotamaphimeia* taxa from the Pleistocene of Taiwan greatly expands its known temporal and spatial existence—the youngest and southernmost record, complicating the evolution and extinction of this fairly large tomistomine lineage (up to 7 m). Future finds and analyses from Taiwan should promise to elucidate the Pleistocene extinction and its megafaunal turnover on the eastern margin of Eurasia.

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### **Taphonomy, Paleoenvironments, & Stratigraphy**

#### ***IN SITU* PRESERVATION OF ARAGONITE IN A TURTLE EGG FROM THE JUDITH RIVER FORMATION (CAMPANIAN) OF MONTANA**

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Turtles are the only vertebrate clade that lays aragonite (one of the polymorphs of CaCO<sub>3</sub>) eggshells. However, because aragonite is an unstable compared to calcite, the only previous unequivocal preservation of aragonite in fossil turtle eggs is from the Pliocene deposits of Rhodes Island, Greece. In this study, we report *in situ* preservation of aragonite in a fossil turtle egg (Museum of the Rockies, MOR 710) for *Testudoolithus zelenitskyae* from the Judith River Formation (Campanian). We analyzed the egg using electron backscatter diffraction (EBSD) and Raman spectroscopy. Whereas EBSD recognizes the crystallographic configurations of minerals, Raman spectroscopy uses the molecular vibration induced by the interaction of light (laser) with the mineral to generate the identification. The EBSD phase map showed the presence of both aragonite and calcite with the former still preserved as needle-like crystals, typical of all turtle eggshells. The coexistence of aragonite and calcite was cross-validated by Raman spectroscopic mapping analysis. This cross-validation approach provides the strongest evidence that Campanian aragonite has been preserved in these Judith River Formation turtle eggs and confirms the record of aragonitic turtle eggshell back to the Campanian. The preservation of aragonite in the fossil record has been a major topic in invertebrate paleontology and paleoecology (e.g., aragonite sea), and this study shows that the fossil aragonite can be not only present in marine deposits, but also in terrestrial deposits. The combination of EBSD and Raman provides a definitive way to identify turtle eggs and future reports of preserved aragonite in fossil turtle eggs will improve our understandings for the preservation of aragonite in fossil records in general.

**Funding Sources** National Research Foundation of Korea Grants 2020R1A6A3A03038316; 2020R1A3B2079815

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**Colbert Poster Prize**

## EVOLUTION OF THE OLD WORLD *EQUUS* AND ORIGIN OF THE ZEBRA-ASS CLADE

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*Equus* evolutionary history has been long debated with a multitude of hypotheses. Currently, there is no consensus on either the taxonomy nor phylogeny of *Equus*. Some hypotheses segregate fossil *Equus* species into three genera, *Plesippus*, *Allohippus* and *Equus*. Also, the evolutionary role of European Pleistocene *Equus stenonis* in the origin of the zebra-ass clade has been debated. Studies based on skull, mandible and dental morphology suggest an evolutionary relationship between North American Pliocene *E. simplicidens* and European and African Pleistocene *Equus*. Herein, we assess the validity of the genera *Plesippus*, *Allohippus* and *Equus* by cladistic analysis combined with morphological and morphometrical comparisons of cranial anatomy. Our cladistic analysis, based on cranial and postcranial elements, supports the monophyly of *Equus*, denies the recognition of *Plesippus* and *Allohippus* as separate genera and supports the derivation of *Equus grevyi*, and members of the zebra-ass clade, from European stenonine horses. We define the following evolutionary steps directly relevant to the phylogeny of extant zebras and asses: *E. simplicidens* - *E. stenonis* - *E. koobiforensis* - *E. grevyi* - zebra-ass clade. The North American Pliocene species *Equus simplicidens* represents the ancestral stock of Old World Pleistocene *Equus* and the zebra-ass clade. Our phylogenetic results uphold the most recent genomic outputs which indicate an age of 4.0–4.5 Ma for the origin and monophyly of *Equus* and identify the Central American *Dinohippus* as the sister genus from which *Equus* evolved.

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### Turtle & Marine Reptile Diversity & Biology

#### AN EXCEPTIONALLY SMALL NEW POLYCOTYLID PLESIOSAUR (REPTILIA: SAUROPTERYGIA) WITH RAPTORIAL EYES

## FROM THE WESTERN INTERIOR SEAWAY OF NORTH AMERICA

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Polycotyliidae is a family of plesiosaurian marine reptiles that evolved during the Early Cretaceous and radiated into multiple genera during the Late Cretaceous, achieving a worldwide distribution. Derived polycotyliids of the subclade Polycotyliinae have a relatively gracile and elongated rostrum, relatively homodont dentition, an extended mandibular symphysis, a reduced or absent pineal foramen, and foreshortened temporal fenestrae. Here we describe a highly derived and relatively small new polycotyliid taxon based on two specimens from the Sharon Springs Formation and one specimen from the Dinosaur Park Formation (all Campanian) of the Western Interior Seaway in North America. A high number of maxillary teeth, partially fused neural arches, propodials with well-defined facets, and heavily remodeled cortical bone establish the specimens as adult individuals, making this taxon the smallest known adult polycotyliid to date. The new taxon has a large orbit with two autapomorphic features: a broad supraorbital ridge that borders its posterodorsal rim and a triangular supraorbital ledge that projects laterally over its anterodorsal margin. Other diagnostic features include a parasphenoid that posteriorly doubles in width, an unusually short postorbital region, a uniquely wide occiput, a retroarticular process consisting of the angular in nearly its entire dorsal margin, and femora that are distally more narrow than those of other polycotyliids. A phylogenetic analysis reveals the new taxon to be deeply nested within Polycotyliinae and differentiated from *Dolichorhynchops osborni*, despite the previous identification of one of the specimens with this species. The analysis places *D. osborni* and *D. herschelensis* in a subclade that is sister to a subclade containing the new taxon and *D. bonneri*, suggesting that the generic name of the latter should be revised. Morphometric analyses confirm the similarity between the two known skulls and quantify their morphological distinction from other polycotyliid taxa, including ontogenetically young polycotyline specimens. Morphological similarity between the supraorbital ledge of the new taxon and the supraorbital processes of raptorial birds suggests a diurnal lifestyle and shallow-water habitat for this taxon and has ecological implications for other polycotyliid taxa.

## Marine Mammals

### RISING FROM THE ASHES: LINKING ANDEAN VOLCANISM, DIATOMS, AND MARINE MAMMAL DIVERSITY WITH THE LATE MIOCENE COOLING EVENT

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The Late Miocene Cooling event (LMC, 7.6 to 5.4 Ma) marks a short-lived but significant drop in global temperatures that has been noted in marine and terrestrial records, foreshadowing the onset of Plio-Pleistocene bipolar glaciation. The cause of this event is unclear but is thought to be related to a dramatic drop in CO<sub>2</sub> that was associated with the establishment of modern cetacean communities (increased abundance of baleenopterids and delphinids, decline of cetotheriids and platanistoids), colonization of the Southern Hemisphere by otariids, and a decline in sirenian diversity. On land, this event is associated with an increase in the global abundance of C<sub>4</sub> grasses and expansion of arid conditions in terrestrial environments. Chemical weathering of Ca-silicate rocks remains the primary hypothesis to explain global Cenozoic cooling via CO<sub>2</sub> drawdown, with the Himalayas and Tibetan Plateau often identified as the most likely source material. Here, we propose an alternative hypothesis that vigorous volcanism from the Andes of western South America enhanced the biological pump through ocean fertilization triggering global cooling during the LMC.

We compiled an exhaustive dataset of >4000 magmatic ages from the Central Andes and identify a significant increase in frequency of volcanic events from 9 to 5 Ma with a peak at 7 Ma. The role of volcanism on global climate remains debated but is most often argued to contribute to global warming through CO<sub>2</sub> release. However, active Andean volcanism and mountain building in the late Miocene would also have fertilized marine surface waters with silica and iron, enhancing diatom productivity and intensifying the biological pump, significantly contributing to carbon burial and CO<sub>2</sub> drawdown in the Cenozoic. Comparison of volcanic activity in the Central Andes with benthic and planktic isotopic records ( $\delta^{13}\text{C}$ ,  $\delta^{18}\text{O}$ ), diatom abundance data, and marine sediment chemical alteration indices from deep sea cores show a strong correlation, supporting a

connection between Cenozoic Andean volcanism and major climatic and biotic events at the LMC. We conclude that volcanism is a key driver of climate change and biotic events over geological times through its ability to contribute both positively and negatively to global temperatures.

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## Preparators'

### PALEO TOOLS VS. THE STONE COMPANY AIR SCRIBES: AN UNOFFICIAL USAGE GUIDE

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After the recent acquisition of new air scribes in the preparation laboratory at The Western Science Center, both staff and volunteers have voiced inquiries regarding their identification and maintenance. Despite hands-on training as well as labels applied to drawers and tools, our preparators have sometimes confused tools made by PaleoTools and The Stone Company. This proposed graphical guide is meant to help with identification of the various types of air scribes available from PaleoTools and The Stone Company, as well as to address inquiries regarding their maintenance requirements. PaleoTools and Stone air scribes have the same application, and thus their appearances can be similar except for some important differences: PaleoTools scribes have no regulator attached to the plastic air hose; while, Stone air scribes have a regulator as well as a cloth covered air hose. While these two main brands of air scribes used in paleontological preparation are similar in appearance, they have different maintenance requirements. For example, PaleoTools requires oil be placed into the tool to inhibit rust and prevent seizure of the tool; in contrast, The Stone Company requires the o-rings on the needle as well as the ones located internally to be lubricated and then excess lubrication to be removed before reassembly. If these two maintenance requirements inadvertently get confused it could result in costly repairs or replacement of the tool. Additionally, there are PSI differences between the various tools to address, as well as the various applications for the different sizes of the air scribes. For



instance, a Micro Jack (PaleoTools) or HW-322 (The Stone Company) is used for fine detail work, versus an ME-91 (PaleoTools) or HW-65 (The Stone Company) that would be applied when removing large amounts of matrix. This guide will be made available online to all institutions in the hope that it will supplement essential hands-on training on the proper identification and maintenance of these important tools and the air compressors that power them.

**Funding Sources** David B. Jones Foundation

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## **Holocene & Pleistocene Mammalian Faunas**

### **INVESTIGATING THE GENETIC AND ECOLOGICAL EFFECTS OF HISTORICAL SYMPATRY AMONG WOLF-LIKE CANIDS OF THE SOUTHERN GREAT PLAINS**

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Human persecution of wolf-like canids (*Canidae*, *Canis*) in North America has severely impacted their geographic range and diversity. This is notably evident within the Southern Great Plains region of the United States, spanning the states of Oklahoma, Texas, and New Mexico. Prior to the end of the 20<sup>th</sup> century, this region supported the now extinct Great Plains wolf (*Canis lupus nubilus*), in addition to the locally extinct gray wolf (*Canis lupus*), red wolf (*Canis rufus*), and Mexican wolf (*Canis lupus baileyi*). Current wolf-like canid diversity in the Southern Great Plains has been reduced to the wild coyote (*Canis latrans*) and domestic dog (*Canis lupus familiaris*), yet effects of wolf presence have not been lost. Wolf-like canid species are known to hybridize, and mesopredators such as coyotes likely experienced an expansion in potential food items following wolf extinction. By applying genomic and isotopic analyses to both modern and subfossil canid specimens, we can investigate the effects of historical sympatry on canid genetic diversity and diet through time. Molecular analyses will include mitochondrial haplotype DNA for

taxonomic identification and measures of relatedness to assess extent of hybridization. Preliminary radiometric data and morphological data collected identified wolf specimens (including skulls, jaws, and teeth), revealing chronological ages from 680 +/- 30 to 100 +/- 30 years before present (YBP). Thus far, mitochondrial DNA sequencing has identified two gray wolves and two domestic dogs, suggesting introgression. Isotopic analyses will include radiocarbon (<sup>14</sup>C) dating and stable isotope analysis of <sup>13</sup>C and <sup>15</sup>N for chronological age and dietary information. DNA sequencing and isotopic analyses of additional specimens are underway. Adding these additional specimens to our existing dataset will allow for more robust time bins and geographic coverage in statistical analyses to assess how inter- and intraspecific dietary composition and relative trophic position changed through time. Comparing coyote populations pre- and post-wolf extinction is of particular interest considering potential differences attributable to mesopredator release. It is imperative that we investigate the impact of wolf occupation on historical communities to inform existing wolf recovery programs and anticipate how natural wolf recolonizations in North America may impact ecosystems in different geographic regions.

**Funding Sources** Native Explorers; Cherokee, Chickasaw, and Choctaw Nations; U.S. Department of Education; OAIMS and Department of Anatomy & Cell Biology at OSU-CHS provided funding.

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## **Stem Tetrapod, Squamate, & Amphibian Diversity & Biology**

### **MORPHOLOGICAL ANALYSIS OF A NECTRIDEAN LEPOSPONDYL, DICERATOSAURUS, FROM LINTON AND FIVE POINTS, OHIO.**

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Lepospondyli traditionally includes five Paleozoic groups: Microsauria, Lysorophia, Nectridea, Aistopoda, and Adelosondyli, which are united by the presence of elongate trunks and holospondylous vertebrae. However, more recent studies have shown these taxa show few consistent similarities and are likely a polyphyletic

assemblage. For example, recent analyses have placed aistopods deep on the tetrapod stem and Lysorophia and Microsauria (in part) with amniotes. Nectridea, which is thought to be quite basal in the early tetrapod phylogeny, has not yet been included in some of these studies. More information needs to be collected to test the interrelationships of nectrideans among early tetrapod groups. This study focuses on *Diceratosaurus*, a nectridean solely known from Linton and Five Points, Ohio. Latex peels of the skull roof and the palate are being analyzed and illustrated by using photography and light microscopy. Preliminary results suggest that *Diceratosaurus* comprises two distinct morphs that range from 14–25 cm in skull length: a broad, round-snouted morph, and a small, narrow-snouted morph which has never been seen in nectrideans before. We test several hypotheses to explain this variation including ontogenetic change, polymorphism, and the presence of multiple species. Examining the smallest specimens, which are the narrow-snouted morphs, to the largest specimens which are the broad-snouted morphs, there seems to be no signs of an ontogenetic difference; the dermal ornamentation is organized with distinct pits and ridges, all bones in the skull roof are ossified, and the sutures are tightly closed in the smaller narrow-snouted morphs. This is not what one would expect if this were a juvenile form of *Diceratosaurus*. Although more work remains to be done documenting the anatomy of the palate, there are differences in the bones of the pre-orbital region of the skull and in the ornamentation around the tabular horn region. We believe that the multiple species hypothesis is the most likely explanation. The discovery of a second morph and these results could further support the conclusion that not only nectrideans, but lepospondyls as a group, are more diverse than originally thought.

**Funding Sources** NSERC through supervisor Dr. Jason Anderson

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## Fishes Evolution & Distribution

### EVOLUTION AND DEVELOPMENT OF AXIAL SKELETAL REGIONALISATION IN GNATHOSTOMES: INSIGHTS FROM FISHES

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The vertebral column is a key feature of the vertebrate skeleton. In amniotes, the vertebral column is divided into at least four anatomical regions, which are determined by the anterior expression boundaries of *Hox* genes. In fishes the backbone is thought to consist of just trunk and tail regions, and the relationship between *Hox* genes and regional boundaries in fishes is poorly understood. Variation in vertebral morphology along the backbone has been documented in several fish species, implying that fish vertebral columns might be more complex than previously appreciated. However, because regional boundaries in fishes are often not as obvious as those in amniotes, a quantitative approach is needed to test for more complex regionalization.

To test for regionalization in fish axial skeletons, we used linear and geometric morphometrics to quantify and compare vertebral shape across taxa, and combined Maximum Likelihood model selection with segmented linear regression to identify region numbers and boundaries. We sampled extant teleosts, non-teleost actinopterygians, and cartilaginous fishes broadly, and included fossil taxa from each major gnathostome lineage. We found that highly regionalized vertebral columns (consisting of four or more regions) are common among fishes (over 80% of analyzed fish taxa). We then used phylogenetic comparative methods to investigate evolutionary patterns of regionalization. High region numbers were reconstructed as ancestral for jawed vertebrates, suggesting that the potential for axial regionalization originated at the base of jawed vertebrates. To test whether *Hox* genes specified axial regions prior to the divergence of bony and cartilaginous fishes, we characterized *Hox* expression patterns in a cartilaginous fish, the skate (*Leucoraja erinacea*), and tracked the skeletal fate of somites at *Hox* expression boundaries. We found that expression patterns of key boundary-marking *Hox* genes only correlate with some regional transitions in skate, suggesting that *Hox* genes played an ancestral role in patterning the jawed vertebrate axial skeleton, but different *Hox* paralogs corresponded to different regional boundaries in divergent lineages. The prevalence of highly regionalized axial skeletons in fishes contrasts with the historical view that fish axial skeletons were simple and unregionalized, and instead points to fish backbones as structures rivaling mammals in their morphological diversity.

**Funding Sources** This research was funded by a Natural Environment Research Council Award (NE/S000739/1) to JJH, JAG, and KEC, with additional data funded by NSF DBI-1701714 (oVert).

## Fishes Evolution & Distribution

### NEW MATERIAL OF *YOUNGOLEPIS* REVEALS THE EVOLUTION OF LUNGFISH DUROPHAGY

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Major paleobiological hypotheses implicate innovations in durophagy—the consumption of prey items protected by hard shells or exoskeletons—in driving major ecological and evolutionary shifts in marine settings over the Phanerozoic. *Diabolepis* from the Early Devonian definitively shows the first example of key functional innovations hallmarking the dipnoan body plan, including tooth plates with dentition in radial rows, a palatal bite, short jaws, and a firmly united mandibular symphysis. However, the order in which these and critical features of dipnoan feeding anatomy evolved remain unclear due to lacking information in closest relatives of lungfishes. *Youngolepis praecursor* is a key member of the diverse sarcopterygian assemblage from the Lower Devonian of Yunnan, China. Current consensus places *Youngolepis* at the base of the lungfish lineage, between the porolepiforms and *Diabolepis*. Therefore, *Youngolepis* is a pivotal taxon for investigating the origin of lungfish anatomical specializations. Its skull shows several distinctive features: loss of the intracranial joints and the presence of neurocranial fossae accommodating origins of jaw adductor musculature. These major changes foreshadow conditions in lungfishes, and suggest *Youngolepis* likely had a distinctive mode of feeding. However, major anatomical systems particularly relevant to the acquisition and processing of prey—the palate, hyoid arch, and branchial skeleton—remain unknown in *Youngolepis*.

Two articulated specimens of *Youngolepis* from the type locality preserve these critical aspects of morphology. 3D models generated from  $\mu$ CT show that *Youngolepis* is substantially more lungfish-like than previously anticipated. Its gill skeleton is like that of porolepiforms, but most surprising is the radical reorganization of palatal dentition, geometry, and suspension. The postorbital region of the palatoquadrate is short and deep, buttressed by a stocky, vertically oriented hyomandibular. The

entopterygoid is thickened and appears to be oriented horizontally, bearing patterned, radial rows of teeth like the tooth plates of *Diabolepis* and other primitive lungfishes. These changes, which are further amplified in lungfishes, indicate changes in biomechanics consistent with the processing of hard prey. *Youngolepis* captures the earliest stages in developing a trophic strategy that has characterized the lungfishes for over 412 million years, the first and longest-lived lineage of durophagous gnathostomes.

**Funding Sources** National Natural Science Foundation of China (41530102), Strategic Priority Research Program of Chinese Academy of Sciences (XDA19050102, XDB26010401).

## Macroecology & Macroevolution

### STABLE STRONTIUM ANALYSES INDICATE HABITAT USE AND FEEDING DIFFERENCES IN CO-OCCURRING LARGE HERBIVORES IN THE LATE CRETACEOUS OF WESTERN NORTH AMERICA

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Large herbivorous dinosaurs in the Cretaceous of Western North America have been hypothesized as particularly sensitive to altitudinal environmental gradients, segregating their niches between closed inland habitats and open coastal habitats, and having latitudinally-restricted ranges. Stable isotope analysis of the enamel of these and other co-occurring vertebrates represents a powerful tool for testing these ecological and environmental hypotheses. We analyzed the  $^{87}\text{Sr}/^{86}\text{Sr}$  ranges of a multi-taxic sample from a vertebrate microfossil bonebed from the Oldman Formation in the Milk River area of Alberta to test hypothesized migration and habitat use differences among ornithischian dinosaurs, while comparing them to a range of co-occurring taxa. Intensive sampling of a single site was performed over mixed formation-level sampling to minimize introduced spatial and temporal biases. Among the sampled taxa, all ornithischians have higher and more variable  $^{87}\text{Sr}/^{86}\text{Sr}$  compositions than co-occurring, and presumably non-migratory, aquatic taxa (crocodylans, freshwater fish). Hadrosaurs have the most

variable  $^{87}\text{Sr}/^{86}\text{Sr}$  values, similar in relative pattern to hadrosaur Sr data in the Dinosaur Park Formation, interpreted as an indication of wider ranges of movement spanning multiple bedrock Sr sources. Thus, our data broadly agree with this interpretation. Interestingly, hadrosaur  $^{87}\text{Sr}/^{86}\text{Sr}$  values continue to be higher than any other taxa sampled or bedrock Sr source known from this area. This could suggest that hadrosaurs from this site in southernmost Alberta were ranging into other unsampled areas with even higher bedrock  $^{87}\text{Sr}/^{86}\text{Sr}$  while avoiding known areas of lower bedrock  $^{87}\text{Sr}/^{86}\text{Sr}$ . As well, ceratopsid and ankylosaur  $^{87}\text{Sr}/^{86}\text{Sr}$  values have no overlap with those of hadrosaurs, suggesting that the differing  $^{87}\text{Sr}/^{86}\text{Sr}$  ranges of ornithischians could also reflect some degree of dietary differentiation, in addition to differences in habitat ranges. This could relate to differential feeding on plant species with deeper vs. shallower roots, and/or plants closer to coastal areas vs. those in inland areas. Large tyrannosaurids preserve  $^{87}\text{Sr}/^{86}\text{Sr}$  compositions which are similarly variable to hadrosaurs, and which overlap with the ranges of all three sampled ornithischian taxa. While additional taxon and site sampling is ongoing, our results so far provide evidence for hypothesized differences in the ecology and paleoenvironmental preferences of these co-occurring species.

**Funding Sources** Natural Sciences and Engineering Research Council of Canada

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## Dinosaur Systematics, Diversity, & Biology

### NEW DRY MESA DINOSAUR QUARRY *SUPERSAURUS VIVIANE* (JENSEN 1985) AXIAL ELEMENTS PROVIDE ADDITIONAL INSIGHT INTO ITS PHYLOGENETIC RELATIONSHIPS AND SIZE, SUGGESTING AN ANIMAL THAT EXCEEDED 39 METERS IN LENGTH

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Newly prepared Dry Mesa Dinosaur Quarry (DMDQ) skeletal material has produced additional gigantic, distorted, disarticulated skeletal elements. The new material not only affirms the synonymy of *Dystylosaurus* with *Supersaurus* and the assignment of the giant cervical vertebra BYU 9024 to *Supersaurus*, but also demonstrates a close taxonomic affinity to *Apatosaurus*. The new

elements indicate *Supersaurus* may have exceeded 39 m in length.

The proximal ~10 *Supersaurus* caudal vertebrae closely resemble those of *Barosaurus*, possessing anteroposteriorly compressed centra with concave anterior and flat posterior centra faces. The ventral centrum surfaces in these positions are flat and lack a ventral sulcus. Beginning with the ~11th caudal vertebra, and persisting to the biconvex whiplash caudal vertebrae, the ventral surfaces are round, and strongly resemble those of *Apatosaurus* sans the narrow "ventral rectangle" present in many, but not all, *Apatosaurus* caudal vertebrae in these positions.

Though disarticulated, paired ischia, pubes, and scapulocoracoids belong to the same individual based on morphology, size, and proximity. The absence of any additional large sauropod material aside from *Brachiosaurus* dorsal vertebrae and a scapulocoracoid, all found ~100 m away from the accumulation of giant diplodocid material, is striking. Parsimony alone suggests the 3 m long right scapulocoracoid belongs to the same individual as that of the 3 m left scapulocoracoid, especially considering their similar morphology, proximity to one another, and the fact the slightly longer of the two is replete with cracks that account for the length disparity. Excavated between these scapulocoracoids, found in approximate life position, was the proximal dorsal vertebra originally assigned to *Dystylosaurus* and the cervical vertebra sometimes attributed to *Barosaurus* (BYU 9024). The *Dystylosaurus* vertebra has undergone significant diagenetic crushing evidenced by directional changes of the bone itself. A 3D reconstruction provides evidence that the pronounced ventral keel is a result of diagenetic factors and that the neural spine is actually bifurcate.

The length of the *Supersaurus* neck, using *Barosaurus* as a guide, exceeds 16 m in length. The actual dorsal + sacral vertebrae, using actual vertebrae, is ~6 m. Extrapolating tail length using known caudal vertebrae and an *Apatosaurus* tail as a model for missing elements yields a 17 m tail, suggesting a length of 40 m+.

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## Permo-Triassic Ecosystems

### AN UPPER TRIASSIC TERRESTRIAL VERTEBRATE ASSEMBLAGE FROM THE FORGOTTEN KOCURY LOCALITY (POLAND) WITH A NEW AETOSAUR TAXON

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Since 1990, several localities within the Keuper (upper Middle to Upper Triassic) strata in southern Poland have yielded remains of numerous terrestrial vertebrate species. Here we report a new Upper Triassic vertebrate assemblage from the rediscovered Kocury locality. An incomplete theropod dinosaur fibula named *Velocipes guerichi* described in 1932 was found there. The site was then forgotten and not explored until our excavations began in 2012, yielding material of a lungfish, a proterochersid turtle, and a new typhothoracin aetosaur *Kocurypelta silvestris* gen. et sp. nov. The new taxon is characterized by autapomorphies of the maxilla: an elongated edentulous posterior portion longer than 80% of the posterior maxillary process, a short medial shelf restricted to the posterior portion of the bone, an anteriorly unroofed maxillary accessory cavity, and lack of a distinct groove for choanal recess on the anteromedial surface of the bone. These new finds improve our knowledge of the vertebrate diversity of the Germanic Basin in the Late Triassic, showing the presence of previously unrecognized taxa. Additionally, the partial cranial aetosaur material emphasizes the issues with aetosaurian taxonomy that is focused mostly on the osteoderm morphology.

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## Biomechanics & Functional Morphology

### BIOMECHANICAL MODELING INDICATES TOOTH POSITION AND ROSTRUM SHAPE AS MAJOR INFLUENCES ON HETERODONTY IN THEROPODA

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Numerous studies have investigated the morphometrics of theropod teeth, typically for the purposes of identifying shed crowns or for phylogenetic analyses. As of yet, little work has looked at how the degree of heterodonty along the dental arcade may affect tooth function. We propose that a tooth's position relative to the jaw hinge is the major driving force in crown variability in ziphodont theropods, and construct a biomechanical model as a predictor of tooth form. Hypothetical jaw shapes were modeled using parabolic equations outlining the rostral margin at variable lengths. This provides a continuous range of variation in jaw shape that is mathematically constrained. Hypothetical, straight teeth were modeled at equal spacing along the jaw, so that jaw shape was the only biological variable. By sweeping the parabolic jaws through three-dimensional graphical space, tooth mechanics at each position could be quantified. Over this range of graphical space, we measured three parameters for each tooth position: 1) the relative force applied to each tooth 2) the arc length needed to contact substrate, and 3) the orientation of the crown's compressed axis relative to the hinge. We also quantified the effects of varying rostral lengths. Results showed the applied force and degree of rotation increased exponentially as crowns were more distally positioned. The compressed axis was relatively parallel to the long axis of the hinge for all but the mesial-most positions; here this axis became perpendicular and rotated about the hinge instead, making tooth damage more likely. These effects were all more pronounced in brevirostrine taxa. The most effective morphotype for modifying compliant substrate predicted by the model included an increase in the distal curvature of the apices in both taller crowns and those in more distal positions. The mesial-most crowns must also increase their labio-lingual bending strengths in order to function. Published databases of dental morphometrics support this model across several theropod families, as typical heterodonty includes a gradual increase in lateral compression and apical curvature, as well as a decrease in height, in the more distal positions. This model also provides functional explanations for unique theropod characters such as D-shaped and procumbent mesial teeth, convex tooth rows, incomplete denticulate carinae, and even partial/full edentulism.

## Dinosaur Systematics, Diversity, & Biology

### A MAZE OF *OMEISAURUS*: OBSERVATIONS ON THE TAXONOMIC STATUS OF *OMEISAURUS JUNGHSIENSIS* (DINOSAURIA: SAUROPODA: MAMENCHISAURIDAE)

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*Omeisaurus junghsiensis* was among the first non-avian dinosaurs named from China. It plays an important taxonomic role as the type species of *Omeisaurus*, which also contains the well-known *O. tianfuensis*. However, the taxonomy of *Omeisaurus* and other long-necked sauropods of Asia such as *Mamenchisaurus* remains poorly understood, and recent phylogenies have suggested that neither *Omeisaurus* nor *Mamenchisaurus* is monophyletic. Unfortunately, the holotype of *O. junghsiensis* has been lost, impeding further study.

To elucidate the taxonomic status of *Omeisaurus junghsiensis*, I included it and the four most complete referred species of *Omeisaurus* (*O. tianfuensis*, *O. maoianus*, *O. jiaoi*, and *O. puxiani*) in a phylogenetic dataset of 116 taxa and 421 characters that includes a diverse set of mamenchisaurids and other non-neosauropod sauropods, and analyzed the dataset with both maximum parsimony and Bayesian inference. Preliminary results support the monophyly of Mamenchisauridae and the inclusion of *O. junghsiensis* in that clade. The referred species *O. jiaoi*, *O. puxiani*, and *O. tianfuensis* form a clade, which is in a polytomy with *O. junghsiensis* and a clade comprising more derived mamenchisaurids. Under maximum parsimony, *O. maoianus* falls within the clade of more derived mamenchisaurids, whereas under Bayesian analysis, it is the sister taxon of *Xinjiangtitan* and the clade comprising the two forms part of the aforementioned polytomy. *Tienschanosaurus* is unstable but occupies a range of phylogenetic positions similar to the species of *Omeisaurus*. *Anhuilong* and *Huangshanlong*, which have recently been recovered as close relatives of *O. tianfuensis*, are not recovered as mamenchisaurids. *O. junghsiensis* possesses a unique combination of characters and can be distinguished from all other adequately-known mamenchisaurids.

These results neither support nor reject the inclusion of *O. jiaoi*, *O. puxiani*, and *O. tianfuensis* in *Omeisaurus*, though the clear differences between *O. tianfuensis* and *O. junghsiensis* and the failure to confirm the monophyly of the four species suggest that further study may justify the splitting of the genus. As has been found in previous

studies, *O. maoianus* is clearly separated from the other species of *Omeisaurus*, and reassignment of it to a new genus is encouraged. Further study of the taxonomy of *Omeisaurus* should take *Tienschanosaurus* into consideration, which occupies a similar phylogenetic position and only differs in a few characters.

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## Macroecology & Macroevolution

### EVOLUTION OF BODY MASS IN SAUROPOD DINOSAURS

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Sauropod dinosaurs are well known for being the largest terrestrial vertebrates. Estimating their body masses has been difficult because it involves substantial extrapolation beyond the body masses of extant terrestrial animals. Linear models developed to predict mass from stylopodial circumferences substantially overestimate body mass in large sauropods relative to 3D modeling approaches; use of quadratic models can reduce this discrepancy. The most comprehensive body mass studies of sauropods have used linear models and estimated body mass in only about half of known species. To gain a more complete picture of sauropod body mass evolution, I employed published and novel robust regression models to predict missing stylopodial circumferences. I used these circumferences to predict body mass using a quadratic model, producing a dataset with body masses of about 30% more sauropod species than has been previously assembled. The body mass distribution of Sauropoda is unimodal and strongly positively skewed, in contrast to the previously reported distribution of body masses within Sauropodomorpha, Ornithischia, or Theropoda. The highest mean sauropod body mass is observed in the Late Jurassic and mid-Cretaceous. No significant linear trend in body mass in Sauropoda as a whole is observed through time; however, the mean body masses of Diplodocoidea, Titanosauriformes, and Titanosauria all decreased through time with the evolution of a number of small-bodied forms in the Cretaceous. The mean body mass for Sauropoda is very similar to the maximum known body masses of both terrestrial mammals and the next-heaviest dinosaurs, hadrosaurs. At least four sauropod clades independently achieved or surpassed the observed upper limit of mammalian and hadrosaur body mass:

Mamenchisauridae, Brachiosauridae, and Turiasauria in the Jurassic and Titanosauria in the Cretaceous.

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## Holocene & Pleistocene Mammalian Faunas

### OVERSIZED KODIAK ISLAND BEARS: DIETARY BEHAVIOR AND BODY SIZE IN *URSUS ARCTOS* AS REVEALED BY DENTAL MICROWEAR TEXTURES

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Alaskan Kodiak Island bears (*Ursus arctos middendorffi*) seem to defy the trend of insular dwarfism that occurs in other mammals, exhibiting both abnormally large body sizes and higher population densities than would be expected for an island population of mammals. Both body size and population density are often closely associated and changes in either of these aspects can indicate changes in hunting or foraging behavior. For example, larger bears in a population could opt to occupy larger territories in order to forage for more fallback food on the mainland while they may instead crowd out other smaller bears from prime fishing spots in island environments. In this study, we seek to understand the differences in diet between Kodiak Island populations (from Kodiak Island), Admiralty Island populations (also known as the Sitka brown bear, *Ursus arctos sitkensis*), and mainland grizzlies (*Ursus arctos*), and what impact body size has on the dietary behavior of these populations. Dental microwear texture analysis is an effective tool in qualifying material properties of foods consumed by ursids and was used to evaluate the diet of grizzly bears throughout Alaska and through time. While Kodiak Island bears are indistinguishable in both complexity and anisotropy from mainland bears, bears from Admiralty Island ate softer foods than both Kodiak and mainland grizzly bears, consistent with a diet of softer foods such as high amounts of salmon. This apparent shift in diet seems to indicate a change in hunting behavior with a higher emphasis on fishing (as opposed to foraging) than mainland grizzlies, especially among larger individuals. The effects of individual body size on dietary behavior is also examined. These data provide insight into the many ways that body size can affect diet in modern and ancient mammals, notably omnivorous ursids.

**Funding Sources** National Science Foundation, USA (1053839), a Vanderbilt University Discovery Grant, Evolution Initiative and the Data Science Institute at Vanderbilt University.

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## Marine Mammals

### REEXAMINATION OF AN EOCENE CETACEAN *EOCETUS SCHWEINFURTHI* (CETACEA, PROTOCETIDAE): NEW DATA ON MORPHOLOGY, PHYLOGENY AND FEEDING STRATEGY

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Protocetidae is a family of middle Eocene semiaquatic cetaceans, dispersed worldwide in warm seas. A lot of protocetids were discovered in Egypt, including first known species, *Protocetus atavus* and *Eocetus schweinfurthi*. *E. schweinfurthi*, perhaps the largest protocetid known to date, is known by holotype, the skull (SMNS 10986). Several vertebrae found in the same sediments as the holotype (Guishi Formation, Bartonian, 40 Ma), were attributed to *Eocetus*. In 2015, Gingerich and Zouhri redefined *Eocetus* as Basilosauridae, based on newly found vertebrae and separate teeth. We reexamined the holotype of *E. schweinfurthi* and found it to be a member of Protocetidae, confirming the original classification by a few diagnostic traits supported by phylogenetic analysis. In particular, two separate roots of P1 are preserved in the maxilla; all the protocetids have the same P1 structure, whereas all the basilosaurids have P1 with one or two fused roots. The parietal foramen between parietal and squamosal is another common diagnostic trait for SMNS 10986 and Protocetidae: unlike them, Basilosauridae have the parietal foramen on the parietal as a common synapomorphy. The palatal surface of the premaxillae of SMNS 10986 is concave and there is a groove near the sagittal suture projecting caudally to P1. This feature is common for Protocetidae and shared by *Basilotritus wardii* among Basilosauridae. This anatomy of the premaxillae could be evidence for suction feeding. However, absence of palatal foramina suggests poorly developed gingiva compared to Pelagiceti. This fact, as well as the heavily worn teeth, argues against suction feeding and better supports raptorial feeding. Large skull

size and long rostrum are common features for *E. schweinfurthi* and *Georgiacetus vogtlensis*, a derived protocetid from North America.

Also, we examined two vertebrae hypothetically assigned to *Eocetus* and consider them belonging to Basilosauridae. This statement is supported by the position of the transverse processes, which are placed on the ventrolateral surfaces of the centra, small pre- and postzygapophyses of SMNS 10934, and the pachyostotic cortex (for NSFM 4470); pachyostosis is unknown for the Protocetidae skeleton. Many basilosaurids sharing this morphology come from the same geological age or even older, so the presence of a mix of protocetid and basilosaurid bones in the same formation is not surprising. Reexamination of such problematic materials helps to clarify phylogenetic relationships of extinct cetaceans.

**Funding Sources** This work was funded by the National Research Foundation of Ukraine (NRFU).

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## Stem Tetrapod, Squamate, & Amphibian Diversity & Biology

### THE SURPRISING LONGEVITY OF STEM-GEKKOTAN LINEAGES

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Gekkota (geckos and pygopods) comprise about 18% of living squamates. Gekkota is nested in the Gekkonomorpha. Within Gekkonomorpha, there are two skull configurations: (1) orbits completely enclosed by bone, seen in stem-Gekkotans such as *Eichstaettisaurus schroederi* from the Jurassic of Germany, *E. gouldi* from the Cretaceous of Italy, and another congener from Catalonia, and *Norellius nyctisaurops* from the Early Cretaceous of Mongolia; and (2) incomplete orbits due to the loss of the postorbital bar, observed in crown gekkotans and a few stem-gekkotans from Asia such *Hoburogekko suchanovi* (Early Cretaceous of Mongolia), *Gobekko cretacicus* (Late Cretaceous of Mongolia), and several geckos preserved in amber from Myanmar (Early and mid-Cretaceous). The latter forms closely resemble

crown gekkotans, but lack all of the derived features present in modern families. Molecular clock estimates place the origin of gekkotans in the Cretaceous, whereas Gekkonomorpha diverged from other squamates during the Jurassic, consistent with the age of these early gekkonomorphs. It was previously thought that gekkonomorphs with complete orbits did not survive beyond the K–T boundary, and that they were eventually replaced by forms with incomplete orbits. Here we report a fossil from the Messel Pit (47 million years ago, Eocene of Germany), which represents the first known Paleogene gekkonomorph with a complete orbit. This finding indicates that stem-gekkotans coexisted with gekkotans for a longer period of time than prior evidence suggested and extends the fossil record of non-Gekkotan gekkonomorphs to 93 million years.

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## Biomechanics & Functional Morphology

### AERODYNAMICS SHOW MEMBRANOUS-WINGED SCANSORIOPTERYGID THEROPODS WERE A POOR GLIDING FLIGHT EXPERIMENT

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The bizarre scansoriopterygid theropods *Yi* and *Ambopteryx* had skin stretched between elongate fingers that form a potential membranous wing used in aerial locomotion, but this has never been tested. Using Laser-Stimulated Fluorescence imaging we re-evaluate their anatomy and perform aerodynamic calculations covering flight potential, other wing-based behaviours and gliding capabilities. We find that *Yi* and *Ambopteryx* were likely



arboreal, highly unlikely to have any form of powered flight, had significant deficiencies in flapping-based locomotion and limited gliding abilities. Our results show that the Scansoriopterygidae are not models for the early evolution of bird flight and that their structurally distinct and inefficient wings differed greatly from contemporaneous paravians, supporting multiple independent origins of flight. We propose that the Scansoriopterygidae represent a unique but failed flight architecture of non-avian theropods and that the battle to capture the vertebrate aerial morphospace in the Middle to Late Jurassic was a dynamic and complex one.

**Funding Sources** HK RGC GRF 17120920 and 17103315, HKU Science RAE Improvement Fund & HKU MOOC Dinosaur Ecosystems (M.P.); HK PhD Fellowship PF16-09281 & M Benton, U of Bristol, UK (A.R.)

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## Late Cenozoic Mammalian Evolution and Ecology

### INFERRING ARCHAIC UNGULATE DIETS USING TWO-DIMENSIONAL DENTARY MORPHOLOGY

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Following the end-Cretaceous extinction, several ungulate lineages appeared and diversified. It is commonly understood that taxa at the beginning of this Paleogene radiation showed little dietary range, being largely generalists or invertivores, while taxa that appeared later in the radiation, including those at the base of the modern ungulate orders, showed a much greater range of diets, including herbivory. While this transition in diet is apparent when observing fossils from the two extremes of the radiation, the dynamics of dietary change within the radiation have not previously been well resolved. Here, we use a geometric morphometric approach to detect changes in diet based on the shape of the dentary. While diet is often inferred from tooth morphology, dentary shape can serve as an alternative when teeth are unavailable, poorly preserved, or worn, and can be analyzed based on two-dimensional photographs. In lateral view, the ramus of the dentary reflects the sizes of the muscles of mastication, and the body of the dentary reflects how the teeth are anchored and the jaw's resistance to stress. Using a discriminant function analysis (DFA), we employed a dataset of modern mammals to

analyze how the shape of the jaw relates to diet. The first two linear discriminants reflect variation in the depth of the mandibular angle, the anteroposterior length of the dentary body relative to the ramus, and the relative positions of the coronoid and condyloid processes. These axes of variation allow the discrimination of broad diet categories and some variation within categories. Among carnivores, a higher and more well-defined condyloid process is associated with consuming invertebrate rather than vertebrate prey. Among herbivores, a ramus that is tall, with a high condyloid process and a deep mandibular angle, suggests folivory over frugivory. When archaic ungulates and early members of modern orders are projected into the DFA, they do not group strongly with one another, but instead are distributed across a large area of the central morphospace described by modern mammals. Earlier ungulates largely group with carnivores and invertivores, while many later ungulates are placed with generalists, frugivores, or at the edge of the frugivore-folivore space, although none reach the extremes of modern folivory. This increase in variation suggests that, during the Paleogene, ungulates radiated into a variety of niches.

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## Colbert Poster Prize

### ELASMOSAURIDS THROUGH TIME: A COLLABORATION ACROSS THE AMERICAS

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Plesiosaurian diapsids have adapted to a fully marine lifestyle in a completely different way to any other vertebrate group. Within this diverse and long-lived clade notably characterized by a vertical four-flipper swimming locomotion and the decoupling of pectoral and pelvic girdles from the axial column, the exclusively Cretaceous Elasmosauridae stand out due to their particularly elongated necks. Ever since the description of *Elamosaurus platyrus* by Edward Cope in 1868, paleobiologists have strived to find a convincing adaptive

explanation integrating feeding and locomotory biomechanical advantages for this peculiar morphology. Why did the unique elasmosaurid body plan explore uncharted ecomorphospace compared with other plesiosaurs? Which ecomorphological insights for Elasmosauridae can be drawn from the study of changes in cranial, cervical, and appendicular anatomy throughout their Cretaceous evolutionary history? These questions are currently addressed in a comparative study of one of the earliest known elasmosaurids (cf. *Callawayasaurus* sp.), from the late Hauterivian–late Aptian Paja Formation, Boyacá, Colombia, and of one of the latest (*Terminonatator ponteixensis*), from the late Campanian Bearpaw Formation of Saskatchewan, Canada. The most notable anatomical differences between both species are observed in the skull and in the neck. For instance, cf. *Callawayasaurus* sp. appears to be part of a basal elasmosaurid clade characterized by an increased cervical count in relation to other plesiosaurs. In contrast, *T. ponteixensis* is a member of the exclusively Late Cretaceous North American Elasmosaurinae (Styxosaurinae), a clade characterized not only by an increased cervical count but also by elongated individual cervical centra. In order to compare the respective biomechanics of these species, such as their possible ranges of neck motion, 3D models of their preserved skeletons have been produced with a portable visible-light scanner during research travel to the *Centro de Investigaciones Paleontológicas* in Villa de Leyva and the Royal Saskatchewan Museum. This project is part of a wider collaboration between the Larsson Lab at McGill University’s Redpath Museum and the former institutions. It is a rare opportunity to unite Canadian and Colombian paleontologists with the help of a fast-developing 3D scanning technology and will eventually lead to reconstructions of both skeletons in their pre-burial state for research and science outreach.

**Funding Sources** McGill University, Canadian Foundation for Innovation

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### Avialan Evolution & Biology

#### THREE-DIMENSIONAL RECONSTRUCTION OF VERTEBRATE MORPHOLOGY AND QUANTIFICATION OF TAPHONOMIC DEFORMATION

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Taphonomic and diagenetic processes during decay, burial, and fossilization often distort the original morphology of fossil remains. Fossil birds are especially vulnerable to taphonomic deformation due to their relatively small size and comparatively delicate skeletons usually characterized by thin bone walls. Such distortion may hinder interpretations of detailed morphology, influence taxonomic diagnoses, and affect phylogenetic hypotheses if important morphological information is directly affected by deformation. Here, we present an idealized three-dimensional reconstruction of the sternum of the crownward stem-bird *Ichthyornis dispar* through application of a novel reconstruction workflow, combining retopology with retrodeformation, and addressing both symmetrical and asymmetrical elements. All known *Ichthyornis* sterna were CT-scanned and segmented to obtain three-dimensional models of the bones free of any matrix. Well-preserved areas of the different *Ichthyornis* sterna were combined into a single, idealized composite representation through superimposition and alignment of the retopologized models, and the composite was subsequently retrodeformed. Our workflow enabled the quantification of the deformation of the individual specimens with respect to our reconstruction, and the determination of major global as well as local taphonomic deformation axes. The proposed workflow can be integrated with geometric morphometric approaches to enable quantitative morphological comparisons between multiple specimens, as well as the direct interpolation of ‘mediotypes’ of axial elements (e.g., missing vertebrae, haemal arches, or ribs)

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### Mesozoic & Paleogene Mammals

#### THE FIRST JUVENILE OF *PANTOLAMBDA BATHMODON* (MAMMALIA, PANTODONTA) FROM THE SAN JUAN BASIN, NEW MEXICO, USA

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Mammals survived the Chicxulub impact sixty-six million years ago and diversified into a wide variety of new ecological niches left by non-avian dinosaurs. Pantodonts, an enigmatic group, quickly achieved hefty post-extinction body sizes to occupy large herbivore niches.

We describe the first juvenile specimen of the Paleocene pantodont *Pantolambda bathmodon* (NMMNH P-27844) consisting of a partial skeleton including parts of the skull, a deciduous upper premolar series, nearly complete forelimbs, and elements of the carpus and hind limb. P-27844 is from the Torrejonian (~62.3 Ma) Tsosie Member of the Nacimiento Formation.

P-27844 has the first deciduous teeth known for *Pantolambda*. dP2 and dP4 are submolariform with a triangular cross-section and a less developed protocone than adults. dP5 is molariform with a large paracone and metacone connected by wing-like cristae to form the w-shaped ectoloph typical of this genus' molars. dP5 also has more pronounced conules than the molars. This molarization style of the ultimate premolar is seen across Pantodonta including in *Alcidedorbignya inopinata*, *Barylambda faberi*, and *Coryphodon* sp. The postcranial morphology of P-27844 is generally concordant with that of adults. This correspondence manifests particularly clearly in the forelimbs. The distal humerus exhibits the base of a posterolaterally directed epicondylar crest which likely anchored the anconeus and the extensor carpi radialis muscles, a deep radial fossa, and an open entepicondylar foramen. The ulna shows a well-developed anconeal process, a pronounced biceps and brachialis fossa, and a shallower groove to accommodate the abductor pollicis longus. The radius possesses a shallow pronator crest that originates near its distal end and extends about two-thirds of the way along the shaft. Interestingly, in contrast to adults, the radial shaft is straight rather than having moderate sigmoidal curvature and has not undergone epiphyseal fusion. Altogether, these osteological features illustrate that, even at its early ontogenetic stage, P-27844 possessed robust forelimb musculature.

Using Developmental Mass Extrapolation from long bone measurements, P-27844's body mass is estimated to be ~17 kg at time of death (~40% of adult body mass). Paleohistological analyses demonstrate the animal experienced a rapid pace of life for its body size and died ~2.5 months after birth. This specimen gives unprecedented insight into the early life history of *Pantolambda*.

**Funding Sources** European Research Council Starting Grant (ERC StG 2017, 756226, PalM); National Science Foundation (NSF; EAR 1654952, DEB 1654949); The Royal Society (NIF\R1\191527)

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## Late Cenozoic Mammalian Evolution and Ecology

### TREE-CLIMBING IN SEARCH OF FRUIT: PALEOECOLOGY OF THE DIPROTODONTID *NIMBADON LAVARACKORUM*

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Diprotodontids, a group of large-bodied wombat-like herbivores, were broadly distributed in Australasian Cenozoic deposits. While most diprotodontids were terrestrial quadrupeds and are often compared to placental herbivores like rhinoceros and hippopotami, the zygomaturine diprotodontid *Nimbadon lavarackorum* is thought to have occupied the treetops. Understanding the dietary ecology of *N. lavarackorum* during the Miocene can help clarify potential motivations for an arboreal lifestyle. Here, we examine dental microwear textures of *N. lavarackorum* specimens from the Riversleigh World Heritage Area using three-dimensional dental microwear texture analysis to assess hard vs. tough food consumption. Despite phylogenetic differences, tapirs are bilophodont like diprotodontids and thus suitable for ecological comparisons. *Nimbadon lavarackorum* displays dental microwear textures (specifically, higher complexity values) most similar to the more frugivorous/hard palm seed eating tapir *Tapirus bairdii* and distinct from the more folivorous *Tapirus terrestris*. Further, when compared to Pleistocene diprotodontids, *N. lavarackorum* shows significantly higher complexity than *Diprotodon* and *Zygomaturus*, suggesting that it consumed distinctly harder food items. When compared to the extant macropodids, including the grazer *Macropus giganteus*, mixed-feeder *Macropus fuliginosus*, specialized browser *Setonix brachyurus*, and mixed woody browser *Wallabia bicolor*, *N. lavarackorum* has significantly greater complexity than all taxa except *W. bicolor*. Much like many extant frugivorous bovids, primates, and tapirs, these data collectively suggest that

*N. lavarackorum* consumed hard and/or more brittle foods with DMTA attributes indistinguishable from a diverse suite of frugivores. Stable carbon isotopes of *N. lavarackorum* (n=14) also indicate the consumption of C<sub>3</sub> food sources, consistent with fruit or foliage of C<sub>3</sub> plants in a forest environment. Fruits may have been a motivation for moving into or staying in the treetops.

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## Fishes Evolution & Distribution

### A NEW SPECIES OF *EUSTHENODON* (SARCOPTERYGII; TETRAPODOMORPHA) AND OTHER TRISTICHOPTERIDS FROM THE CATSKILL FORMATION OF PENNSYLVANIA, USA

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A new species of *Eusthenodon* from the Upper Devonian (Famennian) Catskill Formation was collected from talus blocks at the base of a road cut along the Cogan House exit ramp on US 15/Interstate 99 in Lycoming County, Pennsylvania, USA. The new species is represented by a nearly complete, articulated skull (ANSP 23748) and additional isolated and partially articulated cranial bones, body scales, and pectoral girdle elements. The breadth of anatomy represented by the new fossils, and the quality of their preservation and preparation, enable a detailed anatomical description. The completeness of the articulated skull presents an opportunity to re-diagnose *Eusthenodon*. The original diagnosis of the taxon served only to distinguish it from *Tristichopterus* and *Eusthenopteron*, the only other described tristichopterids at the time. The descriptive qualities of the *Eusthenodon wangsjoi* type material do not diagnose *Eusthenodon* from among the highly nested tristichopterid taxa that have been discovered since the original publication. In an effort to strengthen the taxonomic status and phylogenetic utility of *Eusthenodon*, we propose a revised diagnosis that uses only discrete features that are commonly

preserved and unlikely to be altered by specimen deformation. The new species is the third tristichopterid to be described from the Catskill Formation along with *Hyneria lindae* and *Langlieria radiatus*. All three are large-bodied and in a highly-nested phylogenetic position within the group. Two additional records of large-bodied, highly-nested tristichopterids in the Catskill Formation, from near Port Matilda, Centre County, and from near Trout Run, Lycoming County, appear likely to represent a fourth and fifth species. The presence of a single tristichopterid species at each site highlights temporal and spatial regionalization of the Catskill fauna and may, along with a suite of anatomical features, support the hypothesis that tristichopterids occupied the role of top predator in the freshwater ecosystems of the Catskill Delta complex.

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## Permo-Triassic Ecosystems

### NOTES ON VARIATION IN PELVIC DEVELOPMENT OF THE LATE TRIASSIC AETOSAUR *STAGONOLEPIS OLENKAE* FROM NORTHERN PANGEA

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Heavy armoured aetosaurs (*Pseudosuchia*) are one of the most abundant animals within terrestrial megafaunal assemblages of the Late Triassic. Despite that, only a few forms are described based on complete or articulated material. Many of the species are established solely on the morphology of osteoderms, or minor differences in skull and non-dermal postcrania, especially the pelvis and vertebrae. However, little is known about the intraspecific and ontogenic variance within this group. Here we present our preliminary results on variation in the pelvis of *Stagonolepis olenkae*. We found that ilium thickness increases during ontogeny and causes major changes in the morphology of the iliac blade and acetabulum. In addition, pelvic elements fuse with age, but this process does not have a uniform pattern and is intraspecifically variable. We also recognized some features as being very susceptible to damage due to diagenesis, such as the

orientation of the acetabulum, shape of the iliac blade processes, and the shape and number of pubic foramina. Our studies demonstrate that at least some of the pelvic features used in taxonomy are intraspecifically variable or influenced by taphonomy. Many of those characters are used also for cladistics analysis and constructing hypotheses of locomotion, not only in regard to actosaurs, but also other Triassic pseudosuchians. Better understanding of their variance is a small step for more accurate reconstruction of their evolutionary history and life.

**Funding Sources** NCN grant project number: 2019/33/B/NZ8/01453

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### **Taphonomy, Paleoenvironments, & Stratigraphy**

#### **I LOVE LUCY, FOR DINNER: CROCODYLIAN BITE MARKS AND THE CHALLENGES OF EQUIFINALITY IN THE HOMININ-BEARING HADAR FORMATION OF ETHIOPIA**

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Positively identifying bone surface modifications in hominin-bearing deposits is complicated by convergence between stone tool marks and other taphonomic alterations, including trample marks and crocodylian bite marks. Recent analyses statistically comparing these types of surficial bone damage are helping refine methods for differentiating superficially similar traces. Additionally, ongoing characterization of the total diversity of possible traces associated with these taphonomic agents, instead of concentrating on reporting only diagnostic features, is providing guidance on differentiating suites of characteristic marks. A recent survey of bone surface modifications present within Hadar, a 3.42–3.04 million year old, hominin-bearing fossil site in Ethiopia, reveals an assemblage of crocodylian bite marks ranging from diagnostic to deceptively convergent with some stone tool marks. Tooth marks are present on a variety of prey

remains, including bovids, hippopotamids, suids, and equines. Association with crocodylians is based on the presence of bisected marks, a subscore or notch caused by the carinae of freshly erupted crocodylian teeth. Several hook scores, which are associated with inertial feeding, are present on prey bone. Many of these remains also preserve microstriations, that recently have been associated with modern crocodylian feeding behavior, but which historically were used to identify stone tool marks. Crocodile fossils are common in the Hadar Formation, but all are attributable to a single species of Paleoafrican *Crocodylus*. Associated bite marks are all consistent with the dentition, snout outline, and dental spacing within the tooth row of this species. Size estimates place all of the modified groups within the expected prey sizes of the crocodile population, based on its snout shape, dentition, and size. Additionally, two specimens of *Crocodylus* also bear sets of serial bite marks that are consistent with similarly-sized conspecifics, suggesting that they were the result of intraspecific competition. The generalist morphology of this species of *Crocodylus*, partnered with the frequency and distribution of its bite marks, converge on the interpretation that this semi-aquatic ambush predator was willing and able to consume a wide variety of vertebrates, making nearing the water's edge a particularly dangerous proposition for the fauna of the Hadar Formation, including our early relatives, the australopithecines.

**Funding Sources** NSF DEB 1257786 and the Leakey Foundation

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

#### **A MORPHOMETRIC ANALYSIS OF THE TURTLE MANUS AND ITS IMPLICATIONS FOR THE PALAEOECOLOGY OF EXTINCT TURTLES**

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Among the most widely used predictors of palaeohabitat in fossil turtles is the skeletal proportions of the forelimb (humerus:ulna:manus), yet its application has been criticized because the ternary diagrams used to represent those proportions neither control for phylogeny, nor

provide statistical likelihood estimates for palaeohabitat assignment. In this study, we apply linear statistical modeling to investigate the relationship between forelimb proportions and habitat among turtles, and use them to infer the palaeohabitats of problematic fossil taxa. We performed three morphometric analyses: the first on the major components of the forelimb (humerus, ulna, manus), the second on the manus proper (metacarpals, phalanges, unguis), and the third combining these two datasets (humerus, ulna, metacarpals, phalanges, unguis). For each dataset, we used phylogenetic generalized least squares regression to extract the residuals for subsequent analysis, which are corrected for both size and phylogenetic non-independence of taxa. Each set of residuals was subjected to a linear discriminant analysis (LDA) to determine their predictive accuracy on habitat, which was divided into the following six bins: 'all bodies of water', 'moving or large bodies of water', 'primarily on land', 'primarily on land often in water', 'primarily on land seldom in water', and 'stagnant or small bodies of water'. We then used the discriminant functions to predict the palaeohabitats of the extinct *Basilemys variolosa*, *Palaeochersis talampayensis*, *Proganochelys quenstedti*, *Eunotosaurus africanus*, and *Odontochelys semitestacea*. The manual dataset and combined forelimb and manual dataset performed similarly well, with classification accuracies of approximately 82% and 83%, respectively. The forelimb dataset performed poorest, with a classification accuracy of just 72%. Based on these analyses, *B. variolosa* is resolved as a fully terrestrial turtle that preferred dry environments with well-drained substrates; *Pa. talampayensis* and *Pr. quenstedti* are similarly recovered as highly terrestrial; *E. africanus* was likely primarily terrestrial, occasionally venturing to the water; and *O. semitestacea* was likely semi-aquatic, spending significant periods of time both on land and in the water. Taken together, these results suggest that manual proportions provide a particularly powerful habitat proxy in turtles, and provides still further evidence that stem turtles were primarily terrestrial in nature.

**Funding Sources** NSERC Discovery Grant to JM and an Ontario Graduate Scholarship to TD

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## Fishes Evolution & Distribution

### CHIMAEROID EGG CAPSULES FROM THE LATE JURASSIC LITHOGRAPHIC LIMESTONES OF SOUTHERN GERMANY

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Chimaeroid fishes are all oviparous; the females oviposit distinctive leathery, collagen-rich, multi-layered, proteinaceous egg capsules which enclose both the yolk and the developing embryo which feeds on it. The high organic, low inorganic composition of the egg capsule gives it low preservation potential, so that much taphonomic loss occurs through decomposition, bioerosion, deposition in unsuitable sedimentological facies, etc. This means that chimaeroid egg cases are very rare components of marine ichnofaunas. Despite this, 11 ichnospecies have been recorded in deposits ranging from the Late Triassic onwards.

Chimaeroid egg cases are all somewhat flattened, bilaterally symmetrical structures comprising an ovoid central trunk which tapers posteriorly to an elongate pedicle or tail, and more gradually anteriorly to form a somewhat blunt beak or snout. The spindle-shaped central cavity houses the embryo, whose shape it closely matches. The lateral margins of the case are extended to form a membrane or web which is commonly ornamented by rib-like corrugations or costae, which may be branched or unbranched. Since the case is relatively impermeable to oxygen, movements of the embryo stimulate water entry and through-flow via a system of fine pores enabling efficient exchange of dissolved O<sub>2</sub> and CO<sub>2</sub>. Chimaeroid egg cases are normally laid in pairs and those of the three extant families (Chimaeridae, Rhinochimaeridae, Callorhynchidae) can be distinguished on their external morphology.

The late Jurassic (late Kimmeridgian to Tithonian) lithographic limestones (Plattenkalk) of the Solnhofen and Nusplingen areas in southern Germany have yielded occasional spectacular holomorphic specimens of myriacanthoid (*Chimaeropsis paradoxa*), rhinochimaerid (*Elasmodectes avitus*) and callorhynchid (*Ischyodus quenstedti*) holocephalians. Very rare, single morphotype egg cases also form part of the holocephalian fauna in the Schernfeld area (~8km east of Solnhofen) and are reviewed here. The best example (LF 703) is a double egg case, with each measuring around 489 mm long and 72 mm across. The fusiform central cavity is elongate, extending into the long, slender pedicle. The beak is also quite slender. The relatively narrow lateral web is ornamented by a series of ~50 costae. The overall form

of the case suggests that it belongs to a callorhynchid, and the size makes *Ischyodus quenstedti* a likely producer.

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## Dinosaur Systematics, Diversity, & Biology

### THE BRAINCASE OF A VERY YOUNG INDIVIDUAL OF THE EARLY-DIVERGING IGUANODONTIAN *DRYOSAURUS ELDERAE* (DINOSAURIA: ORNITHOPODA) FROM THE UPPER JURASSIC MORRISON FORMATION OF UTAH: ONTOGENETIC IMPLICATIONS

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Recent 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) provides new insight into intraspecific ontogenetic change in the braincase. 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. Prior analyses indicated clear signs of juvenility in CM 11340, such as its small size, large orbits, short face, and large neurocranium. Our studies confirm those findings, but CT scanning reveals new details of braincase structure. CM 11340 and CM 87688 were microCT scanned at a slice thickness of 25 µm, whereas the slice thickness for CM 3392 was 300 µm. The CT data were analyzed using both watershed and manual segmentation within Amira-Avizo. The braincase of CM 11340 represents one of the ontogenetically youngest and most complete examples among non-hadrosauroid ornithopods, meriting close attention. Preserved elements include the basioccipital, parabasisphenoid, supraoccipital, both otoccipitals, both prootics, both columellae, right laterosphenoid, both frontals, and parts of the parietal, all of which were segmented separately. The surface models were exported to Maya for reassembly, restoration, and comparison with

ontogenetically older conspecifics (CM 3392, CM 87688) and a juvenile individual of the Tanzanian dryosaurid *Dysalotosaurus lettowvorbecki*. Among other findings, the abducens nerves were not captured in canals within the parabasisphenoid in CM 11340, whereas they were in CM 3392 and CM 87688, indicating the extent of the juvenility of CM 11340. Nevertheless, a theropod-like caudal tympanic recess was found in all three *D. elderae* specimens, including CM 11340, raising questions about how widely this feature might be distributed in other ornithopods. The restored braincase of CM 11340 enables the generation of a brain endocast in Maya, allowing comparison to the existing endocast of CM 3392 and analysis of ontogenetic changes in brain shape.

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## Colbert Poster Prize

### REVISIONS TO THE LATE UINTAN MAMMALS OF THE SWIFT CURRENT CREEK LOCALITY, SASKATCHEWAN

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The Swift Current Creek (SCC) local fauna is a diverse assemblage of isolated mammal teeth from a fluvial deposit in southern Saskatchewan, biochronologically dated to the late Uintan NALMA, 44–40 Ma. In addition to previous faunal revisions made by other researchers (*Namatomys fugitivus* = *Metanoiamys fugitivus*; *Wallia scalopidens* upper molars = a molossid; *Procaprolagus vusillus* = *Desmatolagus vusillus*; *Peratherium* = *Herpetotherium*), further faunal revisions made in light of new research include: *Pseudocylindrodon citofluminis* = *P. cf. tobeyi*, Chiroptera sp. 2 = *Bessoecetor sp.*, *Epihippus cf. gracilis* = ?*Orohippus sp.*, *Domnina sp.* = *Domnina cf. sagittariensis*, Brontotheriidae gen et sp. indet. = ?*Rhinotitan cf. kaiseni*, *Hyopsodus fastigatus* = *H. cf. paulus* and *H. cf. sholemi*, *W. scalopidens* lower molars = a talpid, and the confirmation of marsupials closely aligned to those of the Duchesnean Lac Pelletier local fauna (*Herpetotherium cf. marsupium* and *Herpetotherium cf. knighti*). Some taxa described (i.e., Leporidae sp.; *Leptotomus sp.*) are considered incertae

sedis due to poor preservation of material crucial for identification. The upper molars of some taxa (*Janimus* and *Protadjidaumo*) cannot be identified with certainty as these are not known for the type species. The presence of *Janimus*, *Protadjidaumo*, and *Mytonomeryx*, indicate a late Uintan age. The SCC locality represents the last appearance of *Bessoecetor*, and the earliest appearance of talpids in North America. These range extensions will allow refinement of our understanding of middle Eocene North American biochronology. The presence of *?Rhinotitan* in Canada would expand the geographic range of this brontothere genus considered exclusive to Asia.

**Funding Sources** NSERC Discovery Grant to Jessica Theodor

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## Stem Tetrapod, Squamate, & Amphibian Diversity & Biology

### A NEW HERPETOFAUNAL ASSEMBLAGE (AGAMIDS AND RANOIDS) FROM THE LATE EOCENE LOCALITY BQ-2 OF THE FAYUM DEPRESSION, EGYPT.

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Locality BQ-2 (earliest late Eocene, Priabonian ~37 Ma) of Egypt is the oldest site in Africa that unambiguously documents the presence of Anthropoidea (monkeys, apes, and humans), and has yielded some of the most important Paleogene mammal fossils in Afro-Arabia. However, few ectothermic animals (fishes, reptiles, and invertebrates) have been reported from BQ-2. Here, we report on the oldest Paleogene record of Anura from Egypt, represented by dermal bones with pit-and-ridge sculpture that is very similar to that of the ranoid *Thaumastosaurus* from Europe. In addition, the new BQ-2 materials include three distal parts of amphibian humeri. We also report the first “agamid” lizards from the late Eocene of Africa, based on

tricuspid pleuroacrodont toothed bone fragments. The specimens are difficult to diagnose at the species level, however the specimens attest to the previously hypothesized widespread geographical distribution of acrodontans in the northern hemisphere throughout much of the Paleogene. Furthermore, the occurrence of fossil “agamids” and ranoids in Africa during the Eocene allows us to investigate possible dispersal routes to and from Europe and Asia, as reported before for fishes, other squamates, and mammals. Additionally, the new ectothermic fossil material delivers a tentative paleoenvironmental reconstruction for the Fayum Depression and Egypt during the Paleogene period.

**Funding Sources** Mansoura University Research Fund and the American University in Cairo research fund.

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## Fishes Evolution & Distribution

### A LONGIROSTRINE TELEOST FISH FROM THE LATE CRETACEOUS OF LEBANON, AND ITS IMPACT ON THE PHYLOGENY OF TSELFATIIFORMES

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Tselfatiiformes is an enigmatic group of ray-finned fishes, with a relatively short stratigraphic range extending from the Albian to the Campanian. This clade shows its highest diversity during the Late Cretaceous in the Western Interior Seaway of North America. Haqel and Hjoula, two Lebanese Cenomanian localities that represent the richest fish assemblages for the Mesozoic worldwide, also yield a number of tselfatiiformes. Despite being the focus of investigation since the nineteenth century, the phylogenetic position of these fishes is still disputed and the intrarelationships within the clade are far from being resolved. To tackle this issue, we studied new material of Tselfatiiformes from the Cenomanian of Lebanon together with representatives of this clade from other



localities in Europe, Morocco, and the Western Interior Seaway of North America. These form the basis of osteological, phylogenetic, and palaeobiogeographical analyses. New Lebanese material consists of two exceptionally preserved specimens. The first originates from Hjoula. It is complete and was assigned to the genus *Protobrama* of the Lebanese endemic family Protobramidae, based on the absence of pelvic girdle and fins, the proportions of the head, and the fusion of hypurals in a hypural plate. It measures 45 mm in total length suggesting it is a juvenile form of the genus. The second specimen is from Haqel. It is incomplete and shows more affinities with the younger North American genus *Martinichthys* of the family Plethodidae, rather than previously known Lebanese genera. Shared derived features include the presence of the characteristic long rostrum formed by the fusion of two enlarged premaxillae. This *Martinichthys*-like taxon is the first example known from Lebanon. We used these data to include the Tselfatiiformes in a computer-based phylogenetic analysis using a newly created synthetic matrix. This will allow us to evaluate the position of tselfatiiforms among teleost fishes and resolve intrarelationships within the group.

**Funding Sources** This research is funded by the Swiss Government Excellence Scholarships [grant number 2019.0892], and by the Foundation Augustin Lombard and the Schmidheiny Foundation.

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## Fishes Evolution & Distribution

### A NEW MARINE FISH FAUNA DATING TO THE LATEST DANIAN EVENT (LDE – 62.2 MA) OF THE EASTERN DESERT, EGYPT

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The early Paleogene was marked by apparent diversification in several vertebrate clades following the end-Cretaceous extinction. However, gaps in the early Paleocene (Danian) record for many groups are an obstacle to testing competing models of extinction and recovery. This problem is particularly acute for percomorph (perch-like) teleost fishes, a clade containing over 14,000 living species. While diverse marine fish assemblages are known from the Late Cretaceous (e.g., Nardò, Italy) and the early Eocene (e.g., Danata Formation, Turkmenistan), the record of articulated material from the critical Danian interval is restricted to only a handful of sites worldwide. We report a horizon in Gebel Qreiya in the Eastern Desert of Egypt that provides new information on paleotropical (~9°N paleolatitude) marine fishes from the southern Tethys. The fossils occur in the top part of the Dakhla Formation in a dark laminated marl marking the base of the Latest Danian Event, a hyperthermal dated to 62.2 Ma. These fish-bearing layers were deposited in an outer neritic to upper bathyal setting (150–250 m). The fossils are generally articulated and complete, with over 50 specimens recovered during a single field visit. Most individuals measure only a few centimeters in length. Multiple taxa are present based on material collected to date, but the most striking member of the fauna is the moonfish, *Mene*. The fossils from the Latest Danian Event bed predate the earliest previous occurrence of *Mene* by more than 5 million years, and represent the oldest example of an articulated percomorph assignable to an extant genus. They provide an important new temporal constraint on the evolutionary radiation of perch-like fishes, and demonstrate over 60 million years of remarkable anatomical conservatism in menids. Other fishes include an undetermined form with fan-like pelvic fins and a long-based dorsal fin bearing elongated spines. In addition to its critical stratigraphic position, the low-latitude Danian Gebel Qreiya assemblage begins to fill a paleogeographic gap in the record of articulated early Paleogene marine fishes, which so far has been dominated by assemblages from mid-latitude sites in Europe and western Asia.

**Funding Sources** Mansoura University Research Fund and the American University in Cairo research fund.

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## Stem Tetrapod, Squamate, & Amphibian Diversity & Biology

## **DOES REPTILE BODY SIZE TRACK ENVIRONMENTAL TEMPERATURE WITHIN LOCAL ASSEMBLAGES OR ACROSS CONTINENTAL INTERIORS?**

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Metabolic theory for ectothermic vertebrates predicts that maximum body size should correlate with environmental temperature. I have been testing this theory on geologic time scales by investigating patterns of body size evolution in lizards and crocodyliforms in the U.S. Western Interior through major climatic transitions in the Paleogene. My recent studies indicate that maximum body size in lizards corresponds to local terrestrial temperatures through the Paleogene across this geographic area, whereas crocodyliforms do not show a relationship between these variables. But do these patterns emerge within localized community assemblages? Or do they only surface across continental interiors? Here, I test the hypothesis that the observed relationship between lizard maximum body size and environmental temperature is ubiquitous across the intermontane basins of the U.S. Western Interior throughout the Paleogene, and that crocodyliforms do not show a relationship regardless of geographic scale. Using regressions from measurements of extant taxa, I reconstructed snout-vent length (SVL) from individual cranial or limb elements for 271 lizard and 234 crocodyliform fossil specimens from across this geotemporal system. I georeferenced every fossil locality represented and analyzed the taxonomic and body size distribution of each intermontane basin assemblage with respect to local temperature proxies. My results indicate that maximum SVL in the large-bodied lizard families present, Anguidae and Varanidae, indeed tracks local terrestrial temperatures within individual basin assemblages through the Paleogene. This pattern is consistent across contemporaneous and adjacent assemblages. Interestingly, during the warmest interval in the early Eocene, the largest lizards (about 0.9 m) rival some crocodyliforms in body size within basin assemblages. These lizards are insectivorous and likely occupy the same ecological resource space as co-occurring mid-sized insectivorous mammals. In contrast to the lizards, crocodyliform SVL does not appear to track local terrestrial temperatures through deep time at the basin level. Maximum SVL (about 2 m) and SVL range for crocodyliforms are consistently large across the intermontane basins through the Paleogene. These

findings support the hypothesis that the observed relationships between body size and environmental temperature manifest within communities as well as across continental interiors over geologic time.

**Funding Sources** UC Museum of Paleontology, Dept. Integrative Biology at UC Berkeley, SVP, Geological Society of America, Evolving Earth Foundation, Sigma Xi, Burke Museum Natural History

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## **Romer Prize**

### **RADIATION OF AQUATIC PREDATORY DINOSAURS**

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Secondary aquatic adaptations evolved multiple times independently from terrestrial tetrapod ancestors. However, non-avian dinosaurs were largely an exception to this pattern. Only a few species have been hypothesized as aquatic (hadrosaurids, sauropods, spinosaurids, and early dromaeosaurs), but were contested in the absence of unambiguous anatomical indicators of aquatic habits in extinct animals. Therefore, the evolutionary occurrence and distribution of aquatic ecologies among dinosaurs remain unclear, representing a century-long gap in our biological understanding of these animals. The difficulty in inferring aquatic habits from skeletal morphology requires examination of other proxies. Variation in bone compactness provides such possibility. Bone compactness in the femoral diaphysis of 141 extant and extinct amniotes, including novel osteohistological data for non-avian dinosaurs, was quantified to test the association of diaphyseal bone compactness with ecological traits. To test these hypotheses, AICc-based model comparison of phylogenetic multiple regressions was applied, also evaluating the influence of allometry using the maximum diameter of the femur diaphysis as a size proxy. Taxa with known ecology were scored using two categorical explanatory variables that encode the presence of (1) subaqueous foraging, and (2) flying in a comprehensive evolutionary framework. Bone compactness is found as a powerful size-independent proxy to infer diving adaptation across amniotes, including non-avian dinosaurs. This relationship between bone compactness and ecology was applied to establish quantitative predictions of diving behaviour for non-avian dinosaurs

previously suggested to be ecologically linked to water. Spinosauridae, a clade of predatory dinosaurs, was ecomorphologically adapted to a life in water, showing surprising ecological disparity, including subaqueous foraging behavior. These findings greatly increase the ecological disparity of non-avian dinosaurs, challenging the long-standing hypothesis of this group as restricted to terrestrial environments. Spinosaurids are part of the rapid radiation of Tetanurae following the Karoo-Ferrar large igneous province during the Mid Jurassic. Exploration of ecological regimes might have facilitated ecomorphological radiation linked to the invasion of new environments: while multiple dinosaur clades independently evolved flight capabilities, other non-avian dinosaurs explored aquatic ecosystems.

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### Preparators'

#### AN APPROACH TO USE CYCLODODECANE AS PROTECTION FOR MECHANICAL MATRIX REMOVAL OF A THEROPOD TOOTH

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At the Centro Paleontológico de Enciso (La Rioja, Spain), a theropod tooth, preliminary assigned to Carcharodontosauridae, was found half extracted from the matrix. First, a preliminary study of the state of conservation of the tooth was carried out and a proposal for the extraction of the tooth from the matrix was drawn up. The tooth has transverse cracks, so it was decided that was necessary to temporarily protect the tooth for its extraction. Given that the protection of the tooth must be temporary, the use of cyclododecane was proposed. Detailed photographs of the tooth surface were taken using a reflex camera and a Dino-Lite to evaluate the effectiveness of the protection of the tooth. The most effective way to apply cyclododecane was evaluated. Cyclododecane can be applied undissolved using heat or dissolved in an organic solvent. Thanks to the literature, it was possible to check how cyclododecane protects macroporous stone surfaces when it is applied directly with some heat, and dissolved at 80%, 60% and 40%. The

tooth shows a low porosity, analysed by a quick test of a surface tension. Considering this feature and the results published in the literature, it was decided to apply cyclododecane dissolved at 40% in the organic solvent (white spirit) and at 60% in the area with the most damage, on Japanese paper to maximise reversibility and add an extra layer of protection. After removal of the tooth from the matrix, a detailed visual analysis was performed again using Dino-Lite to check the correct protection by this method.

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### Biomechanics & Functional Morphology

#### A FUNCTIONAL ASSESSMENT OF MORPHOLOGICAL HOMOPLASY IN STEM-GNATHOSTOMES

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The Osteostraci and Galeaspida are stem gnathostomes, occupying a key phylogenetic position for resolving the nature of the jawless ancestor from which jawed vertebrates evolved more than 400 million years ago. Both groups are characterized by the presence of rigid headshields that share a number of common morphological traits, in some cases hindering the resolution of their interrelationships and the exact nature of their affinities with jawed vertebrates. Here, we explore the morphological and functional diversity of osteostracan and galeaspid headshields using an innovative approach that combines geometric morphometrics and computational fluid dynamics, thereby constraining the underlying factors that promoted the evolution of their similar morphologies and informing on the ecological scenario under which jawed vertebrates emerged. Phylomorphospace, Mantel analysis, and Stayton metrics demonstrate a high degree of homoplasy. Computational fluid dynamics reveals similar hydrodynamic performance among morphologically convergent species, indicating the independent acquisition of the same morphofunctional traits and, potentially, equivalent

lifestyles. This confirms that a number of the characters typically used to infer the evolutionary relationships among galeaspid, osteostracans, and jawed vertebrates are convergent in nature, potentially obscuring understanding of the assembly of the gnathostome bodyplan. Ultimately, our results reveal that while the jawless relatives of the earliest jawed vertebrates were ecologically diverse, widespread convergence on the same hydrodynamic adaptations suggests they had reached the limits of their potential ecological diversity – overcome by jawed vertebrates and their later innovations.

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## Avialan Evolution & Biology

### MESOZOIC FOSSIL INSIGHT INTO THE PALAEOGNATH–NEOGNATH ANATOMICAL DICHOTOMY

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Among the earliest and most enduring insights into the phylogenetic relationships of living birds was the recognition of the two deepest crown bird subclades on the basis of palate structure: the reciprocally monophyletic Palaeognathae (“ancient jaws”) and Neognathae (“modern jaws”). The palate of palaeognaths is characterized by greatly enlarged basipterygoid processes arising from the parasphenoid rostrum, which buttress a fused pterygoid–palatine complex. Neognaths, by contrast, exhibit either reduced or absent basipterygoid processes, and unfused pterygoid and palatine bones that meet at a mobile joint, conferring a greater capacity for cranial kinesis. In light of these strikingly divergent palate morphologies among extant birds, the nature of the ancestral crown bird palate, whether palaeognathous or neognathous, is uncertain, and the rarity of preservation of delicate palatal bones in crownward Mesozoic avialans has precluded a confident answer to this question. Here, we report a complete, three-dimensionally preserved pterygoid from an as-yet unnamed crownward stem bird,

which fills an important gap in our understanding of crownward avialan palate morphology. Surprisingly, the morphology of this element closely resembles that seen in the extant neognath subclade Galloanserae (chicken-like and duck-like birds), with osteological correlates strongly suggesting that other, unpreserved aspects of the palate would have also been similar to those of extant galloanserans, including short basipterygoid processes, a vertically-oriented quadrate-ptyerygoid contact, and a mobile pterygoid-palatine joint. We infer that the palate of near-crown Mesozoic avialans and the ancestral crown bird would have shared these attributes, suggesting that extant galloanserans may provide the best analogues among living birds for understanding ancestral neornithine palatal morphology and function. Notably, “galloanseran-like” features of the basipterygoid region have been key features used to assess the phylogenetic of a number of lineages of bizarre Cenozoic fossil birds. Recognition that these features may constitute neornithine plesiomorphies instead of galloanseran apomorphies may force reconsideration of the placement of these taxa among crown birds.

**Funding Sources** UKRI Future Leaders Fellowship MR/S032177/1

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## Fishes Evolution & Distribution

### A NEW CARBONIFEROUS–PERMIAN RAY-FINNED FISH (OSTEICHTHYES: ACTINOPTERYGII) HIGHLIGHTS THE MORPHOLOGICAL DIVERSITY OF ENDOCRANIAL ANATOMY OF LATE PALEOZOIC ACTINOPTERYGIANS

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The systematics of Paleozoic ray-finned fishes draws heavily on information from the dermal skull. Limited differentiation and considerable homoplasy in dermal bone patterns likely contribute to a poor understanding of interrelationships among early actinopterygians. Endocranial anatomy represents an important additional source of character data, but current knowledge of Paleozoic actinopterygian endocranial anatomy remains limited. In terms of taxa with well-preserved neurocrania along with branchial and hyoid skeletons, there is a long

stratigraphic gap between examples from the Late Devonian (e.g., *Mimipiscis*, *Moythomasia*, *Raynerius*) and the Early Triassic (e.g., *Pteronisculus*, *Boreosomus*, *Australosomus*, *Saurichthys*). Here we expand on this set of key taxa with a well-preserved three-dimensional skull that falls within this Permo–Carboniferous gap. From the Lontras Shale (Gzhelian–Asselian) of the Paraná Basin, Brazil, this fossil also provides information from the understudied South American fossil record. The specimen exhibits incomplete dermal bone anatomy, mostly represented by the snout and opercular series which are visible superficially. Endocranial anatomy is remarkably well preserved, including the braincase, palate, hyobranchial apparatus and endoskeletal pectoral girdle and fin skeleton. Some characteristics of the specimen, such as a process on the palatoquadrate for articulation with the parasphenoid, well-developed dorsally oriented uncinat processes of the epibranchials, and an articulation for the first epibranchial bordering the otico-occipital fissure, closely resemble conditions in Early Triassic taxa such as *Australosomus*. Other characteristics, such as a basisphenoid bordered laterally by grooves for the internal carotid arteries, a small posterior myodome, large vestibular fontanelles, and marked ridges on the dorsal surface of the braincase, more closely resemble Carboniferous taxa such as *Lawrenciella* and *Kansasiella*. The mixture of characters present in this Brazilian fish is unique among the known late Paleozoic actinopterygians that tend to be easily distinguishable from early Mesozoic taxa. Further studies on Carboniferous and Permian actinopterygians should focus on exploring endocranial features that have the potential to provide a fuller understanding of late Paleozoic actinopterygian diversity and phylogenetic relationships.

**Funding Sources** Department of Earth and Environmental Sciences; College of Literature Science and Arts, University of Michigan

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### Colbert Poster Prize

#### PATTERNS IN THE SCALING OF AMNIOTE DENTINE APPPOSITION

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Incremental lines of von Ebner are ubiquitous light/dark couplets that record daily apposition of dentin in teeth.

The number of incremental lines of von Ebner in a tooth indicates its formation time, whereas their thickness indicates the rate of dentin formation per day. In amniotes, reported daily rates of dentine formation in non-ever-growing teeth range from less than 1 to over 25 microns per day. The latter value has been explained as an approximate upper limit on the activity of odontoblasts in non-ever-growing teeth, a hypothesis supported by the lack of scaling between daily dentin apposition rates and body mass in Dinosauria. To test the validity and generality of this hypothesized constraint, we assembled a dataset of dentin apposition rates and body masses for approximately 100 amniote taxa from the literature and used phylogenetic regression to explore scaling relationships and reconstruct ancestral states of daily dentin apposition in major clades. We find no relationship between body mass and daily dentin apposition rate for non-ever-growing teeth in Amniota as a whole or within major clades such as Mammalia, Primates, Cetacea, Archosauria, Dinosauria, or Crocodylomorpha. Similar daily dentin apposition rates are found in the largest terrestrial mammals, dinosaurs, and marine reptiles, whereas primates, cetaceans, and some smaller marine reptiles independently evolved exceptionally slow daily dentin apposition rates. Ecological and life history factors, but not body mass, appear to tightly control dentin apposition rate in non-ever-growing teeth, which seems to have evolved rapidly at the origin of major clades.

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### Crocodylomorphs & Pterosaurs

#### THE FORELIMB OF *ARCTICODACTYLUS CROMPTONELLUS* (PAN-AVES; PTEROSAURIA) AND THE ASSEMBLY OF THE PTEROSAUR WING

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Pterosaurs represent the earliest-appearing of only three clades of flying vertebrates, the pioneers of aerial vertebrate ecospace, and the lineage to produce the largest known flying organism. The origins of the pterosaurian flight apparatus have been difficult to ascertain, in part due to incomplete or two-dimensional preservation of the earliest (Triassic–Jurassic) pterosaur remains. An exceptional early pterosaur specimen that is preserved in three dimensions, the holotype and only known specimen of *Arcticodactylus cromptonellus* (Upper Triassic; Fleming Fjord Formation, Greenland) may help address these problems. However, it has remained mostly encased within matrix to protect the delicate elements, obscuring external study. Here we present new synchrotron tomographic scan data of the forelimb (wing-forming) elements of *Arcticodactylus cromptonellus*. The forelimb of *Arcticodactylus* possesses a number of features plesiomorphic to Ornithodira (birds+pterosaurs), including the extension of the phalangeal articular surfaces onto the dorsal surface of metacarpals II–III and manual asymmetry (metacarpal I/metacarpal II length  $\leq$  0.80), the latter of which is absent in all but two other Triassic pterosaur taxa (*Carniadactylus* and *Seazzadactylus*). *Arcticodactylus* also possesses several hallmarks of the early pterosaurian wing: a deltopectoral crest that is wider than the humeral mediolateral midshaft width, a fourth digit that is longer than the rest of the forelimb, a fourth metacarpal possessing a ‘roller joint’ articulation with the fourth digit, and a crista metacarpii present on the posterior face of this metacarpal. Notably, the humeral deltopectoral crest of *Arcticodactylus* possesses a straight proximal margin and is separated from the humeral head by a distinct, laterally-facing margin, features found in early ornithodirans but absent in other pterosaurs. The presence of a mosaic of anatomical features found in the forelimbs of early-diverging ornithodirans and of winged pterosaurs (including some found in only the very earliest-diverging pterosaurs) demonstrates that, rather than possessing a “fully developed” pterosaur wing, *Arcticodactylus* is a structural intermediate between early archosaurs and derived pterosaurs. Other Triassic pterosaur specimens, similarly assumed to represent irrelevant “developed” forms, may also preserve distinct, intermediate morphologies that inform the evolution of the pterosaur forelimb from that of terrestrial archosaurs.

## Colbert Poster Prize

### DESCRIPTION OF A NEW UINTATHERE SKULL (MAMMALIA, DINOCERATA) FROM THE UINTA FORMATION, PICEANCE CREEK BASIN, COLORADO AND ITS TAXONOMIC IMPLICATIONS

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Uintatheres (Class Mammalia, Order Dinocerata) are an early Paleogene clade of large-bodied herbivorous mammals characterized by a skull with three pairs of knobby horns and saber-like canine tusks. They inhabited North America and Asia from late Paleocene through middle Eocene time. Their fossils, particularly complete skulls, are rare. The morphologic variation among uintathere skulls has hindered taxonomic classification, especially at the species level. Originally, over 30 species were placed within Uintatheriidae, but the most recent taxonomic revision identifies only two species *Uintatherium anceps* and *Eobasileus cornutus*. Some workers still recognize a transitional genus *Tetheopsis* containing two species. *U. anceps* and *E. basileus* are distinguished by differences in size and horn morphology, with *E. basileus* being the larger form. We report the first nearly complete skull (UCM 102271) of a uintathere recovered from the Uinta Formation in the Piceance Creek Basin, northwestern Colorado. The skull more closely resembles the middle Eocene *U. anceps* than other genera. However, the skull is unusually small with measurements below the smallest observed value for *U. anceps*. The skull length of UCM 102271 is approximately 14% lower than the mean for *U. anceps*. Most cranial and dental measurements compare with subadult specimens of *U. anceps*. The presence of a permanent dentition, dental wear, and fused cranial sutures on UCM 102271 indicate the skull represents an adult specimen. Unique morphological features of UCM 102271 include a parietal horn and occiput that are dorsally elevated beyond what has been documented for *U. anceps*. The region of the skull between the occipital crest and parietal horn is anteroposteriorly shortened compared to *U. anceps*, resembling the derived condition of *Tetheopsis* and *E. cornutus*. The interhorn region of UCM 102271 lacks the dolichocephalic elongation observed in *Tetheopsis* and *Eobasileus*, comparing more favorably with the shortened condition in *U. anceps*. As the first reported uintathere skull from the Piceance Creek

Basin, UCM 102271 appears most similar to *U. anceps*, but nevertheless shows notable differences from the species. Prior to discovery of UCM 102271, the presence of *U. anceps* in the Piceance Creek Basin was suggested from scanty remains. UCM 102271 suggests greater variation in size and morphology exists within *U. anceps* than has been documented by prior studies.

**Funding Sources** University of Colorado Museum of Natural History Museum Student Research Award Program

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## Stem Tetrapod, Squamate, & Amphibian Diversity & Biology

### THE FIRST RECORD OF *LAMPROPELTIS* FROM MCFADDIN BEACH, TEXAS

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McFaddin Beach (MB) is an archeological and paleontological locality extending approximately 20 miles along the coast of Jefferson County, Texas. It is well known for lithics attributed to several Paleoindian groups. Vertebrate fossils recovered from MB include *Bison*, *Mammuthus*, *Equus*, *Mammut*, and *Holmesina*, which indicate a Rancholabrean fauna. A fossil from MB recently donated to Sam Houston State University is a sample of partly cemented matrix containing 29 associated snake vertebrae, some in articulated sections. The fossil was  $\mu$ CT scanned and the individual vertebrae were digitally segmented. The vertebrae are from the preloacal trunk with an average centrum length of 5.62 mm and an average neural arch width of 5.01 mm. The ratios of neural spine length to neural spine height, and cotyle width to cotyle height, are within the range of *Lampropeltis* as reported by previous researchers. The neural spine heights are greater than its lengths. The neural spine also has a posterior overhang. The neural arches are moderately vaulted with convex laminae. The prezygapophyseal accessory processes exhibit lengths less than the greatest lengths of the prezygapophyseal processes and are thick with rounded/blunted ends. The zygapophyses are pronounced laterally and the zygosphenes lack an anteriorly flattened roof. The

subcentral ridges are strongly developed. These characters are all consistent with referral of the specimen to *Lampropeltis*. The genus *Elaphe* has characteristics similar to *Lampropeltis* but was eliminated as a possibility because it has less depressed neural arches, higher and thinner neural spines, and longer, less rounded accessory processes than the MB specimen. The modern ranges for some members of *Lampropeltis* (*L. triangulum*, *L. calligaster*, and *L. getula*) include the Texas coast. Relative to MB, the nearest fossils attributed to the genus are from Bee County, TX approximately 60 miles from the modern Texas coast. *Lampropeltis triangulum*, *L. calligaster*, and *L. getula* have all been identified in fossil deposits of Texas. The vertebrae are the only known articulated fossils from MB. Articulated specimens are unusual at MB because the site is a secondary deposit where elements are redeposited from as of yet unknown primary deposits offshore. An articulated, multi-element skeleton suggests that the specimen may have been rapidly buried, was in a crevasse, was fossorial, or was trapped in a rapid influx of sediment.

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## Stem Tetrapod, Squamate, & Amphibian Diversity & Biology

### CRANIAL OSTEOLOGY OF *PELTOSAURUS*, BASED ON MICROCT SCANS OF TWO EXQUISITE SKULLS

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*Peltosaurus* is a well-represented genus of glyptosaurine anguillid lizard from the Paleogene of North America. Recently reported *Peltosaurus granulosus* specimens from the middle Oligocene (Ar1–Ar2) have extended glyptosaurine temporal records and suggest this genus

was a well-established survivor of the Eocene–Oligocene extinction event, making the species an important case study for understanding paleoherpetofaunal turnovers and how poikilothermic taxa respond to changes in global climate. Most *Peltosaurus* specimens described consist of isolated frontoparietal shields; however, several exquisitely preserved, nearly complete skulls remain almost entirely undescribed. We present high resolution  $\mu$ CT scans of two specimens referred to *Peltosaurus granulosus*, which reveal new details of its morphology including undistorted braincases and inner ears, allowing us to provide a revised diagnosis for the taxon based on comparison to extant and extinct anguillid lizards.

**Funding Sources** Laidlaw Foundation, Macauley Family Endowment, Newt and Calista Gingrich Endowment, NSFGRFP Grant No. 1938103, James Dwight Dana Fellowship, YIBS Small Grant

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## Biomechanics & Functional Morphology

### FUNCTIONAL MORPHOLOGY OF THE INTRAMANDIBULAR JOINT IN DINOSAURS AND OTHER REPTILES

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The amniote mandible is a compound organ formed by rostral (dentary, supradentary, and splenial) and caudal (coronoid, surangular, angular, prearticular, and articular) bony elements joined by a prominent intramandibular joint (IMJ) present among non-mammaliaform tetrapods. The ubiquity of the joint among tetrapods reflects the evolutionary and developmental origins of the mandible but the joint may also be a functionally important articulation. Fundamentally, the IMJ is likely a plane of weakness in the mandible and lineages of reptiles have evolved a variety of morphologies that impact the bending potential of the joint. Whereas crocodylians and birds have each stiffened the IMJ via robust, overlapping sutures or coossification, respectively, non-avian theropod dinosaurs maintain a seemingly flexible arrangement of elements about the joint. However, the relationship between IMJ joint shape, mandible function, and cranial evolution have yet to be explored among dinosaurs. New data on this system are important to not only understand how the mandibles of dinosaurs work and how they have evolved, but also why extant archosaurs modified their

IMJs along their divergent lineages. We collected linear measurements along with landmark data to capture the morphologies of the bony surfaces of the IMJ and tested for correlation of these shapes with biomechanical data gleaned from lever mechanics. We find that the IMJ becomes less vertical as the mandible deepens and adductor muscle volume increases, and that IMJ complexity increases with decreasing mandibular depth. These results suggest two alternative strategies of changing IMJ morphology in order to adequately deal with feeding-induced strain on the mandible— dorsoventrally thin mandibles accommodate feeding forces by developing broad, overlapping sutures while dorsoventrally tall mandibles reorient the IMJ into a position orthogonal to the line of the adductor muscles.

**Funding Sources** NSF IOS-1457319

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## Preparators'

### PALEONTOLOGICAL RADIATION AND RADON MONITORING: A CASE STUDY FROM THE UTAH FIELD HOUSE OF NATURAL HISTORY

Foster, John, Sroka, Steven D., Howells, Thomas F.

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The Utah Field House of Natural History State Park Museum was founded in 1948 and has a collection of geological and paleontological specimens totaling more than 17,000 items. The museum has particular strengths in Eocene and Jurassic fossil material, with specimens from the Uinta, Washakie, and Morrison formations often having elevated radiation output. Following preliminary radon monitoring over five days in November 2019, we tested two fossil-containing spaces (lab and collections) in the collections wing and one control space (classroom/meeting) in the main office wing for one year (Dec 2019–Dec 2020), taking 200 readings semi-daily for 24-hour, 7-day, and long-term averages in pCi/L. We also tested collections spaces for increased radiation and took 0-m and 1-m readings for radioactivity of 50 individual specimens for mRem/hr. Results indicated that six mineral and ore specimens had readings of 1.6 up to 16.0 mRem/hr and up to 36,000 CPM at 0 m. The highest three fossil specimens were two brontotheres from the Washakie and Uinta and a Morrison sauropod humerus, ranging from 0.36 to 1.23 mRem/hr and up to 1860 CPM. The mineral and ore specimens were deaccessioned, as



their levels were considered higher than the museum could properly store, and risk of possible contribution to radon levels was considered to outweigh scientific value. The fossil specimens were retained, labeled as radiation sources, and will be mitigated along with other slightly elevated specimens. Results of radon monitoring indicated a long-term average of 2.00 pCi/L in the control space in the main wing, 4.16 pCi/L in the paleo lab, and 2.83 pCi/L in the collections room; all three spaces collectively had a 7-day average range between 0.85 pCi/L (main wing, Aug 2020) and 6.0 pCi/L (lab, Feb 2020). Short-term (24-hour) average radon levels varied greatly and could only be correlated inversely with local barometric pressure; response to pressure changes appeared to lag somewhat in rough proportion to room volume. Smaller spaces demonstrated more immediate raising or lowering of pCi/L readings with lower or higher barometric pressure, respectively. While degree of response seemed proportionately similar in the large collections space, response time to pressure changes appeared to lag. Other variation in daily averages appeared to be present, but triggers could not be reliably determined. Ventilation of spaces with elevated levels is in the engineering design phase.

**Funding Sources** This project was funded by the Utah Field House of Natural History.

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## Dinosaur Systematics, Diversity, & Biology

### GEOLOGICALLY OLDEST SPECIMEN OF *BRACHIOSAURUS* (SAUROPODA) FROM THE SALT WASH MEMBER OF THE MORRISON FORMATION, SOUTHERN UTAH

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In 2019, a seven-year field study of the Salt Wash Member of the Morrison Formation in southern Utah located the geologically oldest *Brachiosaurus* specimen yet found (FHPR 17108), near the base of the Salt Wash.

Collected in October of that year, the specimen consists of a complete right humerus, a fragmentary left humerus, fragments of scapula(?), and several rib fragments. To date, only two other humeri of *Brachiosaurus* have been described: the holotype, which was collected near Grand Junction in 1900, and a second humerus collected from Potter Creek on the Uncompahgre Plateau in 1955; both sites are from western Colorado. The humeri of FHPR 17108 are the first matched pair known for *Brachiosaurus*. The complete right humerus is 201 cm long and is more intact than either the type specimen from Grand Junction or the Potter Creek specimen; the robustness index of FHPR 17108 is 0.223 and the minimum circumference to length ratio is 0.318. The specimen was collected from a dark greenish-brown siltstone between sandstone units at the ~3 m level in a ~24 m section of Salt Wash Member and a ~120 m section of the Morrison Formation. This stratigraphic position is 12.5% up into the Salt Wash section and 16.7% up into the Morrison Formation overall. The occurrence of the specimen near the base of the Salt Wash Member extends the confirmed lithostratigraphic range of *Brachiosaurus* down from the upper Salt Wash (Jensen-Jensen Quarry near Dinosaur National Monument) to the base. All other occurrences of the genus are either from the overlying Brushy Basin Member or are from high in the formation and/or in Morrison undifferentiated regions to the east or north of the Colorado Plateau in which even lower stratigraphic levels are likely equivalent to the middle to upper units of the formation in Utah and western Colorado. This lower occurrence of *Brachiosaurus* may extend its chronostratigraphic range as much as several million years earlier into the Late Jurassic. Occurrences high in the formation elsewhere (e.g., Oklahoma), along with the new occurrence near the base of the Salt Wash Member in southern Utah, suggest that *Brachiosaurus* ranged from early to probably late Morrison times throughout the Morrison basin. There are not enough characters yet identified in the specimen to determine if it is significantly different from previous specimens.

**Funding Sources** Friends of the Utah Field House, Utah State Parks, and the Bartlett Family

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## Preparators'

### MOUNTING FOSSIL SPECIMENS FOR MICRO-CT SCANNING

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MicroCT scanning is an important tool in paleontological research. A basic understanding of the mechanism of scanning is vital to understanding how to mount specimens for the most informative scan. X-ray beams travel from the source, through a specimen and are captured by the detector. The specimen, sitting on a rotating platform, moves a fraction of a degree and another image is taken. This is repeated for a complete 360°; these images, when rendered, create a 3D volume. A mount for scanning must hold the specimen securely and safely while it spins slowly on the scanner platform. The mount should be created so that the specimen is centered within the scanning frame and must not move while the scan takes place. The mount affects the quality of the scan in other ways, such as whether the beam can be as close to a small specimen as it needs to be. The mounting materials must be invisible to the x-ray beam, having low density and low x-ray absorption: for example polystyrene, polypropylene, gel caps, styrofoam, and florist foam. Floral foams, one of the easiest materials to use, can be carcinogenic with prolonged exposure and other foams can spread particles widely. When even a small particle can damage the detector, every attempt must be made to maintain a clean, dust-free working area. Gloves and N95 respirators should be worn when handling these foam mounting materials. Thin plastic films, like 1-mil plastic wrap can be used to protect the specimen from the mounting materials. Metals, though, should be avoided as they cause scan artifacts. In concept similar to a cavity mount, mounts for CT scanning are created with sculpture tools: serrated knives, X-Acto knives, and wire end modeling tools. The Yale Peabody Museum's procedure for mounting includes documentation, photographing the current condition of the specimen prior to scanning, labeling the mounted specimen with catalog number and element, and tracking possession and travel of specimens from collections, to lab, to scanner and back safely in the collections.

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### **Taphonomy, Paleoenvironments, & Stratigraphy**

#### **INTEGRATED SEDIMENTOLOGY, VERTEBRATE FOSSILS, AND COPROLITES PROVIDE PALEOENVIRONMENTAL CONTEXT**

#### **TO THE "LAST CHANCE THEROPOD" LOCALITY, MUSSENTUCHIT MEMBER, CEDAR MOUNTAIN FORMATION, UTAH, USA**

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The Mussentuchit Member (Cenomanian) of the Cedar Mountain Formation has yielded important insights into the timing of biotic turnover during the mid-Cretaceous in western North America. However, a lack of integrated paleoenvironmental data hampers our understanding of abiotic and biotic interactions. Here we describe sedimentological features, vertebrate faunal remains, and coprolites to interpret the paleoenvironment at the "Last Chance Theropod" locality from the upper Mussentuchit Member. The dominant lithology at the locality consists of thick-bedded mudstones with subordinate silts and sands, identified as water-logged gleysols. Tubular structures with secondary infill (indeterminately root traces or burrows) are also present (BI of 2 to 3). Brecciated clusters of bivalves combined with pervasive evaporites suggest a regionally altered base-level. Vertebrate remains include an associated, disarticulated skeleton of at least two skeletally immature orodromine dinosaurs; 13 isolated crocodylian teeth; two gar scales; and isolated helochelydrid, ornithopod, and theropod remains. Four dark gray spherical to elongate coprolite specimens (24–83 mm length, 11–40 mm diameter) were also recovered from the locality, three of which share similar features and may pertain to a single defecation event. Their identification as coprolites is supported by their overall morphology, distinct elemental composition from the sedimentary matrix, and purported organic inclusions. Pervasive cracking on external surfaces may reflect desiccation. Petrographic thin-sections of one coprolite reveal a circumferential external zone (1–3 mm thickness) dominated by light, granular fabric distinct from a darker, fine-grained interior. Putative plant and other organic inclusions, palynomorphs and/or phytoliths, and amorphous organic matter are observable in thin-section. Definitive bony inclusions were not observed, suggesting an omnivorous or herbivorous producer. This preliminary sedimentological and taphonomic evidence posits that the fossil materials accumulated in water-logged gleysols with minimal hydraulic transport,

consistent with our interpretation of the Mussentuchit paleoenvironment as a paralic depocenter influenced by mixed-waters. Ongoing taphonomic studies specifically coupling fossil data with site-specific paleoenvironmental data will improve these interpretations and begin to unravel ecological aspects of biotic turnover in the Cretaceous of North America.

**Funding Sources** This material is based upon work supported by the National Science Foundation under Grant No. 1925973.

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## Macroecology & Macroevolution

### THE FATE OF THE HELL CREEK TETRAPOD BIOTA: ECOLOGICAL NICHE MODELING REVEALS GEOGRAPHIC AND ENVIRONMENTAL HABITAT CHANGES FOR 106 GENERA ACROSS THE END-CRETACEOUS MASS EXTINCTION

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Extinction survivorship often correlates with geographic range size, which is a product of dispersal constraints, biotic interactions, and abiotic factors. Abiotic factors including long-term climate change have been proposed as contributing mechanisms to mass extinctions such as the end-Cretaceous (K/Pg). Here, we analyze the broader

Hell Creek biota of 106 tetrapod genera (including non-avian dinosaurs, mammals, lissamphibians, squamates, crocodyliforms, and champsosaurs) to test the hypothesis that habitat availability influenced survivorship across the K/Pg extinction independent of the Chicxulub impact. We apply ecological niche modeling (ENM) to relate fossil occurrences to environmental variables, providing quantitative predictions of suitable habitat area and environmental niche breadth pre- and post-extinction. We use >4200 independently, taxonomically, and stratigraphically validated occurrences spanning outcrops of the Williston, Powder River, Cheyenne, and Hanna basins at precise temporal, spatial, and taxonomic resolutions. We consider these to be the minimum for producing realistic/interpretable results. We integrate these occurrences with paleoenvironmental reconstructions using both sedimentological proxies and general circulation models from the late Maastrichtian (68-66 Ma) and early Danian (66-64 Ma). We train ENMs in the late Maastrichtian and project them to the early Danian to determine if suitable habitat and/or abiotic niche size of extinction victims contracted relative to survivors. Results show no consistent relationship between suitable habitat/niche occupation and survivorship. Most extinction victims experienced projected increases in suitable habitat into the Danian, whereas surviving taxa show variable changes in suitable habitat. The diversity of available environments simply appears to be greater in the late Maastrichtian relative to the early Danian (i.e., environments were more heterogeneous pre-K/Pg). Thus, geographic range size is likely decoupled from environmental niche breadth across this interval. Our analyses develop best practices for meaningful ENM in the deep-time terrestrial fossil record, which is pertinent given that ENM is being increasingly expanded to these systems. Overall, these results support a proximate trigger for the K/Pg (i.e., the Chicxulub impact) rather than more gradual causes and offer new insights into mechanisms of extinction selectivity at this critical point in evolutionary history.

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## Education & Outreach

### DINOSAURS ARE FOR EVERYONE: IMPLEMENTING ACCESSIBLE PREHISTORIC PROGRAMMING IN INFORMAL LEARNING INSTITUTIONS FOR DEAF AND HARD OF HEARING STUDENTS

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Virtual programming has traditionally been an educational medium that has been inaccessible for students who require additional auditory assistance (i.e. deaf, hard of hearing, auditory processing disorder, etc.). Various institutions have the options of in-person sign language tours, pre-recorded guided tours, and captioning available for visitors, but there is a lack of live virtual programming and virtual field trips for students. After a few months of fine-tuning our process, we have found success in implementing an accessible virtual floor tour of our paleontology exhibits using a broadcasting software, closed captioning, an American Sign Language (ASL) interpreter, fossil replicas, and paleoart.

Prior to the tour, meetings are conducted with instructors to learn and accommodate for their students' individualized learning objectives, as well as demographic information about the class (ages, learning levels, prior interests in prehistory, etc.). During this meeting, pre-trip materials are also provided to the instructors, such as a list of vocabulary, the slides that will be used during the tour, and coloring pages of animals they will see in the museum. The information and pre-trip materials are also shared with the ASL interpreters. During the tour, it is important for the presenter to tailor their teaching methods to the needs of the students. Examples of this are interpreting the different species names of prehistoric animals (who do not have specific ASL signs), allowing for students to pay attention to the specimens and the ASL interpreter simultaneously, and engaging audiences from pre-kindergarten through high school. Concepts introduced may be reinforced by the use of fossil replicas and paleoart to provide a better visualization of prehistoric life.

After the tour, a survey is sent to instructors about their experience. We use the feedback provided in these surveys as well as any additional feedback provided via email to improve our processes. This is imperative, as it allows the program to be shaped with the input of those within the deaf community. Using these tools, we hope to provide a guideline for other institutions to replicate accessible programming to better serve a broader audience of both abled and differently-abled learners.

**Funding Sources** Funding for the North Carolina Museum of Natural Sciences accessibility tours is provided by grants from Duke Energy and the GlaxoSmithKline Foundation.

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## Mesozoic & Paleogene Mammals

### ***RUDIOMYS* (RODENTIA, APLODONTIDAE) FROM THE JOHN DAY FORMATION OF OREGON**

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Family Aplodontidae consists of a number of species that include the modern mountain beaver as well as considerable phylogenetic and morphological diversity among fossil taxa. We identified several fossils from the John Day Formation of Oregon that can be attributed to the genus *Rudiomys*. JODA 2942 is a partial left mandible with practically unworn dentition and a deciduous premolar from the Turtle Cove Member that has been identified as *Rudiomys mcgrewi*. This is the first documented deciduous tooth attributed to *Rudiomys* and the nearly unworn m1–2 provides dental morphology that is not present on the type and only figured specimen of *Rudiomys*. The type specimen of *Rudiomys* is highly fragmented and preserves a worn dentition. Attribution of this specimen to *Rudiomys* increases the known range of the taxon as well as increasing the known morphology of the genus.

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## **Symposium - Vertebrate dental ecomorphology: Tooth traits that reflect ecology**

### **TRENDS IN NORTH AMERICAN PRIMATE ECOMORPHOLOGICAL DISPARITY IN RESPONSE TO CLIMATE FLUCTUATIONS OVER THE EOCENE**

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Adaptive radiation theory predicts that evolving lineages will expand in ecomorphological diversity in response to ecological opportunity. In the fossil record, intervals of

ecological opportunity are often identified as recoveries from major extinction events or dispersal to new regions without ecological vicars. The fossil record of primates may provide an additional window into the response of an evolving fauna to fluctuations in ecological opportunity over geological time. Primates today flourish in warm climates and Europe and North America supported diverse primate faunas during the relatively warm and wet Eocene. As global climate cooled during the late Eocene and Oligocene, primates disappeared from these northern continents. This suggests that global temperature trends may function as a proxy for primate ecospace availability across continental scales during the Eocene. Primate faunas are expected to show higher disparity during warm intervals and contract in disparity as climates cool during the late Eocene.

We measure disparity in 30 genera of Eocene North American primates in two critical aspects of primate adaptation: body size and dietary adaptation. Body mass is reconstructed using Bayesian models incorporating dental and postcranial skeletal dimensions. Dietary adaptation is quantified using the sums and coefficients of variation of Dirichlet normal energy (DNE) calculated over the surface of the second lower molar. Disparities in body mass and DNE values are calculated as the mean squared Euclidean distances of the genera present during each biochron of the Eocene (Wa0-Du). To account for non-linear temporal trends in disparity and global temperature across the Eocene, a generalized additive model is constructed that predicts disparity using temperature and age splines. The dietary ecologies of the Eocene taxa were also reconstructed using DNE values calculated from an extant strepsirrhine reference sample. Temperature is meaningfully associated with body mass disparity (mean coefficient 0.29), but only weakly associated with disparity in DNE (mean coefficient - 0.01). These results suggest the range of body sizes supported by Eocene environments may have been related to global temperatures but dietary diversification was more responsive to local or lineage-specific patterns of adaptation. Dietary ecology reconstructions from DNE suggest comparatively more members of primate faunas engaged in folivory and insectivory as the Eocene progressed.

**Funding Sources** Duke University Graduate School Research Grant (to ELF); NSF BCS 1552848 (to DMB)

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**Mesozoic & Paleogene Mammals**

## **LIFE HISTORY OF AN ARCHAIC PLACENTAL MAMMAL, *PANTOLAMBDA BATHMODON* (PLACENTALIA, PANTODONTA)**

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The rise of mammals after the extinction of the dinosaurs remains one of the most enigmatic intervals in the evolution of mammals. A relatively sparse Paleocene fossil record and confusing relationships between taxa means that little is known of the evolution, ecology, or biology of these animals. Accordingly, the life history of these organisms remains unstudied, despite likely playing a key role in the rapid proliferation and body size increase of these clades in recovering ecosystems. Here, we present results of an in-depth paleohistological analysis of *Pantolambda bathmodon*, an early, possibly gregarious pantodont, using a new ontogenetic series of specimens. Pantodonts were bizarre, herbivorous eutherians of unknown phylogenetic affinity, and were among the first mammal lineages to reach large body sizes in the Paleocene. In examining both dental and skeletal records of growth from the same individuals, including a juvenile still bearing deciduous teeth, our study is among the most comprehensive paleohistological analyses of any fossil mammal, allowing for unprecedented insights into the life history of this species. Neonatal lines in the teeth indicate that the deciduous premolars and the first upper molar erupted prior to birth, similar to precocious, nidifugous mammals today. Daily incremental lines in the enamel and dentine suggest rapid crown formation times (~70–180 days) and a gestation period of at least 20 weeks. A stress line in the teeth and postcranial bones, recording an anomalous decrease in growth towards the end of this individual's life, may represent weaning. The weanling perished approximately 2.5 months after birth, weighing about 17 kg. Adult individuals exhibiting severe wear on the dentition allow us to estimate maximum longevity in *Pantolambda bathmodon* at about 7 years. In comparison with living mammals, *Pantolambda bathmodon* had gestation and weaning periods below average for a placental of its adult body size (42 kg), but within the range of known variation. However, its lifespan was exceptionally short, falling outside the bounds of comparable living mammals. Together, these lines of evidence suggest a rapid pace of life in *Pantolambda*

*bathmodon*, despite its relatively large body size. Ongoing sampling of more individuals and geochemical analyses should allow for estimation of time to sexual maturity and help to confirm the identity of the weaning line, completing our picture of the life history of this pioneering species.

**Funding Sources** The Royal Society (NIF\R1\191527); European Research Council Starting Grant (ERC StG 2017, 756226, PaLM); National Science Foundation (NSF; EAR 1654952, DEB 1654949)

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## **Taphonomy, Paleoenvironments, & Stratigraphy**

### **A GNAWING QUESTION: EVALUATING TAXON-SPECIFIC BONE MODIFICATION IN AN ARCTIC ECOSYSTEM**

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Gnawing traces on bones record species-interactions and dietary strategies. While many ungulates consume bone in response to nutrient stress, they are rarely the focus of taphonomic studies. As a result, the impacts of ungulates on bone completeness and survival are under-evaluated, despite being generally more abundant than co-occurring carnivorous bone modifiers. We evaluated whether existing criteria adequately identify ungulate gnawing or require further development. We then assessed the exploitation of bones by co-occurring ungulates, carnivores, and rodents to evaluate resource competition among bone modifiers and consumers. We focused on bones accumulating on modern caribou calving grounds of the Arctic National Wildlife Refuge (Alaska), where adult female caribou experience nutrient stresses due to calving and antler regrowth. Exhaustive sampling of standardized surveys yielded over 1,000 antlers and several hundred postcranial bones. Each element was visually inspected for modification features, and compared to established diagnostic criteria for ungulate (*Dama*, *Rangifer*), carnivore (*Ursus*, *Canis*, *Vulpes*) and rodent (*Urocyon*, *Microtus*) gnawing. We identified 22 modification classes with characteristic pits, punctures, furrows, scores, and fractures, which we attributed to caribou (n = 13 classes), carnivores (n = 1), rodents (n =

1), or to non-gnawing damage (n = 7). Among classes of ungulate modification, 10 were previously undocumented, including triangular-shaped punctures. These punctures are consistent with the cusp shape of ungulate cheek teeth but inconsistent with teeth of other modifiers. Triangular punctures are visually distinct and facilitate identification of lower-intensity caribou-modification (~25% of gnawed antlers), which were not identifiable using previously established criteria. We found that ungulates and carnivores target different components of the bone assemblage. Caribou gnawing was recognized on ~96% of all shed antlers, but <10% of postcrania. While carnivore modifications were readily observed on postcrania (>30%), they were not present on shed antlers. Rodent gnawing was limited on antlers (<3%) and postcrania (<5%). Ungulates can be prolific bone modifiers and may drive bone destruction in some settings. Furthermore, co-occurring taxa specializing in different subsets of available bone resources may reduce competition but may also introduce previously unrecognized biases in extant and fossil skeletal assemblages.

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## **Late Cenozoic Mammalian Evolution and Ecology**

### **PROBING THE MAMMALIAN FOSSIL RECORD FOR PATTERNS OF COMPETITIVE EXCLUSION USING COMPUTATIONAL RANDOMIZATION EXPERIMENTS**

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Because they share a recent common ancestor, species that belong to the same genus are expected to be more similar with respect to their phenotype and hence exhibit less niche divergence than species that belong to different genera. As a consequence, species that belong to the same genus are expected to compete intensely for resources, and therefore to be segregated in space. However, empirical evidence in support of this hypothesis of competitive exclusion between congeneric species is at

best limited, despite its longstanding history. In this context, we set out to probe the mammalian fossil record kept in the NOW database (<https://nowdatabase.org/>) for co-occurrence patterns, considering separately Europe during the Neogene, and North America during the Oligocene–Neogene.

We performed a series of computational experiments to compare co-occurrences observed in the fossil record to co-occurrences arising in synthetic baseline datasets where competitive exclusion is obfuscated through randomization. We found that congeneric species occur together notably less than would be expected at random, with large herbivores being more segregated than large carnivores and small mammals.

Our report about these experiments has been submitted as a contribution to the forthcoming special volume of the 'Vertebrate Paleobiology and Paleoanthropology Series' entitled 'Evolution of Cenozoic Land Mammal Faunas and Ecosystems. 25 years of the NOW database of fossil mammals'.

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## Quantitative Paleontological Methods

### MODEL-DISCRIMINATION INFERENCE IN THE BIOGEOGRAPHIC DISTRIBUTION OF EXTINCT BIOTAS

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Study of the geographic distribution of extinct organisms is in a quantitative revolution. Recently developed methods use both phylogenetic relationships among species and various models describing rules of dispersal, extinction, vicariance, and founder effects to determine the historical movements of species around the globe within a statistical framework. Missing from the current suite of biogeographical tools available to paleontologists is a method for detecting the biological heterogeneity of entire communities across a landscape. We developed two model-discrimination methods that compare user-defined geographic distributions of organisms to actual fossil

distribution data. The first method creates a least-squares regression between the pairwise biotic similarity of sites in a series of user-defined simulated presence-absence matrices with the pairwise geographic distance defined for each simulated site. These linear models are then compared to a fossil dataset, which underwent an identical analytical treatment, using the Root-Mean-Square Error test (RMSE); the user-defined model with the lowest RMSE score most closely matches the fossil dataset. A second method also compares user-defined presence-absence matrices to a presence-absence matrix of fossil occurrences, but through analyzing the posterior distribution of overlap between adjacent sites within a Bayesian framework. Model-discrimination is accomplished by calculation of Kullback–Leibler divergence. Simulation tests validate the methods, showing that community distribution models commonly discussed in the literature, such as 'Cosmopolitan', 'Bizonal', or 'Gradational', are differentiated from each other in both the linear regression and Bayesian methods. Tests also show that geographic distribution patterns of ancient communities can be retrieved with a certain level of noise in the data. However, too many undiscovered or misidentified taxa within data decreases the strength of these model-discrimination methods, making biotic occurrences seem like a random distribution of species. These analytical tools can also be utilized to identify changes to ecosystem composition through a stratigraphic section. For decades paleontologists have relied on indirect ordination methods to hypothesize community distribution patterns in the fossil record. It is now possible to redirect paleobiogeographical discourse from informed suppositions towards acknowledgement of all possibilities based on available data.

**Funding Sources** None

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## Permo-Triassic Ecosystems

### TEMNOSPONDYLS ON ICE: NEW INSIGHTS FROM THE TRIASSIC OF ANTARCTICA

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The Fremouw Formation of Antarctica preserves records of Triassic non-marine tetrapods that are of great import for characterizing the recovery of high paleolatitude environments in the wake of the end-Permian mass

extinction. A common component of Triassic paleoenvironments, including those in Antarctica, are temnospondyl amphibians, whose cosmopolitan distribution render them particularly useful tools for exploring biogeography and regional biostratigraphy. The lower Fremouw Formation produced the first temnospondyl material from Antarctica and is considered Early Triassic in age. However, most historic specimens are highly fragmentary, and the validity of the two described taxa, *Austrobrachyops* and *Cryobatrachus*, is considered dubious. The upper Fremouw Formation, which is traditionally considered Middle Triassic in age, has produced unequivocally diagnostic material, but all temnospondyls from this horizon belong to a single clade, Capitosauria, in contrast to greater temnospondyl diversity in coeval deposits from other geographic regions. The middle Fremouw Formation only recently produced diagnostic tetrapod remains for the first time, the study of which remains in its early stages. Here we present findings from our study of the newly collected temnospondyl material, which includes specimens from the lower and middle members of the Fremouw Formation. Firstly, we report *Micropholis stowi* from both the lower and the middle members. *Micropholis* is a diminutive dissorophoid otherwise known only from the *Lystrosaurus declivis* Assemblage Zone (LAZ) and is a rare example of an Early Triassic temnospondyl documented beyond a single narrow region. Its stratigraphic range in Antarctica suggests that both the lower and middle members are equivalent to portions of the LAZ. Secondly, we reassess the putative small-bodied lydekkerinid *Cryobatrachus* from the lower Fremouw Formation and confirm previous suspicions that the holotype is an indeterminate juvenile of a much larger capitosaur. However, we identified more definitive cranial material of a lydekkerinid among the recently recovered material from the lower member. Finally, at least two small-bodied specimens from the middle Fremouw Formation likely represent juvenile capitosaur, which are rare in the fossil record. Their occurrence cannot further inform the age of this member, but it is suggestive of a rarely preserved low-energy paleoenvironment in which adults were absent.

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## Paleohistology & Paleopathology

## PREDOMINANCE OF LUMBAR AND CAUDAL PATHOLOGIES IN THE GIANT GROUND SLOTH *EREMOTHERIUM LAURILLARDI*

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Several species of megamammals inhabited Brazil during the Pleistocene. Among them, the giant ground sloth *Eremotherium laurillardii* has the highest frequency of reported paleopathological lesions. It was affected by a wide range of pathological conditions, including articular and traumatic lesions, and infection injuries. However, most paleopathological studies on megamammals are done based on analyzing few individuals. In this work, we macroscopically analyzed 990 vertebrae belonging to *E. laurillardii* that were recovered from the Toca das Onças (municipality of Jacobina, Bahia, Brazil) and Toca dos Ossos (municipality of Orolândia, Bahia, Brazil) caves, which are located near each other but separated by a river. From all vertebrae, only 34 showed pathological alterations (3 cervical, 12 thoracic, 5 lumbar, and 14 caudal vertebrae). Among them, 25 belonged to adult individuals, and only seven to young individuals. Eight types of bone lesions were diagnosed: congenital anomaly, calcium pyrophosphate deposition disease, spondyloarthropathy, spondylosis deformans, compression fracture, infection, Schmorl's node, and bone tumor. This is the first record of congenital anomaly in *E. laurillardii*, as well as the first report of the association of spondyloarthropathy with a neoplasm, Schmorl's node with infection, and calcium pyrophosphate deposition disease with infection in the same element. The lumbar segment of the column had the highest frequency of injuries (5.55%), followed by the caudal (5.18%), thoracic (2.7%), and cervical (1.63%) segments. As expected from chronic illnesses, our results indicate that most lesions were found in vertebrae belonging to adult individuals. Also expected are the lumbar and caudal vertebrae as the more frequently afflicted elements, as the lumbar segment gives ample support to the body weight, and the affected caudal might be a reflection of the use of the tail as a support for a bipedal posture and defense.

**Funding Sources** PROAP assistance from CAPES



## Education & Outreach

### **BROADCASTING PALEONTOLOGY: YOUTUBE AS A SCIENCE COMMUNICATION AND SOCIAL INTERACTION TOOL DURING PANDEMIC TIMES**

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Covid-19 pandemic brought up a new reality. People are staying longer at home, personal contact ceased or decreased and the exchange of significant social experiences was substantially reduced. Many count exclusively on the internet to connect with other people and several psychological disorders arise from social isolation. In this project, we used our previous engagement with scientific communication on the internet to bring people together remotely and try to alleviate some of the negative effects of isolation while communicating paleontology. We organized biweekly live broadcasts where Brazilian paleontologists were invited to discuss general themes on paleontology with two hosts and the public. A humanist-constructivist approach was used to conduct the conversations, which were essentially guided by viewers' questions. The talks were broadcasted on our YouTube channel (Colecionadores de Ossos/Bone Collectors), which is held in Portuguese and has about 41k followers and over 1.4 million views. The channel is exclusively focused on the communication of paleontology, being one of the largest dedicated to the topic in the Southern Hemisphere. Eighteen live broadcasts were held from May to December 2020. All followed by 5 volunteer moderators responsible for curating the public chat and helping to collect questions. The conversations had varied subjects, mostly focused on vertebrate paleontology (15). The total number of views was 59,184, with an average of 3.303 per broadcast. Each broadcast had an average of 161 simultaneous viewers and 1,435 chat messages, including hundreds of questions. Twenty-one guests participated in the live streams, of which 90% were early-career scientists, 7 women, 6 people of color, and 4 guests reportedly LGBTQI+. Audience engagement was very high, with the average viewing being above the channel standard. Chat interactivity notably helped public retention and we observed no difference in audience numbers between male and female speakers. Themes like

dinosaurs and pterosaurs, however, were considerably more popular. There was very positive feedback both from guests and the public. We argue that the activity could have been more inclusive in terms of the invitees' genre and color. The project was restructured in 2021 and is now designed to be more inclusive. We plan to compare the results by the end of 2021. Recorded videos are available on our channel and can be used as teaching resources for basic and higher education.

**Funding Sources** This project was integrally financed by the 'Colecionadores de Ossos' YouTube channel supporters.

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## Dinosaur Systematics, Diversity, & Biology

### **REASSESSMENT OF THE LOWER CRETACEOUS SOUSA MEGATRACKSITE IN THE BRAZILIAN OUTBACK**

Ghilardi, Aline Marcelle<sup>1</sup>, Aureliano, Tito<sup>2</sup>, Buck, Pedro Victor<sup>3</sup>, de Campos Pimenta e Marques Peixoto, Bernardo<sup>4</sup>, Fernandes, Marcelo A.<sup>4</sup>

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The Vale do Rio do Peixe basin complex encompasses several small sedimentary basins in Northeast Brazil developed during the Late Mesozoic rifting of Gondwana. They record an Early Cretaceous fauna that lived in a semi-arid environment permeated by temporary rivers and lakes. Most of its fossil record is composed of tracks, although recently a few dinosaur body fossils have also been described. Giuseppe Leonardi was the main researcher responsible for studying and describing the local ichnofauna, having published several papers between the 1970s and the 1990s. He helped to describe almost 30 ichnosites and several hundred trackways. Between 2017 and 2019 our team carried out new expeditions to the region, focusing on the Sousa Basin, to map new locations, revisit classic sites, and digitize and reanalyze some trackways using new technologies. The original *Caririchnium*, *Moraesichnium*, *Sousaichnium*, and *Staurichnium* trackways were digitized using photogrammetry in order to save their data and compare

them with the original photos and descriptions. An assessment of the preservation of the main ichnosites was also conducted, because most of them were exposed for decades without conservation initiatives. At least two new ichnosites were discovered during the mapping effort, as well as several new tracks and trackways. Among the new reports are some of the largest theropod footprints identified in the basin, as well as an exceptionally preserved theropod trackway with skin impressions and associated shape with filamentous structures. The type trackways of *Caririchnium*, *Moraesichnium*, *Sousaichnium*, and *Staurichnium* show moderate to high degrees of degradation and urgently need new (or any) conservation strategies. Other tracksites have been almost entirely compromised by weathering and/or anthropic misuse. We are currently conducting a broad comparative analysis with other chronocorrelated ichnofaunas and quantitatively describing the local ichnodiversity. A faunal succession can be observed where ornithopods disappear about the middle of the stratigraphic section and sauropods increasingly dominate the large herbivore niche. The Sousa Basin still can be explored from new perspectives and will help to provide new data on the dinosaur faunas from the equatorial Gondwana prior to the Atlantic rift. Nonetheless, conservation efforts are urgently needed to preserve local ichnosites, whereas the local community exploits this resource as a tourist attraction.

**Funding Sources** Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001

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## Fishes Evolution & Distribution

### **NEW DISCOVERY OF PLEISTOCENE-AGE FOSSIL FISHES (OSTARIOPHYSI: CYPRINIFORMES) FROM SOUTHWESTERN MINNESOTA**

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In 2017, a fossil fish was recovered in a routine core sample during a construction survey in Lyons County, Minnesota, conducted by the Minnesota Department of Transportation. The specimen was collected approximately 40 feet below the surface in a greenish gray silt loam sediment. The specimen is preserved as a part and counterpart with the posterior part of the skull and the entire body preserved. Preliminary preparation recovered a second specimen in the core sample adjacent to the first fish. Examination of anatomy and morphology of the fossil fishes led to identification of a putative new species belonging to the order Cypriniformes based on the presence of a Weberian Apparatus and the morphology of the skull. Similar fossil fishes have been recovered from the Pleistocene of South Dakota, but to our knowledge this is one of the first discoveries of nearly complete fossil fishes from the Pleistocene of southeastern Minnesota. Further detailed analysis of the sediment recovered microorganisms that confirm an age of the sample between 10,000–25,000 years old. We discuss the known distribution of fishes during the Pleistocene in the upper Midwest, and how this enhances our understanding of the distribution of aquatic organisms during a time when Minnesota was impacted by glaciation events. This discovery has the possibility to further our understanding of the evolutionary history of teleost fishes in North America, as well as further clarifying the geologic history of Minnesota.

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## Marine Mammals

### **NEW CORRELATIONS BETWEEN CRANIOFACIAL AND INNER EAR MORPHOLOGIES FOR ECHOLOCATION AND FEEDING IN ODONTOCETES**

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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. We can use CT scanning technology to take detailed measurements of these features. Features of the inner ear that correlate with echolocation include a long secondary

bony lamina, greater inter turn distance, and lower number of turns of the cochlea. Craniofacial features such as cranial asymmetry and posterior migration of the maxilla are also good indicators 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 brevirostry (short rostrum). It is important to understand how the evolution of these structures relate to habitat, behavior and feeding preferences. To determine if there is a relationship between cranial and inner ear features for echolocation and feeding behavior, we look for phylogenetic patterns between measurements of the inner ear and compare them to cranial features for feeding. We have taken existing measurement data of inner ear and cranial features from a total of 48 extinct and extant odontocete species which incorporates most of the major families within the clade. We mapped these characters onto phylogenetic trees and generated them using Mesquite software. We use comparative methods on the phylogenetic trees to assess correlations between cranial features for feeding and cranial and inner ear features for echolocation. We found associations between inner ear measurements on the trees that agree with previous studies, such as a longer secondary bony lamina corresponding to greater inter turn distance. Associations between cranial and inner ear features for echolocation include longer secondary bony lamina and greater cranial asymmetry. We also found associations between cranial features for feeding and inner ear features for echolocation such as longer secondary bony lamina and a lower rostral proportional index (brevirostry). Finding adaptive and functional relationships between these features is an important part of understanding the evolution of odontocetes and how they behave today.

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### **Taphonomy, Paleoenvironments, & Stratigraphy**

#### **MULTIPLE SHARK BITE-SHAKE TRACES ON A MIOCENE BALEEN WHALE RADIUS EVIDENCE SCAVENGING**

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The Calvert Cliffs (Calvert County, Maryland, U.S.A.) are one of the most fossiliferous regions on the east coast of the continental United States. During part of the Miocene epoch (from approximately 22–8 million years ago), the Chesapeake area (i.e., the Salisbury Embayment) was intermittently flooded by the Atlantic Ocean. The shallow marine sediments that now comprise the cliffs abound with marine fossils, including the tests of planktonic organisms, shelled invertebrates, shark teeth, teleosts, turtles, crocodiles, pelagic birds, seals, sirenians, cetaceans, and the isolated remains of large terrestrial mammals. In addition to innumerable body fossils, Calvert Cliffs preserve trace fossils including invertebrate burrows (*Thalassinoides*, *Gyrolithes* and *Ophiomorpha*), coprolites, and shark bite traces, usually on cetacean bone.

An isolated Miocene baleen whale left radius was marked repeatedly by shark bite traces. The radius probably originated from within the Plum Point Member of the Calvert Formation, Calvert Cliffs. At least three successive bite traces made by the same teeth mark the radius. Location and nature of bite traces can indicate the context of the interaction. Deep bites on bones near vital organs are indicative of predation. Bite traces consisting of shallow, thin arching gouges on a bone in an appendage, like the one described here, indicate scavenging rather than active predation.

There are a number of basal thalassotherians (Mysticeti) known from the Calvert and Choptank formations along Calvert Cliffs for which their radius is also known. Of these, the best match is an isolated radius, questionably assigned to the Calvert Formation mysticete, *Diorocetus hiatus*, which is exactly the same length as the radius described here. Although they are not a perfect match morphologically, they are very close. From the sharks that are known from along Calvert Cliffs, we think that the bite traces on the radius could have been made by any one of the following sharks: *Alopias grandis*, *Alopias palatasi*, *Carcharhinus* spp., *Carcharodon hastalis*, *Galeocerdo aduncus*, a juvenile *Otodus megalodon*, *Physogaleus contortus*, or *Sphyrna laevis*.

**Funding Sources** Clarissa and Lincoln Dryden Endowment for Paleontology at the Calvert Marine Museum.

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### **Marine Mammals**

#### **FROZEN IN TIME: UNIQUELY PRESERVED PROTOCETID WHALE ENTOMBED INSIDE**

## DECORATIVE LIMESTONE FROM THE MIDDLE EOCENE OF EGYPT

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A massive block of decorative limestone destined for countertops or sidewalks was cut in a stonecutting yard in Shaq El-Thoaban (Cairo, Egypt), and it was discovered to be riddled with what appeared to be fossilized bones. The limestone block had already been cut into five thick slabs about 4.5 cm thick, and each saw cut removed 3.3 mm of limestone between adjacent plates, inadvertently creating an almost perfect cross-section of what has been identified as a protocetid whale. Protocetidae is a group of extinct whales that fall in the middle of the evolutionary transition of whales from land to sea. Investigation indicates that the block came from Gebel Hof Formation, of Bartonian late middle Eocene age (ca. 42 Ma), north of Khashm el-Raqaba in Wadi Tarfa, Eastern Desert of Egypt, the same locality that had produced the protocetid *Aegyptocetus tarfa*. The new specimen (MUV 502) is an associated partial skeleton represented by a complete cranium, dentaries, many vertebrae, a humerus, an ulna, several ribs, and other unidentified elements. Unique preservation allows the examination of some internal anatomical features of the skull along with its external morphology. The hallmark characters that distinguish MUV 502 from other protocetids include a large skull, measuring over 92 cm, larger than any previously described protocetid; large and robust premolars and molars, larger than any previously described African protocetid; short and fused mandibular symphysis, ending just after the posterior margin of the canine; thinning of the lateral walls of the mandibles; and enlarged mandibular canals. Comparison with related taxa suggests that MUV 502 represents one of the largest protocetid whales on record. This size may have allowed MUV 502 to hunt larger prey within its environment and therefore shifts its role in the ecosystem to that of a semi-aquatic apex predator. In addition to shedding light on a unique taphonomic window, this specimen also delivers an exceptional opportunity for a thorough morphometric assessment over time of morphological trends in earlier cetaceans.

## Permo-Triassic Ecosystems

### ONTOGENETIC INSIGHTS BASED ON A REDESCRIPTION OF THE CRANIAL MORPHOLOGY OF AN IMMATURE ‘*REDONDASAURUS*’ (ARCHOSAURIFORM: PHYTOSAURIA)

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Phytosaurs (archosauriforms) were large, semi-aquatic reptiles whose body plan was converged upon by extant crocodylians and who were an important component of Late Triassic ecosystems. Despite their abundance in Upper Triassic sediments and key phylogenetic position near the divergence of Archosauria, much of phytosaur paleobiology remains poorly understood. One key aspect that is relatively unknown for the group is ontogeny because of the scarcity of skeletally immature specimens. Currently, only two nearly complete skulls of skeletally immature specimens were reported in the literature: *Parasuchus magnoculus* from the Argana Group (Bed XVI), Morocco, and a skull previously identified as ‘*Redondasaurus*’ *gregorii*, from the Rock Point Member (Chinle Formation), at Ghost Ranch, NM. Here we use  $\mu$ CT data to redescribe the latter, NMMNH P-44920. ‘*Redondasaurus*’ represents the most derived North American phytosaur and is characterized by broad postorbital-squamosal bars with medial expansions and supratemporal fenestrae hidden in dorsal view. NMMNH P-44920 previously was recognized as the skull of a skeletally immature individual because of the relatively large orbit with respect to skull length, and it shares diagnostic features with ‘*Redondasaurus*’, such as the thickened rim of the orbit and inflated posterior portions of the nasals. However,  $\mu$ CT data of NMMNH P-44920 reveal mediolaterally narrow dorsal surfaces of the postorbital-squamosal bars, allowing the supratemporal fenestrae to be visible in dorsal view and alluding to ontogenetic features in the temporal region of the skull, an important region in phytosaur systematics. Revisions of the cranial anatomy include reassigning the originally described long, anteriorly-projecting palatines to the premaxilla. This places the premaxilla and maxilla farther posterior in the skull than previously described, consistent with character states associated with phytosaur snout elongation. Assessing ontogeny of phytosaurs can clarify unknown aspects about their evolution, taxonomy, and life history strategies. Because skeletally immature specimens may retain plesiomorphic character states, and

through growth, can shift towards morphologically derived states, understanding phytosaur ontogeny can elucidate the discordant taxonomy and phylogeny within the group and at the base of Archosauria. This study provides key data to track phytosaur cranial ontogeny and identify other skeletally immature phytosaur specimens.

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## Late Cenozoic Mammalian Evolution and Ecology

### FIRST EARLY MIOCENE CAVIOMORPH ASSEMBLAGE FROM LOW LATITUDES OF SOUTH AMERICA

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Caviomorpha are hystricognath rodents endemic to South America. Their rich fossil record indicates an arrival on the continent during the Paleogene, followed by adaptive radiation into the higher latitudes of Patagonia during the Neogene. To date, however, the best record of caviomorph diversity, paleobiology, and evolution is restricted to high-latitude localities with a paucity of information from the low-latitude tropics. Here, from sites in Peru, we describe the first tropical record of caviomorphs from the early Miocene.

Fossils were collected from Site AMD-45, located in the Bala Fm. of the Madre de Dios Basin (13°S) along the Río Alto Madre de Dios. Dates from detrital zircons constrain the locality's minimum depositional age to 17.1 ± 0.7 Ma, making this the only tropical fauna comparable in age to the oldest levels of the Santa Cruz Fm. of Patagonian Argentina (Santacrucian) ranging 48–52°S. At AMD-45, we recognize representatives of the four main caviomorph clades: Chinchilloids are the most abundant and diverse group, with the presence of *Scleromys praecursor* and at least three new taxa ranging from low-crowned brachydonty to euhypsodonty. Pan-Octodontoids are also abundant but less diverse; they are represented by

*Acarechimys minutus*, only known from Patagonia, a new brachydont taxon similar to *Acarechimys* and *Selvamys*, and a new adelphomyine. Erethizontoids are represented by a new lineage similar to *Protosteiomys*. Cavioida is the least abundant clade, with one tooth recognized as *?Luantus*, also only known from Patagonia.

Preliminary study indicates this rodent assemblage has its greatest taxonomic resemblance with those of late Oligocene levels of Contamana and early Oligocene of Shapaja (in Peru), and less resemblance with the middle Miocene of La Venta, Colombia. It extends the ranges of at least two taxa previously known only from the early Miocene of Argentinean Patagonia. Most notable, however, is the observed diversity in crown height. Though we document several brachydont caviomorphs (*Acarechimys minutus*, *Acarechimys* sp. nov., *Erethizontoidea* sp. nov.), many taxa are higher-crowned (*Scleromys praecursor*, *?Luantus*, a new adelphomyine, a low-crowned chinchilloid) or even euhypsodont (new chinchilloid). These findings indicate an early Miocene rodent fauna with great morphological diversity and species richness, comparable to assemblages of higher-latitudes, and provide insight into the tropical radiation and evolution of caviomorphs.

**Funding Sources** This work was supported by NSF grants EAR 1338694 and DDIG 0726134 and National Geographic Society Grants 9920-16 and W449-16.

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## Preparators'

### EXPLORATORY RETRODEFORMATION METHOD ON COMPRESSED FOSSILS USING SLICED SURFACE CONTOURS: A CASE STUDY ON THE OBLIQUELY COMPRESSED METAPODIALS OF AN EGYPTIAN TITANOSAURIAN SAUROPOD DINOSAUR

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A pervasive issue in paleontology is the degree of preservation the fossil experiences from burial to excavation, including breakage, crushing, and deformation. One type of deformation that has the potential to obscure key anatomical features is compression, where a fossil experiences a reduction in

volume and/or shortening along a particular axis or axes. Recent advances in replicating fossils using 3D computer models (e.g., via CT-scanning or photogrammetry), the process of retrodeforming the fossil becomes safely attainable. Retrodeformation on 3D models can be approached in many ways, including localized warping, correction using bilateral symmetry, or the use of landmarks to adjust the model, each seemingly to address specific deformation problems. Here, we explore a computational retrodeformation method for fossils that have undergone drastic compression in their preservation. We aim to see if any conspicuous features may be “decompressed” from the process to better understand the original anatomy.

MB.R.Vb-621-640 is a partial sauropod dinosaur recovered from the Campanian Kharga Oasis, Egypt. The specimen preserves several dorsal vertebrae and various elements from both appendicular girdles. Most recovered elements have been taphonomically compressed. Six metapodials have been recovered and served as our test fossils as these elements have all been obliquely compressed along the long and dorsoventral axes. 3D models were constructed from CT scan data. Since metapodials tend to be boxlike in their overall morphology, we used the proximal and distal surfaces to approximate the orthogonal plane from the direction of compression. Once the angle of the plane was established, numerous slices of the model were taken in consistent intervals along the long axis to demarcate the original dorsoventral axis and obtain surface contours. We then globally warp the element until these sliced contours were perpendicular to the anchored long axis. From there, these contours can be stretched along the certain axes by different factors to decompress the element. Results revealed previously obscured anatomies such as foramina seemingly more canal-like, subtle ridges seemingly more pronounced, and more curved distal condyles. Overall, this decompression technique yielded augmented metapodial models that are more comparable to other titanosaurs. We plan to apply this method to undeformed specimens to establish biologically relevant baselines for this method.

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### Dinosaur Systematics, Diversity, & Biology

#### NEW TITANOSAURIAN SAUROPOD DINOSAUR FOSSILS FROM EASTERN AFRICA: EMERGING INSIGHTS FROM THE CRETACEOUS GALULA FORMATION OF TANZANIA AND REGIONAL

#### FAUNAL PATTERNS ACROSS A CONTINENTAL SCALE

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Over the past decade, numerous new discoveries from middle and Late Cretaceous non-marine units on continental Africa have enhanced our understanding of its role for the diversification of many terrestrial vertebrate groups. Among the most informative clades to date are titanosaurian sauropods, a globally-distributed group of herbivorous dinosaurs. The Late Cretaceous Galula Formation exposed in the Rukwa Rift Basin, southwestern Tanzania has thus far produced three new distinct species (*Rukwatitan bisepultus*, *Shingopana songwensis*, and *Mnyamawamtuka moyowamkia*). Moreover, *Mansourasaurus shahinae* from Egypt is one of the most complete latest Cretaceous dinosaurs of Africa, exhibiting affinities with coeval Eurasian taxa. Recent analyses suggest a coarse northern-southern division of African faunas during the Late Cretaceous, as the Tanzanian taxa exhibit more traditional Gondwanan taxonomic affinities. Other related questions remain concerning a more precise taxonomic and temporal relationship of the Galula Formation, specifically the lower Mtuka Member, with the nearby Dinosaur Beds in Malawi. As yet described titanosaurian fossils from the Galula Formation provide new insights into these persistent questions. One associated specimen consists of an anterior and posterior dorsal vertebra, a partial scapula, and unidentifiable fragments. The anterior dorsal vertebra exhibits similarities with *Malawisaurus dixeyi* from the Dinosaur Beds of Malawi and *Mnyamawamtuka* from the Mtuka Member of the Galula Formation. The posterior dorsal vertebra differs from those of *Mnyamawamtuka* but, interestingly, compares favorably with specimens currently referred to *Malawisaurus*. Moreover, a separate, isolated middle-posterior cervical vertebra is tentatively referred to *Rukwatitan* based on the presence of the unique carotid processes of the holotypic posterior cervical vertebrae—adding new information on the neck of *Rukwatitan*. The absence of neural spine expansion differs from the coeval *Shingopana* and lognkosaurian titanosaurs from elsewhere. This vertebra even differs from those of *Malawisaurus* by being proportionally shorter and taller. Other fossils include a collection of isolated teeth, variably sized femora, and other axial remains. Taken together, these new materials both expand on anatomy of known taxa (e.g., *Rukwatitan*) and provide

additional context for Galula Formation fauna that may illustrate some degree of taxonomic overlap with the Dinosaur Beds of Malawi.

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## Mammalian Skeletal Morphology

### VISUALIZATION OF SLOTH UNGUAL VASCULATURE

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Among the many interesting features of modern sloths is the vasculature of their extremities. While sloths are endothermic, their body temperature is lower and more variable and linked to the ambient temperature than other placental mammals. Like other mammals from environments with temperature extremes, they possess rete arteriovenous bundles, which constitute an effective heat exchange system, where heat from distally flowing arterial blood is transferred to proximally flowing venous blood. In this way the extremities are still supplied with blood, but heat loss is minimized. When core temperature goes down the temperature gradient in the rete increases, thereby cooling the limbs and preserving body heat. When the sloth is warmed, venous return through the superficial venous system increases, promoting cooling. This begs the question of how this complex vasculature system may or may not extend to the distal phalanges and claws of the sloth, perhaps their most distinctive feature. One possibility could be that to work with the limb cooling function of the rete system, the distal phalanx and claw may be poorly vascularized so as not to increase chances for heat loss. However, considering the extensive and important use of their claws, they may require extensive vascularization to withstand the large amount of stress they are often under. This study uses micro CT scans of sloth distal phalanges to visualize their vascular channels. In both modern and extinct giant ground sloths, vascular networks through the bone of the distal phalanx are quite extensive, and are very clearly linked to externally visible channels and impressions left by the proper digital arteries. In ground sloths these internal vascular channels quickly branch on either side and continue distally, letting off smaller branches as they go. These channels are rather large, appearing to be artificial drill holes on a specimen with the distal end broken off. Modern sloths show a similar pattern, but their vascular

channels take up proportionally more space in the bone than in the giant ground sloths. This shows that sloth claws require a significant blood supply, and may indicate that the rete system is effective enough that by the time the arterial blood gets to the distal phalanx it has been sufficiently cooled to not be a significant source of heat loss.

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## Romer Prize

### GROWTH AND SEX: EVOLUTIONARY AND DEVELOPMENTAL ANALYSES OF FORM-FUNCTION RELATIONSHIPS IN THE CRANIAL ORNAMENTATIONS OF NON-AVIAN AND AVIAN DINOSAURS

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Non-avian dinosaurs provide classic examples of ornaments, including the crests of hadrosaurs and frills of ceratopsians, but with unclear biological roles. Neontological frameworks can quantitatively address functional hypotheses in living animals for comparison to extinct taxa. For example, modern cassowaries are compared to ornamented non-avian dinosaurs because of their phylogenetic proximity, similar body size, long lifespans, time to maturity, and superficial similarity of their casques to dinosaur headgear. However, development, disparity, and function(s) of cassowary casques are poorly understood, limiting the circumstances by which previous studies have contextualized them as extant analogs. To set an anatomical baseline, I recently described the cranial osteology of *Casuarius casuarius* by micro-CT imaging a large ontogenetic series (n = 54). The results demonstrate that the casques contain a central bone that is not present in the ornaments of non-avian dinosaurs, suggesting cassowaries are generally not suitable analogs for comparing direct homologies. Despite this, cassowary casques do contain both elaborative and elevatory elements analogous to those in extinct dinosaurs. In order to assess if cassowaries share similar ornament shape disparities, I use geometric morphometric methods on cassowary casques to compare their ornaments to those of non-avian dinosaurs including *Citipati*, *Corythosaurus*, *Parasauolophus*, *Prosaurolophus*, *Protoceratops*, *Saurolophus*, *Stegoceras*, and *Triceratops*. Here, I draw from cassowary life-history

patterns and osteology to test the following hypotheses related to variation in cassowary ornamentation: (1) if casques attain the majority of their size prior to sexual maturity, then they could signal reproductive capability and (2) if variation in intraspecific casque shape is significant between sexes, then it could signal potential mates or competitors. I identify the majority of casque growth in *C. casuarius* prior to sexual maturity, failing to reject hypothesis 1 and supporting previous ontogenetic patterns of the ornaments of hadrosaurs and ceratopsians. I also find that variation in intraspecific casque shape is not significantly different between sexes, rejecting hypothesis 2 and indicating that body size dimorphism may preclude differences in ornament shape—an important consideration for large-bodied, ornamented dinosaurs. Attention to how modern analogs are used is paramount to future fossil ornament studies.

**Funding Sources** National Science Foundation, Western Interior Paleontological Society, American Association for Anatomy, and The Company of Biologists.

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## Biomechanics & Functional Morphology

### PECTORAL AND PELVIC RANGE OF MOTION: CONSTRAINTS ON ORNITHOCHEIRAEAN QUADRUPEDAL LAUNCH

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Pterosaurs were the first vertebrates to develop powered flight as a method of locomotion and subsequently attained sizes unseen in any other flying group. Launch is the most power intensive aspect with regards to flight, requiring the generation of a launch impulse that will provide sufficient velocity and height to safely begin the flapping cycle. As flying animals increase in size, their capacity for muscular force generation does not increase at the same rate, making this launch impulse harder to generate. One hypothesis for how pterosaurs circumvented this issue is that they utilized a quadrupedal launch, allowing them to incorporate the flight muscles in

the launch cycle. Ornithocheiraeans were a clade of Cretaceous pterosaurs including both *Anhanguera* and *Ornithocheirus*. The largest members of this clade reached wingspans of 6 m. By using Range of Motion (ROM) mapping of the pectoral and pelvic girdles of a generalised 5 m wingspan ornithocheiraeon model, we tested the ability of ornithocheiraeans to assume the poses required for quadrupedal launch. Additionally, we were able to simulate the effects of soft tissues on the joint mobility of the girdles. This facilitates expansion of the ROM through cartilaginous offsets and restriction of the ROM by constrictive soft tissues including ligaments and muscles. The ROM maps were then compared against published poses hypothesised to be used in pterosaur launch. Over 197,000 potential poses were tested for the ball-and-socket joint of the pelvic girdle, and over 591,000 potential poses were tested for the more complex semihellar joint seen in the pectoral girdle. The ROM maps generated show that the ornithocheiraeon model can assume the poses required for a quadrupedal launch. Additionally, the ROM maps indicate that the model is incapable of using a bipedal posture to generate a launch impulse, even with the largest cartilage offset. This study demonstrates that medium sized pterosaurs could assume the postures required for quadrupedal launch. Next steps will estimate whether sufficient muscular leverage and power could be generated through a quadrupedal launch cycle.

**Funding Sources** Alan & Charlotte Welch Fund administered by the Geological Society of London; Bob Savage Memorial Fund

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## Paleohistology & Paleopathology

### THE OSTEOHISTOLOGY OF HYOID ELEMENTS PRESERVES A RECORD OF GROWTH IN ARCHOSAURS

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Assessing the ontogenetic maturity of fossilized remains is key to proper interpretation of morphology, but assessing maturity in reptiles is a well-known challenge. One of the most powerful means of assessing maturity is by sampling the histology of long bones. However, histological sampling is almost entirely conducted on



elongate limb elements because their tubular shapes record growth history better than the irregular cranial bones. For individuals known only or primarily from cranial remains, maturity assessment remains difficult. We partially remedy this methodological gap by histologically sampling archosaurian hyoid elements—specifically, the elongate ceratobranchial element. The hyoid apparatus suspends the throat and tongue, and is sometimes preserved in specimens with no known postcrania. To form an extant phylogenetic bracket of archosaurs we sampled ceratobranchials from growth series of Ostrich (*Struthio camelus*, n = 3; hatchling, 2 years old, 5 years old) and *Alligator mississippiensis* (n = 2; <1 m total length, 3.3 m total length). The Ostrich ceratobranchial was composed of well-vascularized fibrolamellar bone and the maturity of the oldest individual was clearly indicated by multiple generations of secondary osteons, indicating extensive remodeling, and a thick endosteal layer. No lines of arrested growth (LAGs) were preserved. The *Alligator* ceratobranchial was largely composed of moderately vascularized lamellar-zonal bone, with minimal secondary remodeling. There are 9–11 LAGs preserved in the large *Alligator* individual. There is no external fundamental system (EFS) in the most mature individuals, which usually indicates the cessation of linear growth in limb bones—unlike limb bones, hyoid elements may not increase in thickness after full size has been reached, and an EFS may not be indicate skeletal maturity in hyoid elements. The proximal portion of the element shaft, not midshaft, preserved the largest proportion of growth record in both taxa. The ceratobranchial clearly preserves a record of growth and is useful for determining maturity in extinct taxa for which suitable postcrania are unavailable. As a case study, once COVID-19 restrictions are lifted we will sample the ceratobranchial of the type specimen of the putative dwarf tyrannosaur ‘*Nanotyrannus lancensis*’ (CMNH 7541) to determine if this specimen represents a mature individual.

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#### Colbert Poster Prize

### MORPHOLOGICAL VARIATION IN GREAT BASIN HETEROMYIDS: THE ROLE OF BODY SIZE AND DIETARY STRATEGY IN DRIVING MANDIBULAR SIZE AND SHAPE OVER THE LAST 13,000 YEARS

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Biotic responses to environmental change play out in a myriad of different ways. Environmental change is a known driver of species range shifts through time. Less is known about how species respond in situ. As primary consumers, small mammals are highly sensitive to shifts in plant communities. Short generation times and small home ranges also make them good candidates for in situ change. We evaluate in situ responses through the lens of morphological change in seven Great Basin small mammals spanning a range of dietary strategies over the Holocene, exploring the degree to which mandible size and shape change are patterned by dietary strategy and body size.

We imaged 433 specimens across two faunal sequences in the Great Basin: Homestead Cave, UT (HC) and Two Ledges Chamber, NV (TLC). These sites experienced similar climates through the Holocene. We quantified mandibular size and shape change via 2D morphometric analysis, placing 13 homologous landmarks along the perimeter of each hemimandible. Perognathine mice (*Chaetodipus formosus*, *Perognathus parvus* and *P. longimembris*), small-bodied granivores, showed a decrease in centroid size and shifted towards a more generalist mandible shape through time at both sites. Larger-bodied kangaroo rats, also dietary specialists, showed disparate responses. At TLC, *Dipodomys microps* (herbivore) and *D. merriami* (granivore) increased in centroid size and shifted slightly towards a more constrained shape, but at HC, *D. microps* and *D. ordii* (granivore) increased then decreased in centroid size and shifted slightly towards a more generalist shape over time. Our non-heteromyid comparator, the omnivorous deer mouse (*Peromyscus maniculatus*), showed no trend in shape and a constant mean centroid size albeit high variability at both sites.

Our results suggest dietary strategy and body size are likely important factors in determining in situ responses to environmental change. Dietary specialists showed the most shape change, while smaller species showed responses consistent with expectations in a warming and drying climate. In the larger kangaroo rats, however, centroid size deviated from climate-based expectations, and the lack of response in the generalist deer mouse suggests less climate sensitivity in this species. Understanding the different factors that determine species responses to environmental change helps us understand which species have potential to remain in-situ versus those who are likely to shift their distributions today.

**Funding Sources** ZoRF index FS025N SZ65

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## Preparators'

### PREPARATION AND RECONSTRUCTION OF *FALCATAKELY FORSTERAE*, AN ENANTIORNITHINE BIRD FROM THE UPPER CRETACEOUS MAEVARANO FORMATION OF MADAGASCAR

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We describe the mechanical and digital preparation of *Falcatakely forsterae* (UA 10015), a high- and narrow-beaked enantiornithine bird from the Upper Cretaceous Maevarano Formation of Madagascar. The preserved rostral and palatal portions of the cranium were remarkably complete given the exceptionally thin bone (<1 mm maxilla thickness), and relatively coarse-grained depositional setting (sandstone). Both of these factors made mechanical preparation especially challenging. Medical-scale computed tomography conducted prior to preparation provided inconclusive resolution as to the anatomical nature of the flattened specimen. Mechanical preparation of the specimen's surface with insect pins and carbide needles under magnification occurred in two phases. A subsequent micro-CT scan at Ohio University served as the basis for digital preparation of morphology inaccessible via mechanical preparation, and also for a digital reconstruction. Segmentation was performed in a taphonomic (rather than strictly anatomical) context, isolating 167 distinctive volumes (elements and/or fragments) from three blocks of collected matrix. Selected materials were enlarged three times and prototyped in polymer for research and initial 3D morphological reconstruction. These results were combined into a single volume in an effort to model the in situ context of the specimen prior to its collection. The in situ model in turn served to create a Beauchêne-style anatomical reconstruction; both of these models were ultimately included as 3D pdfs in the supplemental materials associated with publication. All fragment position changes were recorded and reported for model repeatability. Changes between in situ and in-life position were animated in "rocker" style videos to qualitatively depict the relative displacement of fragments relative to the left maxilla. These processes were essential for allowing the research and data dissemination processes on this remarkable specimen, and will also feature

prominently as part of both digital and physical exhibitions related to various outreach efforts.

**Funding Sources** National Geographic Society (8597-09) and the US National Science Foundation (EAR-0446488, EAR-1525915, EAR-1664432)

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## Biomechanics & Functional Morphology

### TESTING HYPOTHESES ON HETEROSTRACAN FEEDING USING COMPUTATIONAL FLUID DYNAMICS

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Teeth constitute a key innovation underpinning the evolutionary and ecological development of jawed vertebrates. As the earliest jawed vertebrates already possess teeth, we have to study tooth-like structures in stem gnathostomes to learn more about the evolutionary origin of teeth. Heterostracans are a group of extinct, jawless vertebrates, that possess denticle-covered plates in their oral cavity. However, virtually nothing is known about the structure, development or function of these. How did heterostracans feed? Did they use their oral plates as actual teeth for predation or are these structures an adaption to suspension feeding? The lateral sides of the anterior part of the heterostracan oral plates are covered with rows of forward-pointing denticles. The forward-facing orientation of these denticles has previously been hypothesised to be a specific adaption to suspension feeding. To test this hypothesis, we used computational fluid dynamics (CFD), an emerging technique in palaeontology. CFD allows us to model fluid flow and visualise turbulences and velocity patterns around 2D models of heterostracan oral plate denticles. In our analyses we compare flow and velocity patterns of different models with forward-facing denticles to alternative models with rear-facing denticles. Independent of denticle orientation, similar velocity and turbulence patterns develop in the spaces between the individual denticles as well as on the upper surface of the denticles. In general, the models do not show substantial differences in their flow and velocity patterns. We therefore reject the hypothesis of the forward-facing heterostracan oral plate denticles being a specific adaption to suspension feeding.

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**Symposium - Vertebrate dental ecomorphology: Tooth traits that reflect ecology**

**ANTERIORLY DIRECTED MOLAR OCCLUSION IS UNIQUE TO THERIAN MAMMALS AND MAY HAVE FACILITATED THEIR DIETARY DIVERSIFICATION**

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In non-mammalian synapsids and early mammals, evolutionary transformations in the feeding and hearing apparatuses are posited to have been prerequisites for the radiation of extant mammals. Unlike most vertebrates, including many early synapsids, mammals have precise dental occlusion, a lower jaw composed of one bone, and middle ear ossicles derived from ancestral jaw bones. In this study, we illuminate a related functional transition: therian mammals (eutherians and metatherians) evolved anteriorly directed chewing strokes, which are absent in other synapsid lineages. To investigate this transition, we compiled jaw movement directions during postcanine occlusion from the primary literature for a diverse sample of 133 synapsid genera. Results of our meta-analysis indicate that occlusal complexity generally increases among synapsid clades moving phylogenetically crownward from 'pelycosaurs' to mammaliaforms; however, occlusal movement among non-therian synapsids was limited to orthal-dominated shearing and posteriorly directed grinding. In contrast, therian mammals are the only synapsids to exhibit chewing strokes with significant anterior or transverse occlusal movements. Anteriorly directed jaw movement during occlusion necessitates anteriorly directed muscle force vectors, and we posit that a shift in orientation of the superficial masseter and medial pterygoid muscles is reflected in the fossil record by the evolutionary appearance of a posteriorly positioned angular process in cladotherians (therians and their close kin). This change in jaw morphology was accompanied by the evolutionary appearance of the talonid in lower molars, which helped facilitate extended transverse movement during occlusion. Anteriorly directed occlusion might have been absent in earlier synapsids because of the presence of attached middle ear elements in the posterior region of the jaw that

prohibited the posterior insertion of jaw musculature. Taken together, these changes suggest a fundamental shift in the entire masticatory apparatus of early cladotherians, involving transformations of the jaw, muscles, molars, and middle ears. These changes likely permitted the evolution of novel masticatory movements, including grinding in both the anterior and medial directions (e.g., rodents and ungulates, respectively). Thus, this evolutionary transition in early cladotherians may have been a critical prerequisite for the dietary diversification of therians.

**Funding Sources** National Science Foundation (NSF) Postdoctoral Research Fellowship in Biology (DBI-1812126)

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**Mesozoic & Paleogene Mammals**

**DETERMINING INSECT PREY OF EARLY EOCENE PRIMATES FROM TRACE FOSSILS, WILLWOOD FORMATION, BIGHORN BASIN, WYOMING, USA**

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Trace fossil assemblages of the lower Eocene Willwood Formation include a diverse representation of invertebrate taxa as trace makers, several of which were likely consumed by the earliest Euprimates. Comparing insect trace fossils in the Willwood trace fossil assemblage with data on known insect consumption in modern primates offers insights into which insect taxa represented in the Willwood Formation were most likely consumed by principally faunivorous omomyoids and principally omnivorous to frugivorous adapoids. Data on the specific insect prey of modern tarsiers is used to determine likely prey of fossil omomyoids. The record of *Scaphichnium hamatum* and possible *Rebuffoichnus* and *Fictovichnus* suggest that Geotrupidae and other possible beetle taxa were the most likely insects to be consumed by omomyoids, as well as termites suggested by the record of possible remains of termite nests (cfr. *Termitichnus*, cfr. *Laetolichnus*). The diets of various extant frugivorous and omnivorous primates suggest that adapoids also took

advantage of beetles and possibly termites, as well as cicadas indicated by the presence of *Feoichnus*. These insects would have provided adapoids with an easy to obtain source of protein and vitamin C. We acknowledge the Bureau of Land Management and the Denver Museum of Nature and Science for permitting, logistics, and curatorial support.

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## Education & Outreach

### INCORPORATING VISION AND CHANGE CORE CONCEPTS AND COMPETENCIES INTO AN UPPER-LEVEL UNDERGRADUATE PALEONTOLOGY COURSE

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Elmhurst University's Department of Biology has revised its curriculum and learning outcomes to align with the core concepts and competencies of Vision and Change in Undergraduate Biology: A Call to Action. This comprehensive effort guided the development of the Paleontology course, which was developed as an upper-level biology majors' course in the organismal category of the curriculum. Paleontology was taught during the January term as an intense four-week course (class four days per week/6 hours per day) focused on the organismal biology aspects of the field. Due to the COVID-19 pandemic, both lab and lecture portions of the course were taught entirely online, synchronously on Zoom. Fossil specimens and hand lenses from the teaching collection were assembled into take home lab kits that were checked out by the students.

The course explored the types and quality of biological data preserved in fossils and how they can be interpreted, especially given new technologies. Each week was a separate module: preservation, reconstructing anatomy, reconstructing physiology, and reconstructing ecology. Each module's learning outcomes illustrated all five core concepts of biology outlined in Vision and Change: structure and function; information flow, exchange, and storage; pathways and transformations of energy and matter; systems; and evolution.

Each day involved an exploration of the literature, active learning activities, and lab exercises requiring novel hypothesis generation. The course activities allowed students to develop the core competencies outlined in

Vision and Change, such as quantitative analysis, modeling, and interdisciplinary scientific investigation. The course also emphasized the need for equity in Paleontology, exemplifying the Vision and Change core competency of understanding the relationship between science and society. Each day featured the literature and biographies of a diverse group of "paleontologists of the day." Multiple discussions about equity in access to and participation in paleontological training and research were also an integral part of each module.

Assessments throughout the course indicated that over ninety percent of students met each student learning outcome. Pre- and post-course surveys assessing changes in student interest and understanding of paleontology, and the equity challenges in the field, indicated statistically significant gains in those areas.

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## Mesozoic & Paleogene Mammals

### LATERAL DISTRIBUTION OF THE PALEOGENE *ARSINOITHERIUM* IN AFRICA AND THE AFRO-ARABIAN REGION

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The Fayum province, northeast Egypt, is considered one of the best windows for vertebrate evolution during the Eocene–Oligocene of Africa. It is the best site for the occurrence of *Arsinoitherium*, which contains extensive skeletal remains for both *A. zitteli* and *A. andrewsi*. *Arsinoitherium* is a mysterious genus of paenungulate mammal. It resembled extant rhinos in ornamentation with its massive cranium and protuberant horns, and by the great magnitude of its skeletal frame. However, *Arsinoitherium* is more closely related to elephants, which invaded the upper Eocene and lower Oligocene of northern Africa. The upper Paleogene succession in the Fayum province consists of the nearshore marine and fluvial upper Eocene Qasr El Sagha Formation overlain by the fluvial Oligocene Jebel Qatrani Formation, and Widan El Faras Basalt. Preliminary results of the re-evaluation of the previously collected fauna of *Arsinoitherium* from the Fayum province, illustrate a challenge in the lateral distribution of Paleogene *Arsinoitherium* in Africa and the Afro-Arabian region.

We conclude that there is a migration of *Arsinoitherium* from Africa to the Afro-Arabian region through Egypt by the late Eocene and the early Oligocene. This migration is indicated by its presence in Saudi Arabia and Oman in the Afro-Arabian region and its presence in Egypt almost at the same time. By the late Eocene–early Oligocene, *Arsinoitherium* begins its dispersal migration to east Africa and to the Afro-Arabian region through the Egyptian gate. *Arsinoitherium* from the middle Eocene of Namibia is morphologically different from the *Arsinoitherium* in Egypt. By the late Eocene, *Arsinoitherium* is recorded in Tunisia and Egypt. During the early Oligocene, *Arsinoitherium* occurs in Egypt, Ethiopia, Libya, Tunisia, Angola, and Kenya. However, the mysterious appearance and disappearance of *Arsinoitherium* in Egypt and elsewhere in Africa is still a big puzzle.

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## Biomechanics & Functional Morphology

### GOING UP OR COMING DOWN? *ARCHAEOPTERYX* AS THE EARLIEST KNOWN SECONDARILY FLIGHT-REDUCED VERTEBRATE

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The flight capabilities of *Archaeopteryx* continue to be highly contentious. We addressed locomotor performance in this iconic animal using ratios of forelimb to hind limb bone cross-sectional properties. We compared these results to the same ratios in living birds and the dromaeosaurid *Rahonavis*, which provided a critical paravian out-group. Our analysis recovered *Rahonavis* as a capable powered flyer. Conversely, we found *Archaeopteryx* to be a less proficient long-distance flyer than *Rahonavis*, despite being closer to crown group birds. *Archaeopteryx* was highly cursorial and a short-ranged flyer, at most. The scaled humeral/femoral section modulus ratio in *Rahonavis* was 1.49, more than four times higher than the ratio of 0.32 recovered for *Archaeopteryx*. The bone strength ratios in *Rahonavis* are close to (within 99% Confidence Interval) those measured for falcons, pheasants, and egrets: birds that have strong

hind limbs but retain excellent flight abilities (sustained in falcons and egrets, short-range bursts in pheasants). *Archaeopteryx* compares closely in its humeral/femoral strength ratios with secondarily flightless cursorial birds (99% CI). It seems to have possessed a combination of femora that were moderately stronger than expected for its size and humeri that were much more gracile than predicted from regressions of section modulus against body mass for extant birds. Our results are indicative of secondary flight reduction or loss in *Archaeopteryx*, especially when combined with the existing literature data on this legendary taxon. In a secondary flight reduction model, seemingly conflicting results of prior research regarding the flight capabilities of *Archaeopteryx* are explained as variably detecting volant ancestry versus flightless life history. We suggest that *Archaeopteryx* might have had an ecology and locomotor profile like that of living island rails, many of which are secondarily flightless or flight-reduced hunters that use a wide range of wing-assisted behaviors. *Archaeopteryx* may have been a similarly capable island hunter, relying on its exceptionally long and robust hind limbs to chase down small animals and its reduced wings to assist with especially acrobatic terrestrial maneuvers. Our new picture for *Archaeopteryx* is not one of an animal that was “suboptimal” in any respect. Instead, we reconstruct *Archaeopteryx* as a specialized, fast, and agile island endemic.

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## Holocene & Pleistocene Mammalian Faunas

### A BETTER BITE—THE THIRD DIMENSION IN *SMILODON FATALIS* MANDIBLE RECONSTRUCTION

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Sabertooth cats were predators in North America most recently from the Irvingtonian through the Rancholabrean, 1.9 million to approximately 10,000 years ago. Sabertooths are named for their large upper canines that allowed them to capture prey larger and heavier than themselves. Modern studies have tried to determine how *S. fatalis* killed prey, used its canines, and what bite force they may have exerted. Having an undistorted skull and mandible is an important foundation for each of these

studies. Previously the exterior surfaces of skulls have been restored, but these processes have not been able to manipulate the interior of fossilized skulls with accuracy and may have missed possible shrinkage or deformation resulting from the fossilization process. To achieve a more accurate reconstruction of the skull of *S. fatalis*, we used previous work by Haji-Sheikh and Naples wherein placement of the canines fully into their alveoli and the correct size, shape and thickness of the articular disk were determined experimentally. Our results showed how both areas relate to a more realistic jaw alignment, which would result in a better prediction of bite capability. Our work builds on the accurate recreation of the *S. fatalis* cranium. For this study, we used casts of *S. fatalis* made from skulls and mandibles recovered from the Rancho La Brea tar seeps. It is clear from examining casts of the mandibles that the rami have narrowed over time so much that the upper and lower tooth rows do not occlude correctly. We are identifying these deformations by manipulating, reforming or rebuilding some or all of the skull and mandible using a cast and 3-D recreation processes. The skull casts we have studied show that some areas have been deformed over time or from pressure. Our work uses modern techniques, in this case a 3-D scanner, a 3-D printer, and thermal plastic polyester, to rebuild the lower jaw accurately. This modern approach using 3-D tools allows the mandible to be manipulated from the original cast with respect to size, width, and shape to a more correct alignment by widening the mandible so that the markers we used matched all along the maxilla. These manipulations would not be possible with real fossils or even casts and will allow scientists new ways to study fossils in a way that has not been possible. Using these 3-D methods is a new set of tools that can revolutionize the study not only of *Smilodon* but also of all other fossils.

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## Quantitative Paleontological Method

### NEUTRON IMAGING FOR PALEONTOLOGY

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X-ray radiography and computed tomography (CT) reveal hidden subsurface features within fossil specimens embedded in matrix. With X-rays, distinguishing features from the background (i.e., contrast) results from sample density and atomic X-ray attenuation—fundamental properties of the sample. However, even high energy X-rays may poorly resolve hard and soft tissue structures when the matrix has similar density or X-ray attenuation to the fossil. Here, neutron radiography and neutron tomography complement X-ray imaging, as the source of contrast comes instead from how a neutron beam interacts with the sample's atomic nuclei. The contrast is highly nonlinear across the periodic table, and so researchers can see enhanced contrast between adjacent features when X-ray imaging could not. As the signal source is completely different than X-ray imaging, some intuition from X-rays must be discarded. For instance, neutrons quite easily pass through lead, but are blocked by hydrogen.

Since neutron imaging is uncommon within paleontology, we introduce this exciting technology at a high level with an emphasis on applications to paleontology. We cover some basic physics underlying neutron imaging, where one can perform such experiments, and sample considerations. The neutron source, concepts of beam flux, and image resolution will also be covered. As neutron imaging typically complements X-ray imaging, we discuss how to digitally combine modalities for segmentation and inference. We present examples of how neutron imaging informed fossil descriptions. This includes the skull of a Paleocene mammal *Tetraclaenodon* from New Mexico and a variety of Permian vertebrate specimens from Richards Spur, Oklahoma and imaged at the DINGO nuclear imaging facility in Australia.

Though neutron sources will always be difficult to access, we aim to assist interested researchers considering this exciting imaging technology for their paleontology research.

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## Paleohistology & Paleopathology

### ORTHOGONAL VASCULAR HISTOLOGY OF GROWTH SERIES IN THE ORNITHISCHIAN DINOSAURS *CENTROSAURUS* AND *MAIASAURA*

## COMPARED TO THE THEROPOD *GORGOSAURUS*

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Fossil vascularization in paleontological histology is frequently visualized in 2D. Traditional histology is inherently consumptive, and 3D aspects of vascularity require interpretation for vessel orientations, diameters, terminations, bifurcations, and plasmatic volume within the bone tissue. With 3D synchrotron scanning, not only is fossil or modern bone left unconsumed, these 3D interpretations can be visualized and quantified. We examined orthogonal vascular histology of growth series in ornithischian dinosaurs *Centrosaurus* and *Maiasaura*, including histological investigations into cyclical growth marks both pre- and post-LAGs and/or annuli. Ground thin sections on *Maiasaura* have already established large resorption cavities and extensive vascular changes within the woven tissue cortex. In a one-year-old juvenile *Maiasaura* tibia thin section, the osteon vascularity alternates frequently between longitudinal, reticular, and lamellar with sporadic radial canals bisecting these vascular zones. Similar changes in primary osteon canal diameter, bifurcations, and terminations are observed in the humerus of an older *Maiasaura* humerus visualized in 3D rather than ground section. Imaging also reveals that the juvenile *Centrosaurus* is similar to *Maiasaura* with large resorption cavities ringing the medullary canal, but rather than spongy remnants of primary tissue, the medullary cavity is filled by elongated trabecular struts. The cortical vascularity is primarily longitudinal with some reticular and lamellar regions closer to the periosteal surface. *Centrosaurus* imaging reveals that radial canals are sparse, and the outer cortex vascular network is obliquely angled. Juvenile *Centrosaurus* canal diameters also vary per their vascular pattern. Compared with 3D vascularity in a perinate *Gorgosaurus*, the ornithischians have similar primary canal densities but more varying direction, suggesting similarly rapid absolute growth despite being older juveniles. Overall, compared to traditional 2D histological counterparts, 3D methods offer insights into large-scale nutrient transport, vascularity changes, remodeling, and growth cycles throughout ontogeny.

## Education & Outreach

### TRACKING DINOSAUR FOOTPRINTS: USING 3D DIGITAL FOSSIL TRACKS IN STEM LESSONS

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Particularly in the last year, digital teaching assets have been critical to student learning and engagement across all age groups. Moreover, assets that can be conducted asynchronously provide a significant advantage to classes that need to adhere to a variety of schedules. However, creating meaningful inquiry-based lessons that can hold students' attention and align with specific educational standards can be challenging.

Using photogrammetry, we captured 3D surfaces of theropod dinosaur trackways preserved in a rock quarry in Culpeper, Virginia. These fossilized tracks are part of a much larger bed preserving dinosaur footprints from the Triassic, about 211 million years old. From this bedding plane, one trackway (K15) is particularly long and well-preserved, but does have a gap in the middle where the tracks are lost. We decided to utilize this gap to create a STEM lesson centered on the task of recreating the full trackway.

With the help of their teacher or parent, students work in groups to take digital measurements of the high-fidelity dinosaur footprints. They also measure the distance between footprints and are taught how to tell left versus right. This familiarizes the students with the 3D technology as well as the authentic research practice of measuring for scientific inquiry. The students then recreate these footprints at actual size using paper, pencil and scissors, leaving an appropriately sized gap between the two sections. Then using the spacing they measured, the students estimate how many footprints are missing and where they should be within the sequence.

Last, the students 'recreate' the dinosaur by calculating its hip height using a simple mathematical equation correlating with the size of the footprint. They are given an artist's illustration of what the 'track-maker' was thought to look like (i.e., *Dilophosaurus*), and they draw the dinosaur to scale, using either a whiteboard or a large piece of paper.

This lesson is aligned with Next Generation Science

Standards and designed for use in third grade classes, but could easily be scaled to higher or lower grades. It can also be conducted either in the classroom or at home. Instructors are provided with tutorials on downloading digital files, the measuring process, and the lesson includes a powerpoint presentation and an identification guide to fossil tracks. Students who participated in the trial version of this lesson responded positively and appeared highly engaged with the material.

**Funding Sources** NSF award #1510410 (ITEST), in collaboration with Florida Museum of Natural History and University of Florida

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### **Stem Tetrapod, Squamate, & Amphibian Diversity & Biology**

#### **SNAKES FROM THE CHITARWATA FORMATION (OLIGOCENE-EARLY MIOCENE) OF PAKISTAN: FOSSIL EVIDENCE FOR THE EARLY HISTORY OF *ACROCHORDUS*.**

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South Asia possesses some of the highest extant squamate species richness and a fossil record from the Siwalik Group from the Potwar Plateau of Pakistan (late-early Miocene to Pliocene) that include modern faunal components, as well as extralimital distributions of tropical taxa. The initial assembly of South Asian squamate faunas is poorly understood, however, due to a dearth of late Paleogene and early Miocene records. Field research in the Chitarwata Formation in the Zinda Pir Dome of the Sulaiman Range in central Pakistan has produced a diverse micromammal record ranging from early Oligocene to early Miocene in age. Additional vertebrates include snake vertebrae recovered from two localities which provide insights into the origins of Siwalik Group taxa.

Two preloacal vertebrae and a caudal vertebra from the older locality are dated to approximately 28 Ma and represent a small-bodied acrochordid and a possible indeterminate colubroid. The acrochordid specimens indicate a small-bodied animal with a reduced, posteriorly-angled neural spine as in extant *Acrochordus granulatus* and relatively high-angled prezygapophyses as

in Siwalik *A. dehmi*. Preloacal vertebrae from the younger locality, dated to approximately 22 Ma, represent the oldest definitive record of the genus *Acrochordus*. They represent an animal approximately 2 m in length and are distinct from larger *A. dehmi* in the absence of parazygosphenial foramina and in possessing a smaller neural spine. These records extend the history of acrochordids into the Oligocene and potentially constrain the long stratigraphic record of *A. dehmi* to no younger than middle to late-early Miocene. Extant *Acrochordus* climatically restricted to the wet Old World tropics. The Chitarwata and Siwalik records suggest similarly warm and wet continental South Asian temperatures through the late Paleogene to at least middle Neogene.

**Funding Sources** Natural Environment Research Council Award (NE/S000739/1) to JJH

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### **Taphonomy, Paleoenvironments, & Stratigraphy**

#### **PRELIMINARY TAPHONOMIC ASSESSMENT OF THE HOMESTEAD SITE, A NEW REVUELTIAN (UPPER TRIASSIC: MID-LATE NORIAN) MICROVERTEBRATE ASSEMBLAGE FROM EAST-CENTRAL NEW MEXICO: RECONSTRUCTING AN ASSEMBLAGE FROM INCOMPLETE DATA**

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Microvertebrate assemblages (MVAs) are rich sources of information on paleoecosystems, often preserving greater taxonomic and ecological diversity than assemblages of larger bodied taxa. In the Upper Triassic of the American Southwest MVAs of Adamanian (early-mid Norian) age are extensively sampled, but fewer younger, Revueltian MVAs are known. Recently a new MVA from east-central New Mexico, the Homestead Site, has been identified as Revueltian in age based on the abundant teeth of the hybodont *Reticulodus*. The assemblage includes chondrichthyans, actinopterygians, sarcopterygians, “amphibians” and diverse sauropsids,



principally archosauromorphs, and is similar to assemblages known from the Owl Rock Fm of northern Arizona.

The original collector generated an array of tens of thousands of teeth, bones, and coprolites, which was received as one bin (~15kg) of picked concentrate that included many fragmentary fossils (“concentrate” hereafter) and dozens of bags with thousands of more identifiable, yet largely unsorted elements (“picked bags”). The fossils were either surface collected (a few) or screenwashed using paint sieves and picked (most). Other collection details are absent. Complete elements are mm- to cm-scale and preservation ranges from pristine to heavily pitted surfaces.

To estimate sampling bias and form predictions for diversity of future collections from the site we sieved and sorted the “concentrate” into 4, 2, 1, and 0.5 mm size fractions to compare to the “picked bags.” We find that the 4- and 2-mm concentrate is enriched in coprolites and coprolite fragments (> 60%) relative to bones (~25%) and teeth (~15%), whereas the picked bags are primarily bone (50%+) and tooth fragments (~45%) and less than 5% coprolites, revealing an unsurprising bias in the picked bags for more recognizable and/or diagnostic fossils. The similarity of some fossils in picked bags suggests that there may be associated to articulated microvertebrate elements in situ. Careful examination of the picked bags has resulted in the reassembly of many elements broken during collection and screenwashing. These data suggest that careful excavation of the site should result in proportionately more coprolites than seen in the “picked bags,” but also more complete elements of all sizes. Our results are relevant not just to this site, but any MVA from which original collection information is unknown or incomplete and thus taphonomic and sampling biases are poorly constrained.

**Funding Sources** The Lauer Foundation and the Appalachian State University Department of Geological and Environmental Sciences supported this research.

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## Quantitative Paleontological Methods

### QUANTITATIVE MEASURES OF EXTERNAL ORNAMENTATION IN AVIAN AND DINOSAURIAN EGGSHELL USING A NOVEL APPLICATION OF ORIENTATION PATCH COUNT ROTATED

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‘Ornamentation type’ is a criterion used by ootaxonomists to distinguish archosaurian ootaxa that have well-defined external ornamentation on the surface of their eggshells. These range from isolated (‘dispersituberculate’) to rugose systems of nodes (‘sagenotuberculate’), to complex interconnected systems of oriented nodes and ridges (‘anastomotuberculate’ or ‘lineartuberculate’). Although these ornamentation styles are well documented according to the current ootaxonomic system, there is a high degree of potential subjectivity and ambiguity in their discretization (i.e., many samples could easily be assigned to two or more of these categories).

In order to better quantify, and more precisely describe, the particularly prominent external ornamentation patterns in oviraptorosaur eggs, we have used the orientation patch count rotated (OPCR) algorithm within the software MorphoTester to quantitatively assess the complexity of the external topographic surface. OPCR is generally used in paleobiology for studying topography on dental surfaces and our application represents the first known use on external eggshell surfaces. Using microCT scans of an extant *Dromaius* egg and fossil eggs of a putative caenagnathoid dinosaur from the Cedar Mountain Formation of Utah, we created uniform topographic surfaces of 50mm radius using Amira and GeoMagic Wrap, and decimated to a standardized triangle count of 8,000 to allow cross-taxon comparison. Our expectation was that ornamentation with more isolated nodes would produce lower mean 3D-OPCR values compared to the anastomosing and interconnected node and ridges systems.

Our fossil data demonstrate clear differences between the visibly simpler and more complex forms (as previously assigned by qualitative descriptors of ‘ornamentation type’). Samples that look more complex on gross inspection have higher OPCR values than corresponding samples from the same clutch that look relatively simply ornamented. Despite much lower ornamentation heights, relative values across the emu egg from pole-to-pole also produce OPCR values which show variation from more complex poles (OPCR values of c.200) grading to simpler equatorial values (c.50). The adoption of quantitative metrics in the study of eggshell ornamentation patterns may mitigate problems of subjectivity in this key criterion, improving resolution in ootaxonomy and providing new fodder for functional studies.

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## Macroecology & Macroevolution

### THE INFLUENCE OF ANCESTRAL BODY SIZE ON ECOMORPHOLOGICAL TRENDS IN SYNAPSID RADIATIONS

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‘Small-bodied faunivore’ is the dominant ancestral ecomorphotype early in crown mammalian radiations, but it is unknown how far back this trend extends within Synapsida (the mammalian total group). To examine synapsid macroevolutionary patterns in a phylogenetic context, we built a time-calibrated meta-phylogeny of 2,128 synapsid species from the Carboniferous through Eocene (305–34 Ma), based on 211 published character matrices, each weighted according to their dependence on ‘parent’ matrices. All published character matrices focusing on non-mammalian synapsids were included, making the meta-phylogeny comprehensive for non-mammaliaform synapsids. Further, we used the most comprehensive early mammaliaform matrices. We then collected jaw length measurements (as a proxy for body size) and dietary information for 408 synapsid species (37 non-therapsid pelycosaurs, 134 non-cynodont therapsids, 46 non-mammaliaform cynodonts, 80 non-therian mammaliaforms, and 178 therians). We used the meta-phylogeny in conjunction with jaw length measurements to investigate patterns of body-size and dietary evolution during radiations of synapsid subclades.

The results show that faunivory is the typical ancestral diet of each major radiation within Synapsida, but the small-to-large trend in body-size within radiations does not become established until the end-Triassic size bottleneck near the base of Mammaliaformes. Instead, ‘pelycosaur’, ‘therapsid’, and ‘cynodont’ subclades have ancestral jaw lengths that are considerably larger than non-therian mammaliaforms and therians. The shift to small ancestral body sizes is one of several aspects of the mammalian phenotype to emerge in the Late Triassic. Furthermore, by placing ‘mammaliaforms’ and mammals

near their likely lower size limit, this change forced most subsequent body-size diversification to consist of trends toward larger sizes, altering macroevolutionary dynamics for the remainder of synapsid history.

**Funding Sources** This work was funded by the National Science Foundation: DEB-1754502 (to K.D.A) and DBI-1812126 (to D.M.G.).

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## Macroecology & Macroevolution

### NON-AVIALAN THEROPOD ECOSPACE DRIVEN BY EXTINCTION EVENTS, ORIGIN OF FLIGHT, AND RADIATION OF FLOWERING PLANTS

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By giving rise to birds in the Jurassic, theropods are the most morphologically and ecologically diverse clade of dinosaurs. However, even when excluding birds, non-avialan theropods represent an extremely diverse group of Mesozoic dinosaurs (>400 valid species) with a great species richness and a large array of body size, feeding ecologies (carnivores, herbivores, omnivores, piscivores, myrmecophages, etc.) and ecological niches (ground-dwelling, semi-aquatic and scansorial/arboreal). This study aims to identify evolutionary and ecological drivers that have shaped theropod communities throughout the Mesozoic by exploring ecospace modelling using 232 genus-level non-avialan theropod taxa. Five ecological parameters—paleoenvironment, habitat, body size, diet and locomotion—were used to explore ecospace modelling and ecospace occupation in non-avian theropods through time. Diet was considered using three parameters (dietary preference, feeding strategy, and trophic guild), which were assessed and categorized based on the results of a cluster analysis conducted on a data matrix of 60 discrete feeding-related characters. Ecological morphospace and disparity curves were plotted over seven time bins of the Mesozoic and compared with curves on species richness, body mass, and angiosperm within-flora richness and abundance. Our preliminary

results reveal a general increase in ecological disparity throughout the Mesozoic, with a particularly important increase in the Late Jurassic that we correlate with the origin of flight and the emergence of herbivorous theropods. Contrary to species richness, the curve of ecological disparity decreases after the Early and Late Jurassic when the maximum distance is considered. The J/K boundary extinction event best explains a decrease in ecological disparity in non-avian theropods after the Jurassic. Unlike the ecospace occupation of carnivorous theropods, which remains relatively stable from the Middle Jurassic to the early Cretaceous before increasing from the “mid”-Cretaceous, the ecospace occupation of omnivorous/herbivorous theropods constantly increases from the Late Jurassic to the Late Cretaceous. This increase in ecospace occupation, which coincides with an increase in omnivorous/herbivorous theropod richness and abundance during that time, likely results from the colonisation of new ecological niches left vacant by other herbivorous dinosaurs, and by the radiation of flowering plants in the Early Cretaceous.

**Funding Sources** C.H. was supported by the CONICET and Agencia Nacional de Promoción Científica y Tecnológica, Argentina (Beca Pos-doctoral CONICET Legajo 181417)

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## **Stem Tetrapod, Squamate, & Amphibian Diversity & Biology**

### **REGIONALIZATION OF THE SQUAMATE RIBCAGE IN THE EVOLUTION OF THE SNAKE BODY FORM**

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The fossil record demonstrates an abrupt change from limbed lizard ancestors to the snake-like body form in the evolutionary history of Squamates. Little anatomical information is available for intermediate forms, so hypotheses surrounding this transition have previously been based in developmental data. Postulated mechanisms involved axial deregionalization or expansion of a single morphological domain. Recently, retention of axial regionalization in the snake vertebral column has been demonstrated. However, the squamate rib cage has not yet been examined in this context, despite the key role of ribs in limbless locomotion beyond the ventilatory function

seen in limbed taxa. Using anatomical data from extant taxa, we hypothesise and test a more complex history of evolutionary modification of patterning mechanisms in the evolution of limbless Squamate body forms. Using CT scan data from the skeletons of over 50 species of snakes and snake-like squamates as well as limbed taxa, we developed a landmarking scheme that captures shape data of all individual free, pre-cloacal, non-bifid ribs. Using segmented linear regression, we analyzed these shape variables to identify axial regions, as gradients of shape morphologies describe axial regions. Clear morphological regionalization of the dorsal ribs is seen in all squamate taxa studied. Across taxa, there is remarkable consistency in both the number and relative positioning of regional boundaries. When mapped on to molecular and morphological time-calibrated phylogenies, we see clade-specific changes at the base of Lacertoidea and Serpentes, however. The same changes to regional boundaries are not seen consistently across independent instances of the snake-like body form, corroborating the hypothesis that this evolutionary change is not the result of a single patterning shift, but a more complex set of steps. Analysis of the landmark data also allowed examination of changes in rib shape and intracolumnar heterogeneity across the clade. In each of the multiple instances of the snake-like body form, we see convergence of rib shape, reflecting shared functional requirements. Additionally, axial heterogeneity sharply drops compared to limbed relatives. We conclude that all squamate species retain axial regionalization. The abrupt evolutionary transitions seen in the fossil record are therefore not consistent with loss of function of the patterning genes known to be expressed during development.

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## **Avialan Evolution & Biology**

### **SPECIES DISTRIBUTION MODELING OF NON-MIGRATORY AND WINTERING SANDHILL CRANES (*GRUS CANADENSIS*) AT PAST AND FUTURE TIME INTERVALS**

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Sandhill cranes (*Grus canadensis*) are one of the longest-lived species of birds on the planet, with a fossil record stretching back ~2 million years. *G. canadensis*'s long evolutionary history makes it a prime subject with which to explore the relationship between a species and its environment over time. The species' longevity and current widespread distribution raise questions about how sandhill cranes have responded to past environmental conditions and how they might cope in the face of human-mediated climate change. The current study constructs species distribution models of non-migratory and wintering crane populations at three time intervals: modern day, the last interglacial (ca. 130 ka), and in the near future (ca. 2050), based on bioclimatic variables. Both non-migratory and wintering cranes exhibit northward range expansions at both the past and future time intervals compared to the modern. These models predict sandhill cranes to be particularly responsive to the mean temperature of the wettest quarter, and this northward shift may be due in part to warm and wet conditions prevailing under past and future climate regimes.

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## Fishes Evolution & Distribution

### NEW STURGEONS FROM THE LATE CRETACEOUS HELL CREEK FORMATION OF NORTH AMERICA, WITH NOTES ON THE CRETACEOUS RECORD OF THE FAMILY ACIPENSERIDAE

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The modern freshwater fish fauna of North America has been intensively studied, although its early evolution is still poorly understood. In particular, the Cretaceous was a time of great evolutionary transformation for the freshwater fish fauna of North America, although the fossil record of this fauna during that time period is extremely poor, with virtually all remains from this time being fragmentary and isolated bones, limiting their phylogenetic and taxonomic information. In this study, the skeletons of newly discovered whole-body fossils of freshwater fishes from the Late Cretaceous Hell Creek

Formation were examined. Among these specimens are the remains of two distinct undescribed species of sturgeons (Acipenseridae) preserved in a loosely consolidated matrix. One taxon is represented by a partially preserved skull, and can be diagnosed by a relatively elongate preorbital region (i.e., snout). The second species is represented by two body fossils (including the head and relatively complete postcranial remains) and a third specimen of an intact, three-dimensionally preserved skull and pectoral girdle. This taxon can be diagnosed based on features of the opercular elements. Most sturgeons from the Cretaceous are known by undiagnosable fragmentary remains (i.e., scutes and pectoral-fin spines) or poorly preserved remains (e.g., *Protoscaphirhynchus*), with *Priscosturion* and the recently described *Anchiacipenser* (both monotypic) being rare exceptions. Therefore, these fossils give a rare glimpse into the evolution of Acipenseridae at a critical time in their phylogenetic history, and suggest significant morphological and taxonomic diversity within sturgeons early in their evolution.

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## Fishes Evolution & Distribution

### THE LATE MISSISSIPPIAN (VISÉAN) CHONDRICHTHYAN ASSEMBLAGE OF THE ST. LOUIS FORMATION AT MAMMOTH CAVE NATIONAL PARK, KENTUCKY

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Mammoth Cave National Park (MACA) in Kentucky contains the longest known cave system in the world.

Over 400 miles of passages cut through Late Mississippian sedimentary rocks representing three geologic formations. The oldest of these Late Mississippian beds is the Horse Cave Member of the upper portion of the St. Louis Formation. The St. Louis Formation is known for its Viséan-age chondrichthyan fossils from Missouri, Illinois, Iowa, and Kentucky; first described by some of the earliest American paleontologists in the mid to late 1800s. However, many of these early descriptions were not constrained to specific geologic horizons or used vague locality descriptions. Many of these fossils were simply referred as originating from the “St. Louis Limestone.” Recently, three passages cutting through the Horse Cave Member of the St. Louis Formation at Mammoth Cave National Park have yielded a diverse chondrichthyan assemblage in which the occurrence of fossils is documented from a single geologic horizon.

The chondrichthyan assemblage of the St. Louis Formation at Mammoth Cave National Park is presently composed of twenty-three taxa representing ten orders and sixteen families. The order Ctenacanthiformes is represented by *Cladodus marginatus*, *Cladodus elegans*, *Saivodus striatus*, *Glencartius costellatus*, and an indeterminate form. There are two indeterminate forms of Paraselachii and two from the Orodontiformes; *Leiodus clacaratus* and an indeterminate form. Petalodontimorpha is represented by *Chomatodus* sp., *Tanodus pumilis*, *Polyrhizodus concavus*, and *Petalorhynchus pseudosagitatus*. The Holocephali are very diverse with records of *Helodus* sp., *Psephodus* sp., *Cochliodus* sp., *Deltodus* sp., *Sandalodus* sp., *Poecilodus* sp., *Psammodus* sp., *Copodus cornutus*, *Deltoptychius* sp., and *Traguarius* sp.

Our preliminary comparison of the St. Louis Assemblage and the suprajacent Ste. Genevieve Formation chondrichthyan assemblages shows some distinct taxonomic differences with *Cladodus elegans*, *Tanodus pumilis*, *Polyrhizodus concavus*, *Petalorhynchus pseudosagitatus*, and *Copodus cornutus* known only from the St. Louis Formation. We propose that the Mammoth Cave St. Louis chondrichthyan assemblage can be a benchmark to help provide clarity and refinement on the taxonomic records of North American Late Mississippian chondrichthyans, and to help better understand the diversity and plasticity of global chondrichthyan assemblages during the Late Mississippian as a whole.

## A TRANSITIONAL DRUM FISH FROM THE LATE MIOCENE OF FLORIDA

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Despite descending from a marine lineage (Sciaenidae) that is highly specialized for durophagy, the extant freshwater drum fish, *Aplodinotus grunniens*, is not only a freshwater dweller but also a generalist with a very ecologically-variable pharyngeal morphology. When this transition occurred and what factors drive it are poorly understood from fossil records. While the fossil record of sciaenids (including *Pogonias* which is closely related to *Aplodinotus*) spans the Eocene-Quaternary, the fossil record of *Aplodinotus* is limited to the Neogene and primarily consist of calcareous otoliths (inner ear stones) rather than skeletal fossils, which limits both phylogenetic placement and ecological understanding. 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 many osteological elements that belong to a new species of *Aplodinotus*, including the highly diagnostic pharyngeal elements and vertebrae along with a nearly complete neurocranium. Based on vertebrate biochronology, the Montbrook fossil locality is late Hemphillian (ca. 5–5.5 Ma) in age and the *Aplodinotus* fossils represent some of the earliest records of their genus in North America as well as one of the most complete sciaenid fossil taxa known. This particular species is notable for possessing a mixture of osteological traits. While the vertebral column and many cranial features resemble an exceptionally large and somewhat elongated *A. grunniens*, other osteological elements are similar to those found in both the freshwater generalist *Aplodinotus grunniens* and the closely related, marine durophagous specialist *Pogonias cromis*. In particular, the infrapharyngeal is large and robust (similar to *P. cromis*), but possesses the concave lateral edge and smaller, circular pharyngeal teeth of *A. grunniens*. The dentary and premaxilla show both sockets for the large caniniform teeth of *A. grunniens* as well as many rows of very fine villiform sockets as seen in *P. cromis*.

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## Permo-Triassic Ecosystems

### A NEW PSEUDOSUCHIAN ARCHOSAUR FROM THE MIDDLE TRIASSIC OF TANZANIA AND THE EARLY EVOLUTION OF SUCHIANS

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Following the Permo-Triassic mass extinction, archosaurs diversified and rose to global ecological dominance by the Late Triassic. Pseudosuchian archosaurs became particularly speciose and exhibited disparate morphologies related to distinct ecologies. Although that radiation had started by the beginning of the Middle Triassic, as evidenced by the presence of crown archosaurs near the Early–Middle Triassic boundary, many distinct clades (e.g., aetosaurs, ornithosuchids) currently lack Middle Triassic representatives. These absences create a lack of transitional morphologies, obscuring relationships among early-diverging archosaurs, and leaves macroevolutionary questions related to order of trait acquisition and ecological niche-breadth expansion unresolved.

Here we present a new species of pseudosuchian archosaur from the Lifua Member of the Manda Beds, Tanzania. With one mostly complete skeleton with well-preserved cranium, postcrania, and numerous osteoderms, and with two other referred individuals, about ~80% of the total anatomy of this taxon is represented. We assign this taxon to Pseudosuchia based on its ‘crocodile-normal’ crurotarsal ankle joint. The maxillary and dentary dentition is recurved and laterally compressed with mesial and distal serrations. The skull possesses character states shared with aetosaurs and erpetosuchids, such as the jugal contributing to the posterior margin of the antorbital fenestra between two anterior articulation processes, and the postorbital forming the majority of the postorbital bar. In addition to numerous dorsal osteoderms, this taxon has abundant appendicular osteoderms. We recover this new taxon as an early suchian within a larger clade of armored

pseudosuchians, including erpetosuchids and aetosaurs, which splits from paracrocodylomorphs. Character optimizations indicate osteoderm and cranial neurovascular traits are important trait shifts for reconstructing the phylogeny in these early members of Pseudosuchia and shed light on the evolution and expansion of carapaces and a transition from longer-limbed suchian ancestor to a clearly quadrupedal, armored clade. This new taxon highlights the importance of sampling early lineages in rapidly diverging clades to reconstruct character evolution.

#### Funding Sources

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## Non-avian Theropod Systematics, Biology, and Evolution

### ONTOGENETIC IMPLICATIONS OF TWO DISTINCT DROMAEOSAURID MAXILLAE FROM THE CRETACEOUS (CAMPANIAN) TWO MEDICINE FORMATION OF MONTANA, U.S.A.

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Dromaeosaurid material has been found in Campanian rocks throughout western North America with multiple species named. Two species with fairly complete remains include *Saurornitholestes langstoni* and *Bambiraptor feinbergi*. However, little ontogenetic data exists for these taxa and in general, growth changes in dromaeosaurids are not well documented.

Here we describe two dromaeosaurid maxillae recovered in the early 1990s from the Campanian Upper Two Medicine Formation of Montana: the juvenile MOR 9753 and adult MOR 553S-7.30.91.274.

MOR 9753 was recovered from Bob’s Vacation Site in Glacier County, Montana, a site which also yielded frog, pterosaur, troodontid, and *Orodromeus* material, along with a fairly complete adult dromaeosaurid postcranial skeleton not found in association with MOR 9753. MOR 9753 measures 5.5 cm long and represents a juvenile *S. langstoni*. MOR 553S-7.30.91.274 comes from Jack’s birthday site in Glacier County, MT, a locality that also produced numerous other dinosaur remains such as

*Hypacrosaurus*, *Prosaurolophus*, *Gryposaurus*, and *Troodon*. The stratigraphically younger MOR 553S-7.30.91.274 measures 9.4 cm in length, and was identified as an adult *B. feinbergi*.

Previously described maxillae for each respective species include multiple adult *S. langstoni* maxillae and the juvenile *B. feinbergi* holotype (AMNH FR 30556) and allow for ontogenetic comparisons with MOR 553S-7.30.91.274 and MOR 9753. The relatively shorter MOR 9753 is just 15–20% the size of an adult *S. langstoni* (based on TMP 1994.012.0844). The disparity in shape indicates allometric growth, with the maxilla becoming more rostrocaudally elongate with ontogeny. The maxilla of the juvenile *B. feinbergi* holotype, which was previously estimated to be 75% the size of a full grown adult, is only 30–40% the size of MOR 553S-7.30.91.274, but shows similar proportions. There is no change in the position of fenestrae and the bone retains the same overall proportions despite the change in size, indicating isometric growth.

MOR 553S-7.30.91.274 represents the only known adult *B. feinbergi* skull material and may help resolve its place taxonomically within or outside of the saurornitholestinae. MOR 553S-7.30.91.274 also represents a temporal extension for *Bambiraptor*, because the locality of MOR 553S-7.30.91.274 sits much higher stratigraphically than the holotype locality, near the bottom of the upper Two Medicine Formation.

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## Non-avian Theropod Systematics, Biology, and Evolution

### MESOZOIC MEAT-EATER MARKETPLACE: ASSESSING THEROPOD GUILD EVOLUTION BEYOND BODY SIZE

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Cenozoic macropredatory mammalian guilds often show considerable disparity in adaptations of prey acquisition and dispatch (e.g., there are considerable differences in body size and in tooth, skull, claw, and limb morphology in sympatric Plio-Pleistocene ursids, canids, hyaenids, machairodontines, and pantherines.) Recent studies have demonstrated the differences in body size between macropredatory theropods in various Jurassic and Cretaceous faunal assemblages. This study assesses

whether the more taxonomically diverse guilds of the Jurassic through early Late Cretaceous showed higher morphological disparity than the tyrannosaurid-dominated faunas of Late Cretaceous Asiamerica and the abelisaurid- and megaraptoran-dominated faunas of Eurogondwana. Measurements of the teeth, skulls, forelimbs, unguals, pelvis, tail, and hindlimb of diverse theropod taxa were taken to create a set of theoretical and empirical morphospaces. The spread of sympatric assemblages of theropods within these morphospaces were used for a fauna-by-fauna comparison.

It is found that Jurassic assemblages (which often contain the highest taxonomic diversity and/or the most even spread of body sizes) have less morphological disparity of predatory adaptations than the Early-to-mid-Cretaceous carcharodontosaurid-spinosaurid faunas or the Late Cretaceous faunas. This contrasts with an expectation that higher sympatric predator diversity might reinforce greater niche differentiation in food acquisition strategies. Instead, the more morphologically disparate Cretaceous assemblages may reflect an increasing diversity of prey acquisition modes in response to the rise, diversification, and anti-predator defenses of new prey taxa (e.g., titanosaurian sauropods, styracosternan ornithopods, neoceratopsians). Additionally, it is observed that the distribution of different forms of theropod guilds in the Campano-Maastrichtian parallels palynological provinces of that same interval (including variations within Gondwana), suggesting that aspects of the overall environment may be a driver for dinosaurian biogeography and guild structure.

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## Preparators'

### MARINE FOSSILS FROM THE COALEDO FORMATION: A CASE STUDY ILLUSTRATING THE WORKFLOW TO PREPARE AND SHIP AN UNCURATED COLLECTION

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As stewards of paleontological materials at the Natural History Museum of Los Angeles County, collections staff are relied upon to preserve collections and their associated data. A lack of resources, however, contributes to specimens remaining in various curation states after being collected in the field. We present one such example in the

marine vertebrate fossils from the Coaledo Formation, collected many decades prior by a former paleoichthyology curator. This former curator, now retired, wanted to complete the study of the Coaledo Formation material that consists of teeth, vertebrae, spines, and scales of sharks, rays, and teleosts. Using the Coaledo Formation collection as a case study, the following workflow establishes the materials and methods employed to inventory, track, pack, and ship an uncurated marine collection to its original collector for identification, research, publication, and completion of curation. Photographs of the material were taken with a DSLR camera to document their original condition and location. Over 100 specimen trays containing 249 glass vials and 279 elements were inventoried with associated field numbers and tags. Once all trays were assigned a unique number for tracking, each was photographed alongside a printed label using an iPhone or a Nikon point and shoot camera. Custom specimen housings, similar to cavity mounts, were created using a combination of Ethafoam planking, tri-rod, and 1/4" and 1/8" liners affixed using a hot glue gun inside polystyrene containers and pre-made cardboard boxes. Using a Dremel tool, cylindrical holes were drilled into Ethafoam planking to house vials. The specimen housings were packed inside cardboard shipping boxes internally lined with 1/4" Ethafoam with Styrofoam peanuts or air-filled bags to fill empty space. A copy of the images and inventory were sent in the packages and electronically to the collector to aid in the unpacking, identification, and cataloging of the material. This method allowed for over 500 trackable yet uncataloged elements to be shipped to the original collector with approval from the Museum Registrar, resulting in diminished museum backlog and material identification which aids in the completion of curation and publication of research.

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### **Macroecology & Macroevolution**

#### **THE EFFECTS OF ECOSYSTEM CHANGE ON SMALL MAMMAL COMMUNITY ECOLOGY: A HOLARCTIC VIEW**

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Dramatic changes in terrestrial ecosystems through the Neogene have had a significant effect on the evolution of

mammals. Major changes in body size, in diets, in locomotor habits, and in social behavior have been demonstrated by numerous past studies. The increasing dominance of open habitats and cool, seasonal climates have driven greater hypsodonty in ungulate herbivores with an increasingly grassy diet, as well as larger body mass and more frequent cursoriality. Large carnivores likewise see increases in cursoriality and body size to keep pace with their prey. Predatory clades also see new hunting strategies to account for changes in both the prey species themselves and the characteristics of the environments, with longer sight lines and less opportunity for concealment and ambush. Lagging behind our understanding of the larger mammals is our understanding of changes in small mammal ecology. A recent synthesis of North American data using the NOW database revealed that the ecomorphology of small mammals changed much earlier than their larger relatives, with increases in both hypsodonty and open-habitat locomotor adaptations such as digging and hopping. We have added to this dataset to ask how small mammals in Asia and Europe responded to similar changes, given that the timing of the spread of open habitats was similar throughout the Holarctic. Small mammals show some similar changes, but the degree of community change is less dramatic in Europe than it is in North America, with more of the continent still forested even into the Pleistocene. This apparently smaller change is likely exacerbated by the underrepresentation of the more forested eastern half of the North American continent in published Neogene fossil occurrences. Asia's rodent diversity bears more resemblance to that of North America, with greater diversity of open-habitat-adapted small mammal taxa through much of the Neogene, before ungulates and large carnivores become well-adapted to open ecosystems. This finding shows the importance of small mammals, which respond more rapidly to environmental change than their larger cousins, to detecting the timing of ecosystem changes. The distinct responses in Europe and Asia also highlight global differences in patterns of ecological change, making it all the more important to add data from South America, Australia, and Africa to these databases in order to get a clear sense of the relationship between mammals and ecosystem change.

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### **Mesozoic & Paleogene Mammals**

#### **NEW RECORDS OF EARLIEST TORREJONIAN (TO1) PLESIADAPIFORMS FROM**



## NORTHEASTERN MONTANA, USA, PROVIDE WINDOW INTO THE EARLY DIVERSIFICATION OF STEM PRIMATES

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Plesiadapiforms (stem primates) appear in the fossil record shortly after the Cretaceous/Paleogene (K/Pg) boundary and subsequently radiated throughout the Paleocene into a taxonomically and ecomorphologically diverse group. The spatiotemporal patterns surrounding the plesiadapiform radiation are thus important for understanding their evolutionary history and the post-K/Pg recovery and diversification of placental mammals more broadly. The oldest confirmed occurrences of plesiadapiforms come from deposits in northeastern Montana dated to the earliest Puercan (Pu1) North American Land Mammal ‘age’ (NALMA), and all records of Puercan plesiadapiforms are taxonomically restricted to members of the Purgatoriidae and two species of the enigmatic plesiadapiform *Pandemonium* (family incertae sedis). Plesiadapiform diversity substantially increased in the Torrejonian NALMA with the appearance of five families that exhibit a wide range of dental morphologies. However, the sparse record of compositionally intermediate faunas between the Puercan and the more well-known middle and late Torrejonian NALMAs has hampered our understanding of this crucial interval of diversification in primate evolutionary history. Here we report a large sample of plesiadapiform dental fossils recovered from the To1 Farrand Channel and Horsethief Canyon localities in the uppermost part of the Tullock Member of the Fort Union Formation in northeastern Montana. This assemblage includes over 100 isolated teeth and dentigerous dentary fragments and records members of the Purgatoriidae, Paromomyidae, and provisionally the Palaechthonidae. Notably, these new records provide further evidence that the temporal range of the Purgatoriidae extended into the Torrejonian. Large sample sizes also allowed us to document intraspecific variability and one previously unknown tooth position of the earliest known paromomyid, *Paromomys farrandi*. New observations shed light on changes in dental morphology within the Purgatoriidae and Paromomyidae that occurred in the earliest Torrejonian, which might also help clarify evolutionary relationships with at least some members of the likely non-monophyletic Palaechthonidae. Further, this

assemblage records a key interval in the evolutionary history of plesiadapiforms that bridges the gap between their relatively low taxonomic richness in the Puercan and their comparatively higher taxonomic richness and range of morphologies in the middle and late Torrejonian.

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## Stem Tetrapod, Squamate, & Amphibian Diversity & Biology

### INFERRING HOMOPLASY IN CRANIAL MORPHOLOGY ASSOCIATED WITH FOSSORIALITY IN SNAKES

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Reconstructing ancestral ecologies of snakes, particularly in reference to the evolution of the clade from limbed squamates, has been the subject of considerable debate. Phylogenetic hypotheses based on either morphological or molecular data recover divergent topologies especially interrelationships of fossorial taxa such as the ‘anilioid’ pipe snakes.

To test whether cranial morphology associated with fossoriality is homoplastically distributed throughout snake phylogeny, we examined the parietal bone of 67 extant species of snakes from all major snake clades, including ‘anilioids,’ and fossorial and terrestrial members of the booids, elapoids, and colubroids, as well as the Late Cretaceous stem snake *Dinilysia patagonica*. We chose the parietal because it is the primary skull roof bone of snakes, enclosing the braincase and ophthalmic nerves, shows considerable morphological diversity, and is preserved in fossil taxa. Shape differences were quantified using geometric morphometric analysis of 19 homologous landmarks. Procrustes rescaled landmarks were then analysed using principal component analysis to define shape variables along major axes of variation. Analysis reveals repeated independent occupations of a fossorial morphospace by multiple clades of snakes, including *Anilius*, uropeltoids, colubroid, and elapoid taxa. This pattern holds regardless of competing hypotheses of relatedness based on either molecular or morphological data. Our results are consistent with the hypothesis that independent specialisations to a fossorial ecology results in homoplasy of morphological characters in snakes, and support molecular phylogenetic hypotheses of fossorial ecomorphologies being widely distributed

within basal divisions of Alethinophidia. Our results also predict fossorial habits for *Dinilysia*, supporting previous inferences based on inner ear morphology. These results highlight the need to understand how morphological characters relate to ecology when using those characters to reconstruct phylogenetic relationships, and the usefulness of homoplastic characters in predicting the ecology of extinct organisms.

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### Mesozoic & Paleogene Mammals

#### STILL EXPLORING CONFLICTING MOLECULAR AND MORPHOLOGICAL SIGNALS IN THE PHYLOGENETIC ASSESSMENT OF FOSSILS—A CRITICAL LOOK AT THE EARLY HISTORY OF PRIMATES

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Perhaps all systematically minded paleontologists would agree that the long and ongoing dialectic regarding what to do when morphological and molecular phylogenetic signals are in conflict has been witness to plenty of thesis and antithesis, but little in the way of synthesis. Total evidence remains a viable solution but seldom produces what most would consider to be a truly integrative result. Somewhat paradoxically, what we are often left with when analyzing fossils is a direct comparison between topologies derived solely from morphological matrices, where fossils differ from extant tips only in the extent of their completeness, and molecular backbones, where fossils are stripped of any ability to overturn the underlying phylogenetic framework. Here, we use the well-studied group Primates to explore the utility of a previously implemented comparative strategy wherein morphological characters are weighted based on their congruence with the molecular topology. While we recognize this strategy falls short of a truly synthetic solution, it provides comparative metrics preferred over those of a strict molecular scaffold. This is because the approach permits the fossil record an opportunity to meaningfully shape the result while still incorporating the heuristic power of molecular sequence data. Our results retained many hallmarks of paleontological

analyses with several fossil taxa being unstable because of a scarcity of data and a clustering of the historically volatile omomyioids and adapoids around the crown clade defined by the Strepsirrhini-Haplorhini split. Interestingly, the weighted hard-morphology-exclusive dataset successfully recovered a monophyletic Haplorhini. We also found that seemingly small adjustments of the data matrix had a major effect on phylogeny and associated statistics. In particular, we found that as little as 3% of all characters can have a major effect on the resulting topology, and applying weight to characters, even equally, can result in significant change in bootstrap support value. In addition, we found that a considerable number of characters were deemed phylogenetically uninformative based on the assigned weight. Even if such weighted results are ultimately rejected as the preferred tree based on theoretical grounds, calculating and comparing these results does provide nuanced information that can aid interpretation.

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### Dinosaur Systematics, Diversity, & Biology

#### POSTCRANIAL AUTAPOMORPHIES AND A NEW OCCURRENCE OF *PARKSOSAURUS WARRENI* (DINOSAURIA: ORNITHISCHIA) IN THE HORSESHOE CANYON FORMATION

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Thescelosaurids are typically diagnosed based on unique autapomorphic character combinations present in the skull, and few members of the group can be taxonomically assigned on postcranial autapomorphies. Accordingly, establishing postcranial autapomorphies for various thescelosaurids will be crucial for enabling researchers to classify taxa at the genus or species level based on fragmentary postcranial remains. Examination of the postcranium of *Parksosaurus warreni* (ROM 804) led to the establishment of new autapomorphies of the ilium and ischium that distinguish this taxon from other ornithischians. This unique character combination includes a dorsoventrally thin distal ischium that is paddle-shaped and expands mediolaterally as a sheet of bone; a concave dorsal margin of the ischial shaft; a mound-like obturator process that marks the proximal expansion of the paddle-shaped portion of the ischium;

and a narrow, oval brevis shelf is oriented lateroventrally. In the light of these postcranial autapomorphies, a new *P. warreni* specimen (UALVP 56885) is identified from the Horseshoe Canyon Formation (HCF). Its phylogenetic position among ornithischians is assessed using a previously published character matrix. UALVP 56885 consists of a partially articulated sacrum with paired ilia and ischia and fragmentary caudal vertebrae. Character codings for ROM 804 and UALVP 56885 in the context of the published matrix are identical. UALVP 56885 represents the only *P. warreni* specimen to have been discovered within the last century. Referral of UALVP 56885 to *P. warreni* is based on anatomical comparisons (postcranial autapomorphies and character coding are identical) with the *P. warreni* holotype. Future basal ornithischian research should concentrate in part on documenting postcranial differences, including autapomorphies, in basal neornithischians. Such studies will improve the ability of researchers to test hypotheses and establish robust systematic relationships with respect to the taxa in question.

**Funding Sources** Grande Prairie Regional College, NSERC Discovery Grant (RGPIN-2017-06246), and an endowment from the Philip J. Currie Professorship at the University of Alberta

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## Mesozoic & Paleogene Mammals

### A CARBONIFEROUS SYNAPSID JAW WITH CANINIFORM TEETH AND A REAPPRAISAL OF MANDIBULAR SIZE-SHAPE HETERODONTY IN THE ORIGIN OF MAMMALS

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Permian sphenacodontian synapsids like *Dimetrodon* and nonmammalian therapsids were among the oldest terrestrial apex predators, some having enlarged caniniform teeth. Though canine-like teeth are recognized

anecdotally in the maxillary dentition of some early synapsids, the homologies of the corresponding mandibular dentition and their role in prey processing are understudied. Here, we describe a new sphenacodontian from the late Carboniferous Halgaito Formation of southern Utah based on a well-preserved dentary and jaw fragments. The specimens came from a conglomerate at the base of a recently described bonebed featuring small and large freshwater and semi-terrestrial vertebrates, and terrestrial synapsids and reptiles. The postcanine morphology resembles the wide triangular teeth of *Ianthodon*, but there is a unique conspicuous caniniform tooth on a separate raised buttress. Additionally, the new taxon shares with *Sphenacodon* and *Dimetrodon limbatus* enlarged anterior dentary teeth, a dorsoventrally deepened symphysis, and low-crowned postcanines with clover-shaped plicidentine. A phylogenetic analysis of 20 taxa and 155 characters places the new taxon in a position near the evolutionary divergence of Sphenacodontidae and Therapsida (Sphenacodontoidea). A two-dimensional morphometric analysis of mandibular heterodonty was conducted on 65 Carboniferous–Permian taxa using semilandmarks and a Principal Component Analysis to explore overall variation in the toothrow. The variance of PC1 (which accounts for 58.2% of the variation) was evaluated as a continuous proxy for functional heterodonty and compared in time series in 11 major clades of basal synapsids and therapsids. Increasing PC1 variance in medium to large carnivores, however, preceded the diversifications of any large-bodied herbivore clades by several million years. These data may emphasize the increasing terrestrialization of tetrapod predator-prey interactions; the enlarged anterior dentitions of early sphenacodontoids enhanced raptorial biting (puncture and gripping) to aid prey capture, but this behavior was likely an evolutionary antecedent to more complex processing (shearing and tearing) of larger prey by the late Early-to-Middle Permian. As one of the oldest and anatomically plesiomorphic representatives of Sphenacodontoidea, the Halgaito taxon supports the notion that the predatory feeding ecology of sphenacodontoids had emerged in paleotropical western Pangea by late Carboniferous times.

**Funding Sources** U.S. Bureau of Land Management's National Conservation Lands Grants and the Canyonlands Natural History Association

## **Non-avian Theropod Systematics, Biology, and Evolution**

### **PALEOBIODIVERSITY OF THEROPOD DINOSAURS OF THE LOWER CRETACEOUS CAMEROS BASIN, NORTHERN SPAIN**

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The Cameros Basin is one of the most important Iberian basins in order to study the European dinosaur faunas and associated biota during the Early Cretaceous. The Cameros Basin is located north of Spain (Burgos, La Rioja and Soria) and is part of the Iberian Mesozoic Rift. The basin was formed in the second rifting stage that took place during the Late Jurassic and the Early Cretaceous (Tithonian–early Aptian). Material found in recent years has led to the description of new sauropod taxa such as *Demandasaurus* and *Europatitan*, and the identification of other dinosaur groups like ornithomimids, thyreophorans, and theropods. Nevertheless, the theropod fossil record is scarce and fragmentary.

The theropod fossil record of the Cameros Basin consists mainly of isolated teeth, but cranial and postcranial material has also been recovered representing several theropod lineages. In the upper Hauterivian–lower Barremian Golmayo and Pinilla de los Moros formations, skeletal remains have been attributed to Allosauroidea, Baryonychinae, Dromaeosauridae and Theropoda indet. In the upper Barremian–lower Aptian Castrillo de La Reina Formation and Enciso Group, instead, carcharodontosaurids, spinosaurids (baryonychines and spinosaurines), dromaeosaurids and other coelurosaurians, as well as indeterminate theropods, have been identified on the basis of skeletal material.

Spinosaurids, especially baryonychines, dominate the medium-large size theropod record of the basin. They are abundant in the lacustrine-palustrine deposits of La Rioja and fluvio-lacustrine environments of Burgos. In addition

to the tooth sample, spinosaurids are represented by cranial and postcranial remains in Burgos and La Rioja. A partially articulated skeleton and a second specimen with dorsal vertebrae from Igea (La Rioja), currently under study, probably belong to Spinosauridae.

The fact that different clades have been identified in the same sites shows direct evidence that distinct theropods co-habited the fluvial environments of the Cameros Basin during the Early Cretaceous. Considering the fossil material found up till now in the Cameros Basin in the lacustrine-palustrine environments, spinosaurids might be virtually the only clade of medium- to large sized theropods represented.

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## **Stem Tetrapod, Squamate, & Amphibian Diversity & Biology**

### **MIDDLE TRUNK VERTEBRAL SHAPE AND THE ECOMETRICS OF LOCOMOTION AND TEMPERATURE IN NORTH AMERICAN SNAKES**

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Ecometrics examines community trait-environment relationships across space and time. As such, ecometric methods are useful proxies for reconstructing past environments and community-level organismal trait variation. A framework for snake middle trunk vertebral (MTV) shape as an ecometric has been established, as MTV shape relates to vegetation cover, ecological province, and temperature. Functionally, snakes use the axial skeleton to locomote and thus, vertebral shape and the necessities of limbless movement influence each other. Snake locomotor specialization allows for unique methods of movement through the environment. This ecometric is then based on ecomorphological variation in MTV shape and geographic and evolutionary responses to environmental change. Although previous work established ecomorphological and ecometric signals in MTV shape, that evaluation was limited to neural spine height. In addition, little work has been done to implement ecometric models of MTV shape to estimate paleoenvironmental conditions.

Here, we assess more aspects of vertebral shape using 23

landmarks. We increased previous sample sizes to include vertebrae from 118 extant snake species from the United States and Canada. We used geometric morphometrics to quantify vertebral shape with Generalized Procrustes Superimposition and a Principal Component Analysis to ordinate landmarks and extract shape scores. We found the first six PC axes composed 86% of all variation in MTV shape. Species-level linear regressions showed PCs 2, 5, and 6 performed best overall when related to temperature variables. These PCs are chiefly associated with prezygapophyseal orientation and relative length, prezygapophyseal articular facet orientation and relative width, and anterior articulation proportions compared to vertebral compactness, respectively. We compiled community-level shapes (mean and standard deviation) for coincident snake species occurring at 50 km equidistant points across our study area and built an ecometric trait space using maximum likelihood of mean annual temperature (MAT) given the shape summaries. Altogether, our results indicate several community-level aspects of snake MTV shape that relate to the environment and can be used to estimate past MAT; combining shapes led to better estimations. The relationship with MAT makes our ecometric a useful tool for examining and predicting how snake assemblages morphologically change as climates and biomes change across space and time.

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## Late Cenozoic Mammalian Evolution and Ecology

### DID MIOCENE DIDACTYL STHENURINE KANGAROOS WALK LIKE THE PLIO-PLEISTOCENE MONODACTYL ONES?

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Sthenurine kangaroos (Macropodidae: †Sthenurinae) have been proposed as bipedal striders, with this gait perhaps replacing hopping in the larger forms, but likely an alternative to quadrupedal slow gaits. Investigations to date have mainly considered the Plio-Pleistocene monodactyl forms; however, Miocene sthenurines retained the fifth pedal digit seen in other macropodids, which might imply that their gaits were more macropodine-like. Here we investigate some aspects of

the anatomy of the early late Miocene *Rhizosthenurus flanneryi* (~ 25 kg) and the late late Miocene *Hadronomas puckeridgei* (~75 kg). Two-dimensional geometric morphometric analysis of the fourth proximal pedal phalanx shows two distinct areas of morphospace: monodactyl sthenurines have a relatively shorter and broader (especially at the articular ends) phalanx than macropodines, and a more distal position of the scar for the attachment of the oblique sesamoidean ligaments (the V scar). Allometry is not the issue in this shape difference, as extinct 'giant' macropodines (e.g., *Macropus titan*) cluster with other macropodines. This difference in pedal morphology may instead reflect more robust phalanges, with better ligamentous support, for alternate-leg weight bearing. Linear morphometric studies of the calcaneum show that, while the length of the calcaneal head of all macropodids scales approximately with allometry, the length of the heel scales differently in the two subfamilies: with slight positive allometry in macropodines, but with negative allometry in sthenurines. The ratio of the calcaneal heel:head is high in most macropodines, but lower in ones that do not hop (*Hypsiprymmodon moschatus*, the musky rat-kangaroo) or hop only rarely (e.g., *Dendrolagus* spp., tree kangaroos). Monodactyl sthenurines all have low ratios, supporting a non-hopping locomotor mode in these species. The long calcaneal heel of hopping macropodids may be related to resisting rotational forces at the ankle joint: larger hoppers cannot reduce these forces by attaining a less-crouched posture (as do large quadrupedal mammals). Considering the morphology of the Miocene sthenurines, *R. flanneryi* shows the phalangeal proportions and calcaneal ratio of similarly-sized macropodines, while *H. puckeridgei* resembles those of the smaller monodactyl sthenurines (such as *Sthenurus andersoni*). These results imply that the transition to sthenurine bipedal striding took place by the late late Miocene, preceding the loss of the fifth pedal digit.

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## Permo-Triassic Ecosystems

### A NEW SPHENODONTIAN FROM THE LATE TRIASSIC OF GERMANY

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The Arnstadt Formation of Saxony-Anhalt, Germany is known for its rich fossil record, and has yielded some of Germany's most substantial Triassic finds, including the sauropodomorph *Plateosaurus* and the early turtle *Proganochelys*. Besides these larger taxa, the formation also bears some small reptiles, such as the diapsid *Elachistosuchus huenei*. Here we describe the remains of a small, almost complete skull and mandible of a new sphenodontian, using  $\mu$ CT scanning. Sphenodontia is a lepidosauromorph group that was very diverse in the Mesozoic, but whose Triassic fossil record still remains quite poor. The skull was discovered together with *Elachistosuchus* from the middle to late Norian, making the new taxon the oldest and most complete sphenodontian skull from Europe. Small size and poor ossification of parts of the nasals, parietals, palate, and braincase suggest an immature ontogenetic stage. Important features of the new taxon are the absence of lacrimals, supratemporals and splenials, along with a heterodont dentition similar to the sphenodontian *Diphydontosaurus*, with small, narrow teeth in the front and broad, conical teeth in the back of the maxilla. The type of tooth implantation, however, could not be determined with certainty due to poor internal resolution of the material. Despite these similarities, the material differs from *Diphydontosaurus* in having a pronounced coronoid process in the mandible, a long posterior process of the postorbital, and postfrontals that extend beyond the fronto-parietal suture. Phylogenetic analysis recovers the new taxon as more closely related to *Planocephalosaurus* and *Eusphenodontia* than *Diphydontosaurus*. Inclusion of the new taxon in an evolutionary change rates analysis resulted in the destabilization of previously obtained rates for Mesozoic sphenodontians, yielding only one pulse of significantly (>50%) increased change rates. Previous studies have suggested either multiple pulses of increased rates or stable morphological rates before the origin of *Eusphenodontia*. The new taxon adds to our knowledge of Triassic sphenodontians of Europe and indicates the presence of a hidden morphological diversity in the early evolution of the group.

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### Late Cenozoic Mammalian Evolution and Ecology

## BIODIVERSITY AND CARNIVORAN FAUNAL DYNAMICS IN SOUTHWESTERN ASIA AND NORTH AMERICA DURING THE MIOCENE–PLIOCENE

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Recent field work yielding valuable new specimens is providing new insights into the mammalian carnivores from the Siwalik Group/Siwaliks during the Miocene and Pliocene epochs. These, combined with previously described Siwalik carnivores and data of extant carnivorans, provide information about community dynamics (e.g., immigration, emigration, and extinction) and evolution of this group. Our new data not only further confirm that most terrestrial mammalian carnivore groups in the region today were present by the middle Miocene, but also that hyaenodontid creodonts, along with amphicyonids and percrocitids, were mostly gone by the end of the Miocene. This is especially applicable to creodonts who barely crossed into the early late Miocene. However, recent collection now suggests amphicyonids may have held on in relict populations into the Pliocene. Concurrently, hyaenid biodiversity increased throughout this time, potentially filling newly open niches, including those of osteophagous carnivores. Conversely, felids and mustelids maintained relatively high biodiversity, making up 60% of the carnivoran fauna by the Upper Siwaliks, similar to modern carnivoran biodiversity in the region. Canids, although a late arriving group, are the third most diverse group of carnivorans in the region today. Also, with data compiled from the Paleobiology Database on the Miocene–Pliocene carnivorans of North America, we compared carnivorans of North America with those of southwestern Asia at this critical time. Distinct from the Siwaliks, canids made up 40% of carnivoran biodiversity in the early Miocene, dropping in diversity through time. Musteloids account for around 25% of carnivoran diversity at this time, resulting in these two groups accounting for the majority of that paleobiodiversity. Like southwestern Asia, felid and musteloid diversity increases through time, also similar to the modern North American carnivoran fauna. Conversely, canids decrease in diversity in North America, while they do not show up until late in the Siwaliks. In contrast, hyaenids show up late in North America, potentially due to expansion barriers, and do not survive there for very long, while they remain a key component throughout the Siwaliks. Further work must be

done investigating body size and diets, potentially in addition to increasing abundances, to further understand the dynamics and changes in mammalian carnivore communities during this important time in their evolution.

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### Paleohistology & Paleopathology

#### BIMODAL TRAJECTORIES AND UNRESOLVED EARLY GROWTH STAGES IN *TYRANNOSAURUS REX* GROWTH

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Two decades of intense investigation has rendered *T. rex* an exemplar of dinosaurian growth studies. Early models used terminal age and body mass of individuals that died during multiple growth stages to create a species composite curve. More recently, researchers have begun to study individual growth records in detail; however, these studies have either used individual records to explore the macroevolution of theropod gigantism or test alpha-taxonomic hypotheses via microstructural descriptions of bone histology. Individual growth records demonstrate heterogeneity in *T. rex* growth, leading to hypotheses that it regulated annual growth based on environmental stressors. In addition, the documentation of skeletal immaturity in specimens hypothesized to represent “*Nanotyrannus*,” has been used to refute its validity and support secondary metamorphosis in *T. rex*, with pronounced implications for the community composition and macroecology of Campano-Maastrichtian assemblages across Laurasia. To explore individual variation and further test these hypotheses, we modeled the entire preserved growth record in multiple specimens referred to *T. rex*. We gathered femoral and tibial LAG circumference data and body mass data from seven published specimens spanning multiple growth stages and sampled one undescribed juvenile femur. Following established methods, we fit these data with several non-linear models to determine a species average model, an optimal fit for each specimen, and statistically compare curves. Our preliminary results infer a significantly different bimodal distribution of *T. rex* growth ( $p < 0.00382$ ) with half of individuals reaching

skeletal maturity  $> 8,000$  kg and half between 5,000–7000 kg. Composition of these “groups” does not parse out by stratigraphy, nor previous identifications of “robust” and “gracile” morphs. Recently, researchers have criticized the hypothesis that dinosaurs reached sexual maturity prior to a marked decrease in growth rate in contrast to other vertebrates. Truncation of growth in a large percentage of individuals, combined with medullary bone in this group, suggests the possibility of cryptic sexual dimorphism in growth strategy unobservable with species-specific curves. However, we cannot rule out general intraspecific variability. Finally, we are currently unable to link the growth curve of BMRP 2006.4.4 with other *T. rex* specimens. Intermediate specimens (2,000–4,000 kg) are needed to resolve this discrepancy.

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### Stem Tetrapod, Squamate, & Amphibian Diversity & Biology

#### PALEO-ECOMORPHOLOGICAL DISPARITY OF THE CRYPTOBRANCHOIDEA SALAMANDERS (AMPHIBIA, URODELA) —INSIGHTS FROM GEOMETRIC MORPHOMETRIC ANALYSES OF THE PALATE

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Cryptobranchioidea are an early-branching clade of crown group salamanders (Urodela) that contain two extant families with different life history strategy and ecological preferences. Cryptobranchidae are obligate neotenes that live in water permanently by retaining larval features (e.g., gill slits) at adult stage, whereas Hynobiidae are predominantly metamorphic with most-metamorphosed hynobiids living in water, on land, or being semiaquatic out of breeding season. In the past two decades, ten cryptobranchoids have been reported from the Middle Jurassic to Lower Cretaceous of northern China, with most of which recently identified as stem hynobiids. Benefited from well-preserved soft tissue impressions, the paleoecology of few taxa have been interpreted (neotenic/aquatic *Chunerpeton*, metamorphic/semiaquatic “*Liaoxitriton daohugouensis*”), whereas that for the majority remains unexplored largely due to an insufficiency of direct paleoenvironmental evidences and

of morphological studies on extant cryptobranchoids. Here we conduct 2D landmark-based geometric morphometric analyses on the palatal region (vomer and parasphenoid) based on Micro-CT scanned images of 67 adult specimens that represent 10 fossil and 25 extant species across all extant genera of Cryptobranchoidea, basal salamandroids and stem urodeles. Our results reveal that asymmetry and allometry accounts for 3.78% and 9.07% of the total shape variations, respectively. Terrestrial and aquatic taxa occupy constricted and distinctive zones within the morphospace of the palate constructed from symmetric shape components with or without allometric shape components, whereas semiaquatic taxa are more widely distributed. Expansion of the vomer, elongation of the parasphenoid, and reduction in the width of the cultriform process of parasphenoid are three main sources of shape variations associated with PCs 1–3, respectively. Results of Procrustes ANOVAs reveal the shape of the palate is also significantly correlated with taxonomy, life history strategy and phylogeny, with the morphospace mainly shaped by evolutionary constraints. Most metamorphosed fossil taxa including *Nuominerpeton* are terrestrial or semiaquatic whereas *Liaoxitriton zhongjiani* is aquatic. The semiaquatic stem hynobiid “*L. daohugouensis*” is unique in having a typical terrestrial type of palate. Our study indicates that most of the current morphospace of the palate has been occupied by stem hynobiids by the Early Cretaceous.

**Funding Sources** NSFC 41702002/41672003/41872008

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

### **LIFE HISTORY TRAITS OF TWO MOSASAUROID SPECIMENS REVEALED BY RIB HISTOLOGY**

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Mosasauroidea is a highly evolved and specialized group of squamate reptiles that radiated rapidly into the oceans of the world, reaching gigantic body sizes and streamlined body shapes during the Late Cretaceous. However, how they reached such a body size and mass remains unclear. Bone histology has been a key tool in reconstructing life

histories in fossil and extant vertebrates, because bones provide mechanical support and reveal information about the animal's anatomy, biology, behavior, and ecology. Previous research shows that rib bones of sauropods preserve a good growth record due to their simple morphology and relatively low bone apposition rate. Here we show the utility of mosasauroid rib fragments for histological analyses of life history and ontogeny, based on the principle that rib growth happens primarily from proximal to distal, producing a change in cross-sectional shape during ontogeny. Two complete dorsal ribs, one of *Platecarpus* sp. and the other of *Clidastes propython*, were sectioned in seven different positions along the proximodistal axis. Both taxa show a similar microanatomy of longitudinally vascularized primary bone tissue that is replaced by secondary cancellous bone surrounding the medullary cavity. Rib growth shows distinct cycles, ending in lines of arrested growth. After mapping the histology along the ribs, the best growth record was found to be located just distal to the rib head, about one third of the rib shaft. The best record of primary cortical bone is preserved here because it is least replaced by secondary cancellous bone, and at most one growth cycle was lost to remodeling. Despite their phylogenetic distance, both mosasauroid lizards reached skeletal maturity at an age of approximately 10 years old. This is indicated by the initiation of an external fundamental system at this cycle count. In the *Platecarpus* sp. specimen, sexual maturity was reached at the age of 7 years old, while in the *Clidastes propython* specimen it was reached at the age of 9 years old, both events visible in the thin section as a sudden decrease in growth mark spacing. Considering that both individuals must have had a body mass of several hundred kilograms, their life history resembles that of similar-sized cetaceans. This suggests a higher basal metabolic rate in mosasauroids than in extant squamates.

**Funding Sources** Alexander von Humboldt Stiftung/Foundation

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## **Colbert Poster Prize**

### **THE HIGH VALLEY PROJECT: NEW FOSSIL VERTEBRATE LOCALITIES FROM THE WHITE RIVER GROUP OF NORTHEASTERN COLORADO**

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Beginning with the very first field expedition of O.C. Marsh in 1870, the White River Group of northeastern Colorado has been known for its rich fossil record of early mammalian fossils from the late Eocene to the middle Oligocene (~36–28 Ma). However, after early investigations extending into the 1950s, these exposures became largely neglected, due to the difficulty of public access to many areas requiring private landowner permission. Among the goals of the High Valley Project are to establish a liaison with local landowners to develop a geological conspectus of the paleoenvironment and paleontology of the area ultimately, leading to the protection of important sites and fossils from the region. The primary vertebrate fossil localities described here are located on two different private properties, spanning a full township and range, with the principal sites situated on a family-owned property called the High Valley Ranch. On this property and its neighbor, six localities have been documented and been analyzed, with an additional five having been surveyed. This has led to the identification and study of some smaller ancient ecosystems within the White River Group of Colorado. Within these smaller locality ecosystems, a plethora of mammal fossils have been found, including the titanotheres *Megacerops riggsi* and *M. acer*, the camel *Leptomeryx*, the mustelid *Drassonax*, at least one oreodont, and an unidentified felid. Several fossil reptiles are also known, including a dentition of *Exostius serratus*. These new vertebrate-bearing localities promise to significantly enhance paleoecological analyses of this neglected, southern region of the White River Group.

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## Biomechanics & Functional Morphology

### BIOMECHANICAL PERFORMANCE OF THE CRANIA OF TYRANNOSAUROIDS AND COMPARATIVE IMPLICATIONS FOR THEROPOD FEEDING

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The theropod dinosaur *Tyrannosaurus rex* is viewed as a model organism, with numerous studies analyzing its

biomechanics, feeding behavior, and diet. Bite force models indicate *Tyrannosaurus* was capable of exerting a high bite force with its robust teeth. Additional biomechanical studies indicate that an adult *T. rex* had a reinforced skull that was capable of resisting high forces. The evolution of feeding behavior and biomechanics has been under-addressed in Tyrannosauoidea, especially in basal tyrannosauroids (e.g. *Guanlong*, *Yutyrannus*, *Dilong*). Here we use muscle force reconstruction and finite element analysis (FEA) to quantify how the crania of tyrannosauroids responded to high forces. We used a combination of 3D and 2D models.

The 3D models consisted of an adult and juvenile *Tyrannosaurus*, *Teratophoneus*, and *Raptorex*, to reflect the ontogeny and phylogeny of feeding behavior of *Tyrannosaurus* and similarly sized tyrannosauroids. The 2D models were used for a larger sample size to (1) analyze the evolution of feeding behavior of Tyrannosauoidea and (2) compare the stress magnitudes with the 3D models. The 2D models display stress magnitudes similar to the 3D models, supporting their utilization in FEA. All 2D models were set to the same length as an adult *T. rex*, with individual jaw muscle forces derived from the adult *T. rex* specimen, USNM 555000.

We defined and sampled homologous points of the tyrannosauroid crania that show areas of high stress and input their stress values as quantitative phylogenetic character data in Mesquite. Using squared-change parsimony ancestral state reconstructions of stress values at each of the defined skull points we found that tyrannosauroids' crania show moderate to low stress values. To provide a more detailed phylogenetic comparison, we incorporated non-tyrannosauroid theropods and compared their cranial stress values with those of Tyrannosauoidea

At the internal branches of Tyrannosauoidea, hypothetical common ancestors exhibit low cranial stress values. These traits may have been passed down to later tyrannosauroids, enabling them to handle high forces. We found that non-tyrannosauroid theropods' crania exhibited higher stress values than the crania of Tyrannosauoidea. Combining 3D and 2D FEA provides significant information on the evolution of feeding mechanics and behavior in a dinosaur clade.

**Funding Sources** The Jurassic Foundation

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## Mesozoic & Paleogene Mammals

## THE EARLIEST ASIAN BATS AND IMPLICATIONS FOR EVOLUTION AND BIOGEOGRAPHY OF EOCENE BATS

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Bats (Mammalia, Chiroptera) first appear in the fossil record during the earliest Eocene as fragmentary dental remains known from western Europe and Australia. The oldest complete skeletons of bats, from western North America, are known from later early Eocene sites, several million years younger than the oldest bats. These North American Eocene bat taxa were fully capable of powered flight and some were able to echolocate. These data suggest two major gaps in our knowledge of the bat fossil record: a morphological gap separating definitive bats from their closest non-bat relatives; and a biogeographical gap, with the earliest bats already known from geographically disparate parts of the globe. Both of these gaps are partly filled by isolated bat upper molars from the earliest Eocene of the Junggar Basin (northwestern China). These teeth share morphological similarities with other small, early Paleogene insectivores (e.g., distinct conules) while exhibiting clear bat synapomorphies (e.g., dilambdodonty, lack of a mesostyle), thereby improving our understanding of dental evolution in the early bat families Onychonycteridae, Icaronycteridae, and Archaeonycteridae. The Junggar Basin teeth suggest that the latter two families are not characterized by unambiguous dental synapomorphies. The presence of early Eocene bats in central Asia expands the known range of stem bats and brings the bat fossil record in line with that of other Laurasiatheres. The primitive nature of these fossils also suggests that central Asia may have played an important role in the earliest phases of bat evolution, as has been documented for rodents and lagomorphs.

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## Mesozoic & Paleogene Mammals

### NORTH AMERICAN MAMMAL PREDATOR DIVERSITY AND FUNCTIONAL TRAIT RESPONSE TO CLIMATE CHANGE ACROSS THE PALEOGENE

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The general trend of global cooling across the Cenozoic transformed the North American Paleogene landscape, where early Eocene forests gave rise to more open environments in the early Oligocene. Many studies document the traits that arose in the North American mammalian herbivores as a response to this environmental transition: as habitats became more open, herbivores evolved dietary and locomotory adaptations including high-crowned dentition and more elongate, cursorial limbs. However, absent from many of these studies is a view of the coevolving predators. Here we examine the broad patterns of faunal change in North American mammalian predators across the Paleogene. We assembled a dataset containing body mass estimates and relative blade length (RBL) of the first lower molar, an index of carnivory, for nearly all Paleogene and extant North American mammal predators (Creodonta and Carnivora). To establish the degree to which predator functional traits correlate with environment, we tested our extant dataset for association between the measured functional traits and diet and habitat type, respectively. Next, we applied a model comparison approach to find the best-fit configuration of distinct shifts in both taxonomic composition and functional trait distributions in order to detect if any correspond to global climate change events. While we found no association with body mass, we found a significant association between RBL and both habitat type and diet, with higher RBL taxa preferentially found more open environments. Within the Paleogene, our best-fit models found a total of seven distinct shifts: three shifts in taxonomic composition, one shift in body mass distribution, and three shifts in RBL

distribution. Only two shifts coincide with global climate change events: a shift in taxonomic composition at the Paleocene–Eocene Thermal Maximum, and shift to higher RBL distribution at the Early Eocene Climatic Optimum. Additionally, the mean RBL increases sharply in the late Eocene, with the Oligocene predator faunas having a consistently higher mean RBL than those in the Paleocene and early Eocene. This pattern of increasing mean RBL is consistent with the decline of forested environments following the Eocene–Oligocene Transition. These results indicate a potential functional response, rather than simply phylogenetic replacement, in North American predators to large-scale environmental changes across the Paleogene.

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### Colbert Poster Prize

#### A NEW MID-CENOMANIAN FISH FAUNA FROM SOUTHEASTERN NEBRASKA, USA

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The mid-Cenomanian time approximately 100 million years ago is when the Late Cretaceous epicontinental Western Interior Seaway began to spread over the North American continent. Here, we describe a previously unreported marine fish fauna that captures that critical timeframe in the history of the seaway. Rock samples, that belong to the University of Nebraska State Museum, were collected most certainly from one of the intertonguing sandy beds occurring at the transition zone from the Dakota Sandstone to the overlying Graneros Shale in southeastern Nebraska, USA. The Dakota Sandstone is predominantly a terrestrial deposit, and the Graneros Shale represents the first fully marine deposit formed in the Western Interior Seaway. This land-to-sea transition, marked by small pulses of transgression and regression, is thought to have taken place from the latest early Cenomanian to the earliest middle Cenomanian. The examined rock samples are dense in small bones and teeth of marine fishes in calcium carbonate-supported sandy matrix, and acetic acid was used to disaggregate vertebrate remains. The fossil fauna includes elasmobranch taxa, such as *Meristodonoides* sp., *Cenocarcharias* sp., *Haimirichia amonensis*, *Cretoxyrhina mantelli*, *Squalicorax curvatus*, *Ischyryhiza texana*, *Onchopristis dunklei*, and *Ptychotrygon* sp., as

well as bony fishes such as *Enchodus gladiolus* and multiple other teleost species. The occurrence of hybodontid *Meristodonoides* sp. is indicative of a nearshore environment, and the abundance of multiple benthic taxa, such as batomorph *Ischyryhiza*, *Onchopristis*, and *Ptychotrygon*, suggests a well-oxygenated water. More importantly, the composition of this fossil fauna is broadly consistent with other previously identified North American Cenomanian localities that are mostly slightly younger geologically, suggesting that the establishment of the marine fish community in the Western Interior Seaway took place quite rapidly.

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### Mesozoic & Paleogene Mammals

#### PALEOGENE RODENTS OF THE HUAYABAMBA FORMATION, OF THE ALTO RÍO MADRE DE DIOS AND ITS TRIBUTARIES, AMAZONIAN PERU

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The fossil record of South America includes caviomorph rodents and anthropoid primates of proposed Paleogene African origin. Interpreting their origins and early evolution is obscure due to their best fossil record being in high latitudes with a scarcity of fossils from the tropics where major radiations or oldest representatives might be found. Recent excavations at two sites in the Huayabamba Formation (HF) along the Río Alto Madre de Dios in the Peruvian Amazon (13 °S) have yielded new faunas of small rodents, expanding the geographical and temporal ranges of Paleogene tropical rodents. The HF is the oldest Cenozoic formation within the Madre de Dios basin,

based on dated detrital zircon samples from two caviomorph-bearing localities. Distinctive features of the zircons include: (1) Over half the zircons are sourced from the west, meaning the Andes were a major sediment supply to a foreland basin by at least ~58 Ma. (2) Zircons with Cenozoic ages are rare, accounting for only ~1% of the total, indicating no major volcanic sources were proximate to the Madre de Dios basin during deposition. Site RA-1 is located on the Río Aguaroa, with a minimum depositional age of  $30.28 \pm 0.74$  Ma. RA-1 documents a fluvial sedimentary environment with abundant paleosols containing rodents, metatherians, and other terrestrial vertebrates. Two rodent genera, *Eobranisomys* and *Cachiyacuy*, are represented, having been previously documented at Contamana, Peru (7 °S, late middle Eocene Pozo Formation) and Santa Rosa, Peru (9 °S, lower Oligocene Yahuarango Formation). *Eobranisomys* is also known from La Cantera, Chubut Province Argentina (46°S; lower Oligocene Sarmiento Formation). Site RC-1 on the Río Carbón is assigned to the HF on the basis of overall similarity to the zircon provenance profile of RA-1 and a distinctive ~235 Ma zircon age peak absent from younger formations, though it has yet to yield any Cenozoic zircon grains. RC-1 has produced *Cachiyacuy kummeli* and *Pozomys*, hitherto recorded at Contamana and Santa Rosa. Several other new rodent taxa are also recorded, including the first subtropical record of Acaremyidae, a family previously restricted to the late Oligocene–middle Miocene of Argentina. These new records from the HF reveal considerable taxonomic diversity, but not a corresponding morphological disparity. Notably, all rodents from these Paleogene localities are brachyodont, unlike the wide range of hypsodonty characterizing rodent faunas in Neogene localities.

**Funding Sources** This work was supported by NSF grants EAR 1338694 and DDIG 0726134 and National Geographic Society Grants 9920-16 and W449-16.

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### **Symposium - Vertebrate dental ecomorphology: Tooth traits that reflect ecology**

#### **MICROMAMMAL DENTAL ECOMORPHOLOGY FROM THE PLEISTOCENE TO THE PRESENT AT HALL'S CAVE, TEXAS**

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At Hall's Cave in Central Texas, the micromammal community persisted from the Pleistocene to the present with minor turnover despite considerable climate- and extinction-mediated ecosystem restructuring. To characterize the long-term ecological consequences of climate change and biodiversity loss, we studied the superabundant fossil record of ten micromammal taxa (*Geomys*, *Thomomys*, *Neotoma*, *Sigmodon*, *Microtus*, *Chaetodipus*, *Onychomys*, *Reithrodontomys*, and two *Peromyscus* morphotypes) across the last 22,000 years. To understand how these animals adapted in situ, we evaluated changes in microCT-derived 3D dental ecomorphology in relation to stable isotope analyses of bone collagen ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) and shifts in body size inferred from tooth row length. While body size for several micromammal taxa waxed and waned with climate consistent with Bergmann's rule, *Onychomys* grasshopper mice defied this trend immediately post-extinction, nearly doubling in size during a warming period. Moreover, body size was positively correlated to elevated  $\delta^{15}\text{N}$  levels suggesting increased carnivory. We found significantly higher occlusal convexity (OCC), a measure of tooth pointiness, at the same time, suggesting dental morphology may have evolved rapidly to match a dietary shift. Dental ecomorphology for other taxa also changed over time, both with and without concomitant shifts in stable isotopes or body size. For example, volumetric relief index (vRFI), a measure correlating with degree of folivory, was significantly greater in Pleistocene *Chaetodipus* pocket mice than their isotopically similar Holocene counterparts. While Pleistocene *Chaetodipus* specimens were still classified as granivores using an ecomorphology discriminant function model, we suggest they may have consumed greater proportions of foliage in the greener Pleistocene than modern, more arid-adapted conspecifics. For all taxa, we find low variation in 3D dental ecomorphological variables within but not among time bins, supporting clear ecomorphological change over time unconfounded by time-averaging. Overall, we reveal rapid dental ecomorphological adaptation in micromammal communities over the Pleistocene–Holocene transition. We recommend that 3D dental ecomorphological approaches be used to complement other paleoecology proxies such as stable isotope and body size analyses because ecomorphology can both corroborate shifts in other proxies and reveal additional nuances in fast-adapting micromammal ecology.

**Funding Sources** Funding sources included the UNM Gaudin scholarship, American Society of Mammalogists, Geological Society of America, and NSF (DEB grant #1555525 to FAS, SKL, & SDN).

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## Holocene & Pleistocene Mammalian Faunas

### NICHE STABILITY THROUGH ENVIRONMENTAL CHANGE: A LATE PLEISTOCENE CHRONOLOGY OF *BISON PRISCUS* PALEOECOLOGY FROM YUKON TERRITORY, CANADA

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Do species respond to environmental change by shifting their niche? The late Pleistocene permafrost-preserved record of fossil mammals provides a rare opportunity to address this question because specimens are abundant, well-preserved, and can be precisely dated. We developed a high-resolution time series of *Bison priscus* paleoecology spanning the last ~50 ky from the Klondike region of Yukon Territory, Canada. Since bison may occupy grazing, browsing, and mixed-feeding niches, we hypothesized that Pleistocene *B. priscus* in the Klondike exhibited dietary flexibility through time. We tested whether environmental fluctuations since 50 ka resulted in changes to diet, body size, and/or relative population size. We radiocarbon (<sup>14</sup>C) dated all relatively intact bison mandibles and maxillae curated at the Yukon Paleontology Program (n = 88), and evaluated dental mesowear, dental microwear (Dental Microwear Texture Analysis) and stable isotopes (collagen  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  values) to assess *B. priscus* diet and paleoenvironment. We used molar size measurements to evaluate changes in body size. To model changes in relative abundance, we evaluated the age-frequency distribution of preserved specimens and estimates from published ancient DNA analyses. We found that *B. priscus* body size is weakly positively correlated with relative abundance, which

peaks first during relatively warm/wet interstadial intervals at ~39 ka and again during the Bølling Allerød (BA) event at ~14 ka. Also during the BA,  $\delta^{15}\text{N}$  values decrease significantly by ~2 ‰, likely reflecting increased moisture availability. Mean dental mesowear, microwear and  $\delta^{13}\text{C}$  values are consistent through time. Thus, despite changes in body size and  $\delta^{15}\text{N}$  values, we find millennial-scale stability in at least some aspects of dietary ecology (i.e., food textural properties and  $\delta^{13}\text{C}$  values). Contrary to expectations, *B. priscus* did not respond to changing environmental conditions by altering their dietary niche; rather, *B. priscus* thrived when conditions were favorable and suffered population contraction during the colder, drier interval of the Last Glacial Maximum. However, the variances of proxies for body size and diet were significantly and universally reduced during BA warming, despite increased *B. priscus* abundance. Reduced variance may be indicative of *B. priscus* becoming focused into isolated, graminoid-dominated ‘refugia’ or ‘islands’ amongst an expanding boreal forest towards the end of the Pleistocene.

**Funding Sources** Student Grants in Aid from the Geological Society of America, University of Cincinnati Sigma Xi and National Sigma Xi, American Society of Mammalogists, and NSF 1053839.

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## Late Cenozoic Mammalian Evolution and Ecology

### POSTCRANIAL TRAITS DIFFERENTIATE SPECIES OF THE LATE CENOZOIC KANGAROO GENUS *PROTEMNODON* BETTER THAN TEETH

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Prior to their extinction ~40,000 years ago, kangaroos of the genus *Protemnodon* Owen, 1874 (Marsupialia, Macropodidae) were widespread across the Australian continent during the Pliocene and Pleistocene. Large and robust, they were among the largest kangaroos ever, with body mass estimates of up to 180 kg. The Pleistocene Australian species are poorly delimited, diagnosed on slight, inconsistently recognisable dental differences, resulting in 150 years of taxonomic confusion and that negatively affected broader studies of historic trends (e.g., palaeoclimate).

3D scans and photographs were taken of 735 specimens

from 13 institutions in four countries. Digital measurements were collected and morphometric data visualised, while detailed morphological comparisons were made. These analyses found that only some species could be differentiated on dental characteristics. However, profound morphological and proportional differences in hindlimb and cervical vertebrae not attributable to sexual dimorphism were evident between specimens with indistinguishable dentitions. Some specimens have long, gracile hindlimbs, proportionally similar to the arid-adapted, fast-hopping red kangaroo. Others have shorter, more robust hindlimbs and very short, broad cervical vertebrae, suggestive of slow hopping through dense vegetation. The geographic distribution of these morphotypes, which are interpreted as distinct species, is consistent with such ecomorphological inferences and a reminder that herbivore divergences may be driven as much by varying locomotor adaptations to different habitats as by diet. The overriding historical focus on teeth in mammalian taxonomy is often due to their higher chance of preservation, but where elemental associations exist we must interrogate further and generate a more complete understanding of evolutionary patterns and processes.

**Funding Sources** Australian Research Council  
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## Fishes Evolution & Distribution

### NEW FOSSILS FROM THE MIDDLE-LATE MIOCENE OF KENYA ILLUMINATE THE HISTORY OF CICHLID FISHES LIVING IN ALKALINE LAKES

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Tropical freshwater fishes of the family Cichlidae have gained iconic status in evolutionary biology studies due to their extraordinary ability to radiate, sometimes even under extremely adverse conditions. An intriguing recent

example is the radiation in the highly saline and highly alkaline Lakes Magadi, Natron, and Manyara near the border between Kenya and Tanzania in East Africa. These alkaline lakes host the only known modern clade of alkaliphile cichlids from the African continent. However, little is known about the evolutionary history of alkaliphilia in cichlids in general and of this lineage in particular. To help bridge this gap, we describe new skeleton-based material of fossil cichlids from middle to late Miocene deposits in central Kenya (East Africa) that can be assigned to alkaline paleolakes. The studied material comes from two newly discovered localities, dated to about 11 Ma (site Rebekka) and 12 Ma (site Yatianin). We examined the osteology of these fossils by using  $\mu$ CT technology and light microscopy. Moreover, we gathered comparative anatomical data for more than 360 modern cichlid species representing all major African lineages, based on X-ray imaging,  $\mu$ CT scans and ethanol-preserved specimens. Two new species from each of the two sites were described, for which we introduced the genus †*Rebakkachromis* Kevrekidis, Valtl and Reichenbacher, 2019. From the site Yatianin, we described further five individuals of †*Rebakkachromis*, each possessing a unique combination of characters. This is interpreted as evidence of diversification and the possible presence of a (nascent) species flock. Based on the anatomical data, we place †*Rebakkachromis* in the tribe Oreochromini, one of the most speciose modern cichlid lineages. This tribe includes, among other species, the modern alkaliphile cichlids, which bear a close morphological resemblance to †*Rebakkachromis*. Further, we are constructing a morphological character matrix, which so far includes 122 characters of 67 modern African cichlid species distributed over all tribes. Based on this matrix, Parsimony and Bayesian phylogenetic analyzes recover †*Rebakkachromis* in a clade with the modern alkaliphile cichlids. Thus, our research indicates that the ability of cichlids to thrive in highly alkaline lakes had already evolved in the middle-late Miocene by relatives of the modern alkaliphile cichlids.

**Funding Sources** We acknowledge funding from the Deutsche Forschungsgemeinschaft (RE 1113/18-1&2) and the LMU Mentoring Program (2020).

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## Holocene & Pleistocene Mammalian Faunas

### PLEISTOCENE PROBOSCIDEANS FROM THE SARDHOK PABBI HILLS, PAKISTAN

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Pabbi Hills, the fluvial deposits with a total sediment thickness of ca. 1000 m in northern Pakistan, are one of the youngest (2.6–0.6 Ma) anticlines in the world. The Pabbi Hills are representative of the Quaternary Siwalik deposits in northern Pakistan and were formed under a monsoonal regime with strong seasonal contrasts between a relatively cool winter season and a hot wet summer monsoon. Sardhok is one of the few localities in Pakistan having well-exposed Pleistocene outcrops of the Siwalik Group. Chronologically, the Sardhok outcrops correspond to the Pleistocene. Like other-Pleistocene localities, the remains of Elephantidae are well-preserved in these outcrops along with the typical Asian cousins stegodonts (family Stegodontidae).

Here we describe some newly discovered remains of *Palaeoloxodon namadicus*, *Elephas planifrons*, *Stegodon bombifrons* and *Stegodon pinjorensis*. In addition, geological, stratigraphical and biostratigraphical correlations have been attempted to determine the position of this locality within the paleomagnetically well-known localities of the same age in Pakistan and India.

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## Macroecology & Macroevolution

### DIVERSITY AND PROPOSED BIOZONES OF VERTEBRATES FROM THE LATE CRETACEOUS WESTERN INTERIOR SEAWAY IN MANITOBA, CANADA

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Stratigraphic distributions and diversity of vertebrate faunal assemblages from Upper Cretaceous deposits in Manitoba (MB) were analyzed in order to define stratigraphic positions and changes in vertebrate diversity that occurred along the east–central margin of the Late Cretaceous Western Interior Seaway (WIS). Class-specific and standing vertebrate diversity estimated from museum specimen counts of all nine Upper Cretaceous

lithostratigraphic members of MB indicate cartilaginous and bony fish were the most diverse groups from the mid-Cenomanian to the early Campanian, and hesperornithiform birds, marine reptiles, and bony fish the most diverse groups from the early Campanian to early Maastrichtian. Peaks of highest standing vertebrate diversity occur in the mid-Cenomanian with 30 known genera, late Cenomanian to early Turonian with 22 known genera, and the early Campanian with 21 known genera. Periods of lowest diversity occur from the late Turonian to early Coniacian with at least two genera and in late Maastrichtian time with at least one genus. Coverage-standardized diversity estimates are presented alongside previously defined inoceramid, ammonite, and foraminiferal biozones for comparison with invertebrate faunal turnovers, as well as lithological and chemical profiles in order to correlate apparent changes in diversity with potentially associated changes in depositional environments. These defined stratigraphic occurrences allow for the observation of diversification and extirpation events as well as the proposal of stratigraphic biozones to represent the Late Cretaceous vertebrate assemblages of MB.

Six biozones named after the dominant taxa known from seven lithostratigraphic members are proposed, from oldest to youngest: 1) *Rouletia canadensis*–*Archaeolamna kopingensis*, 2) *Squalicorax curvatus*–*Xiphactinus audax*, 3) *Palaeoanacorax pawpawensis*–*Squalicorax curvatus*, 4) *Enchodus petrosus*–*gladiolus*, 5) *Archaeolamna* sp., and 6) *Hesperornis* sp. These proposed biozones are significant because they represent the first vertebrate biozone scheme for the Late Cretaceous of MB and allow for general comparisons of dominant vertebrate taxa with those of other North American regions containing coeval WIS deposits.

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## Colbert Poster Prize

### A RELATIONSHIP BETWEEN EGGSHELL THICKNESS AND MICROSTRUCTURE TO SHOW A POSSIBLE MECHANISM FOR HATCHING OF THICK-SHELLED DINOSAUR EGGS

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Despite the great structural difference between dinosaur eggs, thick-shelled eggs exceeding the thickness of 4 mm occur in three major clades: ornithopods, sauropods, and avian theropods (*Aepyornis*, elephant bird). Most previous studies on thick eggshells have focused on parataxonomic classification, but the exceptionally thick eggshells raise the question of how an embryo could hatch through it. To determine the relationship of eggshell thickness with microstructures, we examined the allometry of avian and non-avian dinosaur eggs and performed electron backscatter diffraction (EBSD) analyses. Equivalent Spherical Radius (ESR), defined as the radius of a sphere of equal volume, was plotted against the eggshell thickness of 430 avian and 71 non-avian dinosaur egg specimens. While non-avian theropod and avian eggs show a strong linear correlation between ESR and thickness, most non-theropod dinosaur eggs were plotted much thicker than the avian ones, although they are randomly distributed. This result is counter-intuitive because non-theropod dinosaur eggs have no reason to be thick, unlike avian eggs designed to support the heavy incubators' weight. We hypothesized that the eggshell ultrastructure might relate to the eggshell strength, and therefore, the eggshell thickness can vary with it. EBSD analyses on 30 avian and 24 non-avian eggshells were conducted, covering a wide range of eggshell thickness (0.09–4.11 mm). The results show that all eggshells thicker than 1.5 mm have a low median misorientation angle ( $<40^\circ$ ), while those below 1.5 mm span a wide range of misorientation angles between  $10^\circ$ – $62^\circ$ . Because crystals with a low misorientation angle are more fragile than those with a high one, thick eggshells might have no problem being hatched due to fragility. On the other hand, eggshells of Neognathae with a high misorientation angle might prevent an embryo from hatching successfully if the rigid eggshells were too thick. Although ornithopod, sauropod, and paleognath eggs are known to be independently calcified with various eggshell thicknesses, the eggshell crystal structure with a low misorientation angle seems essential for thick-shelled eggs.

**Funding Sources** National Research Foundation of Korea (Grant Number 2019R1A2B5B02070240)

## THE NEUROANATOMY, OLFACTORY ABILITY, AND TROPHIC ECOLOGY OF *TERATONIS* *MERRIAMI* (AVES: TERATORNITHIDAE)

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*Teratornis*, one of the most recognizable large-bodied genera of birds of the late Pleistocene from North America, is known from multiple localities from Arizona, California, Florida, and Nevada; however, the only known complete braincases are from the tar pits of Rancho La Brea. Since its discovery in the early 1900s, the diet of the species *T. merriami* has been debated due to the mosaic of characters present in the skull and postcranial anatomy of the species. Early on, a scavenging diet was assumed due to its large nares, it being found with other contemporaneous condors and vultures at La Brea, and the presence of late Pleistocene megafauna found within the La Brea tar pits. Other studies retrieved *T. merriami* as a carnivore or piscivore based on different aspects of craniofacial anatomy. Here, CT scanning was used to reconstruct the first cranial endocast for the teratorn *T. merriami*. Unsurprisingly, the gross anatomy of the endocast does not notably differ from the general avian form: the cerebrum is enlarged and the widest aspect of the endocast, the optic lobes are laterally oriented and large, the flocculi are elongate, and both flexure angles are near  $90^\circ$ . The endocast morphology is more similar to accipiters rather than cathartids in that the cerebrum is pyriform when viewed dorsally rather than constricted. The olfactory lobes are barely noticeable on the endocast and comprise only 0.06% of the total endocranial volume. Considering that some modern scavenging avian taxa, such as vultures, have an olfactory lobe volume that is 2.09% of the total endocranial volume, the disparity between scavenging and other ectomorphs for *T. merriami* is dramatic. This lends support that, neurologically speaking, a carnivorous or piscivorous trophic ecology was more likely than scavenging. This supports earlier discriminant function analyses that cast doubts on a scavenging lifestyle for *T. merriami* based on measurements taken from the cranium.

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### Avialan Evolution & Biology



## **Stem Tetrapod, Squamate, & Amphibian Diversity & Biology**

### **NEW LATE TRIASSIC STEM-CAECILIAN FROM SOUTHWESTERN NORTH AMERICA STRENGTHENS EVIDENCE FOR LISSAMPHIBIAN MONOPHYLY, AND ILLUMINATES THE ANATOMICAL, FUNCTIONAL, AND GEOGRAPHIC ORIGINS OF LIVING CAECILIANS**

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The early evolutionary history of living amphibians (Lissamphibia: frogs, salamanders, and caecilians) is clouded by a paucity of fossils chronicling the evolutionary steps between Paleozoic amphibians and the oldest known fossil representatives of crown-group Lissamphibia from the early Mesozoic. This problem is particularly acute in the caecilian record, where an absence of unambiguous fossils prior to the Early Jurassic obscures their early anatomy, biology, and geography – evidence critical not only to resolving caecilian origins, but also interrelationships of all crown-lissamphibian lineages and their affinities to Paleozoic amphibians. Here we report the discovery of the geologically oldest stem-group caecilian (*Gymnophionomorpha*) from the Upper Triassic (~220 Ma) Chinle Formation of Petrified Forest National Park, Arizona, USA, pulling back their known record by at least 35 million years. Microcomputed tomographic scans and histological analysis of these three-dimensional fossils reveal a mosaic of derived caecilian features in addition to character states shared with batrachians (frogs and salamanders) and albanerpetontids. A monophyletic Lissamphibia including caecilians, batrachians, and albanerpetontids is suggested by the structure of the jaw joint and posterior portion of the lower jaw, while the presence of craniomandibular coossifications, parallel double-rows of pedicellate teeth, and osteological correlates of the tentacular organ indicate at least a Late Triassic acquisition of these body-plan specializations unique to the caecilian lineage. Our osteohistological analysis of a pseudodentary reveals possible osteological correlates of glands to secrete friction-reducing lubrication as in living caecilians, one of several features found in these specimens associated with subterranean burrowing, showing the antiquity of

fossorial life habits in caecilian evolution. The provenance of these fossils may suggest caecilian origins in the paleotropics of central Pangaea prior to supercontinent breakup, with a post-Triassic biogeographic history driven by vicariance through plate tectonics and ecosystem restriction or fragmentation. The paleotropical occurrence of these and all other extinct caecilians suggests biogeographic constraints tied to climate, now reflected in their exclusively tropical extant distribution.

**Funding Sources** Virginia Tech Department of Geosciences, Petrified Forest National Park, Petrified Forest National Park Museum Association, the David B. Jones Foundation

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## **Macroecology & Macroevolution**

### **HOW TO TUNA FISH: DRIVERS OF DIVERSITY IN PELAGIARIA (TUNAS, MACKERELS AND THEIR KIN)**

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Teleost fishes represent the most taxonomically diverse group of living vertebrates and have evolved to occupy a vast range of ecological niches in marine and freshwater habitats. Morphological diversity is particularly notable in the skull. Understanding how this diversity has evolved in the ~250 million year history of teleost evolution presents a challenge because of the complex three-dimensional structure of the teleost skull and the vast number of species involved. Modularity, or the division of complex structures such as the skull into a smaller number of integrated, independent units known as modules, provides a solution to this problem.

Several studies have shown that the skulls of many tetrapod clades are highly modular but studies on fish tend to focus on the neurocranium or overall body form. Here we present an analysis of skull modularity in ~100 species of the morphologically diverse but numerically tractable teleost group Pelagiaria. Using three-dimensional geometric morphometrics, our analysis encompasses the neurocranium, jaws, suspensorium, and opercular series, enabling an analysis of morphological

diversity across the entire skull and allowing a more direct comparison to previous tetrapod studies. We also analyze shape and mechanical properties of the mandible independently from the rest of the skull, incorporating several three-dimensionally preserved fossil specimens including *Eocoelopoma* and *Scombramphodon* from the Eocene London Clay.

Our results show that the teleost skull is highly modular, and that morphological disparity is highest around the supraoccipital crest, the posterior region of the maxilla, and at the junction of the dentary and articular of the mandible. The otic capsule region shows the lowest disparity. These findings reflect variation in body shape and jaw morphology, and suggest that modularity plays an important role in shaping morphological diversity in this clade. Furthermore, mandible shape diversity is strongly linked with the diversification of mechanical properties, with different clades within Pelagiaria occupying different adaptive peaks in morphospace. Our findings represent an important first step towards broader investigations of teleost modularity and a more comprehensive understanding of drivers of vertebrate biodiversity.

**Funding Sources** This project is funded by a Leverhulme Trust grant number RPG-2019-113

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## Dinosaur Systematics, Diversity, & Biology

### A CAUDALLY-DIVERTED VAGAL CANAL IS A POTENTIAL ORNITHOSCELIDAN SYNAPOMORPHY

Knoll, Fabien

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In adults of neognaths and the kiwi, the glossopharyngeal (CN IX) and vagoaccessory (CN X-XI) nerves exit the braincase through separate apertures resulting from the subdivision of the embryonic fissura metotica, the recessus scalae tympani rostrally, and the foramen vagi caudally. It was believed that this configuration occurred once at some point along the neotheropodan lineage and that in all more basal theropods and, in fact, all other dinosaurs, CN IX–XI exited the neurocranial cavity through the same aperture (foramen metoticum). However, the issue was compounded by the difficulty in distinguishing the foramen vagi from a foramen hypoglossi in lateral view of the neurocranium. The fact is that the number of hypoglossal canals varies across

Dinosauria, and these are also enclosed within the otocipital. Considerable progress in our knowledge of the palaeoneurology of dinosaurs over the last decade reveals that a vagal (or vago-accessorial) canal could be identified next to a variable number of hypoglossal canals (generally one or two) in the vast majority of Mesozoic theropods (including basal forms such as *Dilophosaurus*) in which the courses of the caudal cranial nerves could be reconstructed adequately. A caudally-diverted vagal canal seems to have been widespread in ornithischians too. Its presence is supported by some observational evidence in *Heterodontosaurus*, the basal thyreophoran *Scelidosaurus* and the basal neornithischian *Lesothosaurus*. It seems to have been the general configuration in ornithopods, pachycephalosaurs and ceratopsians. The situation in derived thyreophorans is not as clear, but some stegosaurs at least (e.g., *Tuojiangosaurus*) seem to have had a diverted vagal canal. Thus, the configuration of the metotic region in theropods and ornithischians is similar and stands in sharp contrast to the arrangement in all sauropodomorphs (including primitive taxa such as *Buriolestes*) and dinosaur close outgroups (e.g., *Silesaurus*), in which CN IX–XI exits the neurocranium undivided through a relatively large metotic foramen. Although it cannot be ruled out that a caudally-diverted vagal canal has appeared independently in theropods and ornithischians or was reverted in sauropodomorphs, it may well be a reliable marker of phylogenetic history since it is relatively complex and apparently non-adaptative. If true, it would suggest that theropods and ornithischians are indeed sister groups.

**Funding Sources** Research projects CGL2017-89123-P funded by ERDF/Spanish Ministry of Science and Innovation-State Research Agency

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## Dinosaur Systematics, Diversity, & Biology

### A NEW BASAL HADROSAURID (DINOSAURIA: ORNITHISCHIA) FROM THE LATEST CRETACEOUS KITA-AMA FORMATION IN JAPAN ILLUMINATES THE ORIGIN OF HADROSAURIDS

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Here we present a partial hadrosaurid skeleton from the marine Maastrichtian Kita-ama Formation in Japan as a new taxon, *Yamatosaurus izanagii* gen. et sp. nov., based on unique characters in the dentition (only a single tooth as a minimum number of functional teeth per tooth position in the middle of the dentary dental battery and the complete absence of the “branched ridges” on the dentary tooth occlusal surface). Our phylogenetic analysis demonstrates *Yamatosaurus izanagii* belongs to Hadrosauridae, composed of *Hadrosaurus foulkii*+(*Yamatosaurus izanagii*+(Saurolophinae+Lambeosaurinae)). The coracoid lacks a biceps tubercle as in non-hadrosaurid hadrosauroids, suggesting its presence is a key feature for the clade of Saurolophinae and Lambeosaurinae. The evolutionary rates analysis further supports that shoulder and forelimb features, which are likely to have been involved in locomotion, were important for the early evolution of Hadrosauridae in addition to changes in jaw elements and dentition. Our biogeographic analyses show that basal hadrosaurids were widely distributed in Asia and Appalachia, and that the clade of Saurolophinae and Lambeosaurinae originated in Asia and subsequently dispersed into the Laramidia subcontinent. *Yamatosaurus izanagii* shows the longest ghost lineage duration of roughly 30 my among hadrosaurids. Interestingly, given the length of the ghost lineages of the Maastrichtian non-hadrosaurid hadrosauroids *Plesiohadros djadokhtaensis* from Mongolia and *Tanius sinensis* from China, considered with the ghost lineage represented by *Yamatosaurus izanagii*, it may be that eastern Asia (Japan, Mongolia and China) served as a refugium of relict hadrosauroid taxa. The contemporaneous occurrence of basal (*Yamatosaurus izanagii*) and derived (*Kamuysaurus japonicus*) hadrosaurids during the Maastrichtian in Japan is the first record in Asia. This contemporaneous occurrence may be due to a different paleoenvironment preserved, where Japan was more coastal in nature and richer in vegetation with plants such as plane trees, elm, and cycads than the fluvial environments preserved in the mainland Asian continent. Alternatively, because of the long geographical distance between these localities, they likely did not co-exist, but instead demonstrate some level of provinciality.

**Funding Sources** JSPS KAKENHI Grant Number JP19K04052 to Y.K. and 20J01696 to R.T.

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## Holocene & Pleistocene Mammalian Faunas

### NEW LATE PLEISTOCENE FOSSIL RODENT REMAINS FROM THE MIDDLE ATBARA, SUDAN

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Since 2018, paleontological and archeological field research along the Atbara River in eastern Sudan has recovered a diverse fossil assemblage, with over 30 vertebrate species including hominins and their stone tool technologies. Among the small mammals are fossils of cane rats (Thryonomyidae) and gerbils (Muridae, Gerbillinae). High-density OSL and <sup>14</sup>C dating suggests the deposits are between ~200 and ~15 ka. Fossil rodent remains include two *Thryonomys* sp. specimens, a partial dentary with dP<sup>4</sup>-M<sup>2</sup> and a partial maxilla with M<sup>1-2</sup>. Though these specimens most likely represent living species, they indicate a northern extension of the geographic range of *Thryonomys* during the late Pleistocene; today cane rats are restricted to sub-Saharan Africa and are not found in Sudan. Additionally, living cane rats are most commonly found in riverine and marsh systems, which is consistent with our preliminary paleosol and sedimentary analyses showing increased grassland-woodland habitats and a more complex fluvial system in this area during the late Pleistocene as compared to today. We also recovered a well-preserved fossil gerbil cranium most closely resembling the extant genus *Gerbilliscus*, today represented by three Sudanese species. This cranium does not exhibit the extreme hypertrophy of the tympanic bullae seen in many arid-adapted gerbillines, also suggesting that the Pleistocene landscape was less arid than today. Overall, these small mammal remains provide important information on late Pleistocene biogeography and the emergence of modern ecosystems

in the Nile River Basin, and our findings provide support for consistently wetter and more vegetated environments in this part of the African continent during the last ~100 ky.

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### Stem Tetrapod, Squamate, & Amphibian Diversity & Biology

#### DIMINUTIVE 'METOPOSAURUS' BAKERI MATERIAL IS MORPHOLOGICALLY DISTINCT FROM STRATIGRAPHICALLY YOUNGER SMALL-BODIED METOPOSAURIDS

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Recent attention has been given to the early ontogeny of metoposaurids and how our poor understanding of their early life appearance may influence alpha taxonomy of fragmentary or even relatively complete remains. Much of this work has focused on the purportedly diagnostic elongate, cylindrical intercentra of *Apachesaurus gregorii* as well as some aspects of the skull. Complete ontogenetic series of metoposaurids that overlap in size range between the large-bodied taxa (e.g., *Anaschisma browni* and '*Metoposaurus' bakeri*) and the small-bodied taxon *Apachesaurus* are virtually non-existent. A recently excavated, metoposaurid-dominated bone bed from the Popo Agie Formation (Late Triassic) of Wyoming (BLM permit PA16-WY-252) has yielded abundant remains diagnostic of '*Metoposaurus' bakeri*. Among these are several nearly complete crania that are similar in size to the holotype cranium of *Apachesaurus gregorii*. These crania possess the typical deep otic notch and well-developed tabular horn of large-bodied metoposaurids. In addition, some exceptionally small, putative metoposaurid remains – predominantly postcrania – have been recovered and differ significantly from *Apachesaurus* material. This diagnosis is based on the dorsally closed, cylindrical intercentra found in association with ribs, a femur, and an ilium. Preparation of the bone bed is still underway, and it is plausible that more small metoposaurid material will be recovered.

**Funding Sources** The David B. Jones Foundation

### Holocene & Pleistocene Mammalian Faunas

#### A JUVENILE *PANTHERA* FROM X CAVE, BOLT'S FARM, GAUTENG, SOUTH AFRICA

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Large *Panthera* fossils in the fossil record of southern Africa are rare to date. The Cradle of Humankind in South Africa has produced a few lion-sized pantherine fossils over the years from sites such as Gladysvale, Sterkfontein, Kromdraai, Swartkrans and Bolt's Farm (*Felis shawi*). More recently the Bridge Cave and Aves Cave deposits of Bolt's Farm have also yielded large bodied pantherine fossils. In 2009, a South African-French palaeontological team recovered numerous fossils from multiple sites within the palaeokarst system known as Bolt's Farm. One of these fossil deposits is X Cave. While to date X Cave has only had preliminary excavations completed, it yielded a plethora of carnivore fossil remains. Of note are specimens XC26, a calcaneus of a large-bodied *Panthera*; XC100, a proximal phalanx of a lion-sized *Panthera*; and XC10, a mandible of a juvenile lion-sized *Panthera*. XC10 is in four pieces and comprises deciduous premolars, incisors and canine dentition. In addition, the m1 is visible in the crypt and starting to erupt. Here we discuss the presence of lion-sized felids at X Cave, and in particular look at the relative age of the individual based upon eruption data compared to that of modern lion (*Panthera leo*) and tiger (*Panthera tigris*).

**Funding Sources** Paleoproterozoic Mineralization (PPM) Research Group

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### Macroecology & Macroevolution

#### BAYESIAN REANALYSIS OF THE EVOLUTION OF PHORUSRHACIDAE (AVES, CARIAMIFORMES)

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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. We present a revised evolutionary tree for the family Phorusrhacidae, with analyses on body size evolution. Using previous studies 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. Due to the poor preservation record of Phorusrhacidae, multiple size proxies were evaluated. Those which reliably correlate to femur length within a phylogenetically normalized regression are presented here as possible alternative metrics for body size.

Measurements were then used to test for the directional selection of gigantism and variability in body size within and between various lineages. This 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, composed of all phorusrhacids excluding Psilopterinae and Mesembriornithinae. Notably the largest individual species appear to form a distinct clade, comprising two lineages with no biostratigraphic overlap. Overall, we observe a continuous trend of multiple co-occurring phorusrhacid species within the same ecosystem, each occupying a non-overlapping range of body sizes. Discrete size ranges associated with specific clades persisted even as ecosystems were restructured over geologic time. Individual clades remained within a constrained size range, with no significant shifts observed except when directly following the extinction of another lineage.

This revised Phorusrhacid tree clarifies how this group evolved and with additional inquiry may have further implications regarding Phorusrhacid ecology. No directionality in body size evolution was detected, which we ascribe to the early divergence of size constrained clades. Species divergence rather was associated with long-term stabilizing selection, or niche filling following extinction. Body size thus appears to be strongly associated with the maintenance of high phorusrhacid diversity and the partitionment of the terrestrial predator niche within mid-Cenozoic South American grasslands.

**Funding Sources** Montana State University:  
Undergraduate Scholars Program

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## Late Cenozoic Mammalian Evolution and Ecology

### A NEW GENUS OF GOMPHOTHERE (MAMMALIA, PROBOSCIDEA, GOMPHOTHERIIDAE) FROM THE MIOCENE CHOPTANK FORMATION OF VIRGINIA, AND A REVIEW OF BARSTOVIAN AND CLARENDONIAN GOMPHOTHERES FROM THE CHESAPEAKE BAY REGION

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Published studies on the diversity of North American gomphotheres usually focus on the West, Great Plains, and Florida. However, a substantial number of important gomphothere discoveries have been made in the middle to late Miocene sediments of the Chesapeake Bay region of Maryland and Virginia on the Atlantic Coastal Plain, including one of the earliest known records of *Gomphotherium* in North America. This record is reviewed here.

Reflecting the importance of the Chesapeake region for gomphothere diversity, three species are identified: *Gomphotherium calvertense* from the Barstovian Calvert Formation (Fm); a species similar to “*Amebelodon*” *floridanus* from the early Clarendonian (Cl2) Choptank Fm; and an unusual new species represented by associated partial left and right mandibles with m2–m3 and partial upper and lower tusks from the Cl2 Choptank Fm from a cliff along the Potomac River in Virginia (hereafter referred to as the CPG). Although the upper and lower tusks of the CPG resemble those of typical *Gomphotherium*, the cheek teeth possess a unique combination of conservative and progressive gomphothere features. The m2 is very progressive, being both strongly double-trefoiled and incipiently tetralophodont by virtue of a large conulid. The m3 is elongated, having five lophids rather than the four to four-plus typically found in conservative (i.e., *Gomphotherium*-like) gomphotheres, and shows partially suppressed single trefoiling, the only trefoils being found

on the first two lophids (with those being weakly developed).

This unusual combination of dental characters makes it difficult to refer the CPG to any known genus. The double-trefoiled, incipiently tetralophodont m2 and elongated m3 separate the CPG from all conservative gomphotheres, while the lower tusk morphology rules out any shovel-tusked gomphotheres, progressive or conservative (e.g., *Amebelodon*, *Konobelodon*, or *Platybelodon*). The CPG most closely resembles *Pediolophodon*, with which it shares an m3 that is both elongated and shows single, partially suppressed trefoiling, but differs in having the m2 strongly double-trefoiled and only incipiently tetralophodont compared to *Pediolophodon* in which the m2 is single-trefoiled and strongly tetralophodont. The CPG does not appear to belong to any known gomphothere genus, and we here propose that it belongs to a new, and as yet not formally described, genus.

**Funding Sources** Clarissa and Lincoln Dryden Endowment for Paleontology at the Calvert Marine Museum

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### Colbert Poster Prize

#### THE CRANIAL ENDOCAST OF *BREAGYPS CLARKI* (AVES: CATHARTIDAE) AND THE EVOLUTION OF CONDOR OLFACTORY LOBES

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The La Brea tar pits of southern California are known for their well-preserved late Pleistocene taxa – including large-bodied birds such as condors. One of these condors, *Breagyps clarki*, represents the basalmost condor for which a 3D braincase is known among fossil taxa. Using CT scan data, the digital endocast of *B. clarki* was reconstructed in Avizo (v.9.7.0) and the anatomy described. The cranial endocast of *B. clarki* is typical for an avian: the cerebrum is enlarged, the optic lobes are large and laterally oriented, and the flexure angles are small making for a compact form. *B. clarki*'s cerebrum is constricted laterally forming a figure-eight shape when viewed dorsally – much like the cerebra of modern condors. The olfactory bulbs of *B. clarki* are of specific

interest based on their shape and olfactory bulb-to-endocast volume. In modern scavenging birds, the olfactory bulbs are volumetrically enlarged when compared to birds from other trophic ecologies. The volume of the olfactory lobes measures 0.02 g/cm<sup>3</sup> and accounts for approximately 0.06% of the total endocranial volume (31.8 g/cm<sup>3</sup>). The olfactory lobes of *B. clarki* are, volumetrically, six times smaller than those found in the extant condors *Gymnogyps californianus* and *Vultur gryphus*. The olfactory bulb volume is closer to modern predacious accipiters such as *Aquila chrysaetos* and the contemporaneous extinct teratorn *Teratornis merriami*. Morphologically, the olfactory bulbs of *B. clarki* are elongate, thin, and protrude from the body of the endocast as a single stalk rather than two distinct lobes. This indicates two different trends in the evolution of olfactory lobes in condors. First, sometime during or prior to the Pleistocene the olfactory bulbs of condors were more similar to those found in closely related accipiters and teratorns in volume and rapidly expanded in volume during the late Pleistocene. Secondly, the morphology of the olfactory apparatus has altered through time as the osteology of the skull changed. This may be evidence that the scavenging trophic ecology that is well-known in modern condors is relatively recent and shifted from a more predacious diet.

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### Marine Mammals

#### DEVELOPING A TASTE: CONNECTING SKULL SHAPE ONTOGENY AND EVOLUTION OF DIFFERENT FEEDING ADAPTATIONS IN CETACEA USING 3D GEOMETRIC MORPHOMETRICS

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Baleen and toothed whales (Mysticeti and Odontoceti, Cetacea), while sharing a deep evolutionary history, present distinct adaptations. Mysticeti have a highly specialized skull allowing them to engulf water and filter out the prey using their characteristic keratinous plates (baleen). Odontoceti instead present a variety of feeding adaptations, from short snouted suction feeders like the beluga, to the extremely long rostra of the primarily fish-

eating river dolphins. Ontogeny plays a key role in the evolution of organisms, as changes during this complex process can allow for new traits to arise. Identifying changes in allometry—the relationship between skull shape and size during growth—from fossil representatives and ancestors to modern groups can reveal important insights into the evolutionary processes at play. In the case of Cetacea, it can illuminate how they acquired the variety of feeding adaptations and skull shapes seen in living taxa while having evolved from a common ancestor. We hypothesize that, despite their close phylogenetic link, Mysticeti and Odontoceti present markedly different allometric trajectories, and, further, that within toothed whales differences in ontogeny are recognizable among families with different skull morphologies and associated feeding adaptations. To test these hypotheses, we assembled a 3D dataset of over 120 specimens, spanning the developmental and phylogenetic spectrum: from fetal stages to adults, and representing two-thirds of the living Cetacea genera. Skull shape morphology was acquired using both X-ray CT and surface scanning methods. We quantified the differences in skull shapes in the ontogeny of these taxa using 3D geometric morphometrics, with a total of 48 fixed landmarks and four semi-landmark curves, and conducted Procrustes ANOVA and ancestral state reconstruction analyses in R. The analyses revealed that Odontoceti and Mysticeti have distinct allometric trajectories, with baleen whales displaying a decelerated growth relative to the reconstructed ancestral trajectory. Odontoceti present instead an accelerated growth, with significant differences among families with different skull morphologies, which persist even after taking phylogeny into account. This shows the profound influence of developmental changes in the evolution of the disparate feeding adaptations present in modern Cetacea. Adding fossil taxa to the dataset will allow to quantify which areas of the skull primarily drive this pattern.

**Funding Sources** Marie Skłodowska-Curie Individual Fellowship 2019—Project: 894584—Evo-Devo-Whales

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## Turtle & Marine Reptile Diversity & Biology

### MESOZOIC TURTLES (TESTUDINES) FROM THE BOWSER BASIN OF BRITISH COLUMBIA, CANADA

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Terrestrial Cretaceous fossil vertebrates from British Columbia, Canada, remain rare. Here we report three well-preserved turtle specimens from the Late Jurassic to Early Cretaceous Bowser Lake Group of the Bowser Basin in the Skeena Mountains. RBCM P122, from the Jenkins Creek Assemblage, was deposited in a low-gradient fluvial system with no marine influence. It is a partial articulated carapace and plastron with articulated elements of the left hind limb. Though worn, the carapace preserves parts of the right costals 5–8, the left costals 6–8, and the associated neural elements. The right xiphiplastron is preserved largely as an impression, but the left xiphiplastron is largely intact and preserves the anal-femoral sulcus. A xiphiplastral notch is absent. The surface texture is vermiculate, similar to *Glyptops* and *Trititichelys*. RBCM P1048 and RBCM P1049 are from the Groundhog-Gunanoot Assemblage, which is deltaic in origin with only slight marine influences. They are both complete left hyoplastra of differing size but similar proportions. However, their ventral surfaces remain unprepared, limiting the exposure of diagnostic characters. These fossils represent the only fossil turtles in this part of North America and may represent a rarely sampled portion of the Mesozoic terrestrial fauna.

**Funding Sources** Royal BC Museum to DL and VA; Funding to VA was also provided by NSERC Discovery Grant RGPIN-2020-04012

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## Mammalian Skeletal Morphology

### NEW SKULL MATERIAL OF *HAPLOMYS* (RODENTIA, APLODONTIIDAE) GIVES WAY TO NEW MORPHOLOGICAL DETAILS

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Today there is only one living species of rodent in the family Aplodontiidae, *Aplodontia rufa*, the mountain beaver, which can be found in Northwestern North America. *A. rufa* is a ground-dwelling mammal that primarily feeds on small shrubs and ferns; however, their evolutionary history spans a wide range of ecological roles. Throughout the last 30 million years, there have been over 100 species attributed to the Aplodontiidae family spanning in order of magnitude in body sizes and a

wide range of habitat types. Aplodontiid fossils are abundant and diverse in the Turtle Cove Member of the John Day Formation, located in eastern Oregon. The Turtle Cove Member from the Arikareean North American Land Mammal Age includes fossils ranging from middle to late Oligocene in age. While the diverse members of the derived allomyine and meniscomyine clade have been used to subdivide the John Day Formation stratigraphy, the lower Turtle Cove member has only a single known aplodontiid species, *Haplomys liolophus*, described exclusively from teeth. Unpublished material of *Haplomys* in the collection at the University of California Museum of Paleontology includes a skull and postcrania, making it one of the most well-preserved *Haplomys* specimens found to date, offering insights into the cranial and postcranial morphology of an early member of this diverse lineage. This is the first time that a *Haplomys* specimen of such quality is being figured and analyzed in public literature. Analysis of skull and dental morphology has given way to new insights such as molar mesostyle and lower premolar cusp structures, dental size variation within the species, and basicranial and postcranial anatomy. Additionally, measurements suggest that *Haplomys liolophus* is substantially larger than other species and genus of the Aplodontiidae family. This specimen reveals the close morphological similarity of the cranial anatomy of prosciurine aplodontiids and early members of the Sciuridae, striking given the significantly specialized cranial morphology of *Meniscomys* less than five million years later. No postcrania have been documented for the *Haplomys* genus, and this new specimen shines light on morphological origins of the Aplodontiidae.

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## Holocene & Pleistocene Mammalian Faunas

### A RARE FINDING OF A *HYLOCHOERUS* (MAMMALIA, SUIDAE) TOOTH FROM LATE PLEISTOCENE RUSINGA ISLAND, KENYA: PALEOECOLOGICAL AND PALEOENVIRONMENTAL IMPLICATIONS

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Despite the rich eastern African Plio-Pleistocene fossil record, the latest part of the Pleistocene is sparsely sampled. As a result, the recent evolutionary history of many African taxa remains uncharted, including that of African forest hogs (genus *Hylochoerus*). Forest hogs are, together with warthogs, the evolutionary end product of a well-documented African Plio-Pleistocene suid radiation. Contrary to warthogs and various other extinct suid species, which developed highly derived craniodental adaptations to grazing diets in response to the expansion of C4-grassland ecosystems, forest hogs became adapted to mixed diets and to living in Afro-tropical forests and thick bushlands. *Hylochoerus* likely evolved from the extinct eastern African Pleistocene species *Kolpochoerus majus*, but its most recent evolutionary history is virtually unknown. The only securely dated and well-identified fossils of *Hylochoerus* are those from Member III of the Kibish Formation ~0.1 Ma. Here, we redescribe a partial right lower third molar of *Hylochoerus* from the late Pleistocene Wasiriya Beds of Rusinga Island dated to ~50–36 ka, which was previously assigned to *Kolpochoerus*. The crowns are mesiodistally compressed in a bunolophodont fashion and arranged in relatively tall columnar pillars that resemble those of extant forest hogs. Using micro-computed tomography, we show that the hypsodonty index (HI) of the Rusinga third molar crown was like those of extant *Hylochoerus* (HI = 1.8–2.0). We also report the results of stable carbon isotope analyses, including previously unpublished data on extant *Hylochoerus*. These data suggest that the diet of the Rusinga specimen ( $\delta^{13}\text{C} = -17.0\text{‰}$ ) was isotopically similar to that of extant forest hogs ( $\delta^{13}\text{C}$  average =  $-17.6\text{‰}$ ). This is the most negative carbon isotope value of any mammal in the whole African Neogene–Quaternary fossil record and contrasts strikingly with those of other fossil large herbivores at Rusinga ( $\delta^{13}\text{C}$  average =  $-0.7\text{‰}$ ). The presence of forest hogs in this site suggests that the late Pleistocene paleoenvironments were more heterogeneous than previously considered and may have included closed-canopy woodland in the highlands of Rusinga.

**Funding Sources** Humboldt Postdoctoral Fellowship, National Science Foundation grant (#1740383), Museum für Naturkunde Berlin, Natural History Museum of Utah, National Museums of Kenya

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## Education & Outreach



## **INCLUSIVE DESIGN HELPS MORE STUDENTS FEEL INCLUDED IN ONLINE UNDERGRADUATE STEM AND PALEONTOLOGY COURSES**

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How can we make our college courses more accessible and inclusive to those with and without disabilities? If we teach our undergraduate students how to use concepts of inclusive design, which increases accessibility for people with disabilities, we can make a positive shift. During summer and fall 2020, we designed and implemented a 6-week-long digital media project in a temporarily online, undergraduate non-majors human biology course with strong paleontology and paleoanthropology frameworks. During this culminating project, students were challenged with the task of producing a digital product; a video, podcast, or series of curated social media posts that explained aspects of human evolution and genetics. In addition to their broader science communication goals, students also incorporated an aspect of inclusive design such as closed captioning for d/Deaf and Hard of Hearing audiences, audio narration for blind or low vision audiences, colorblind accessible palettes, or alt text for social media posts. Students were provided with pedagogical scaffolding to introduce them to inclusive design concepts and methods of implementing them, including reflections from disabled persons on their experiences with inclusive design barriers.

Based on student post-course Likert-scale reflections (n = 336 of 672 total class size), over 96% of students responded they strongly or somewhat agreed that they had “grown in [their] awareness of disability and accessibility accommodation”, 93.5% responded that they agreed they had “grown in [their] sense of compassion for others”, 94% felt they were “more motivated to advocate for disability accommodation in the future”, and 93.8% “now consider disability to be a part of human diversity more than before this project or course”. In addition, 85.5% of student respondents shared that they agreed with the statement, “as a student, I feel more included in science because of this project or course.” Interviews were also conducted with the intent of refining the survey instrument and gathering feedback from student participants with and without disabilities.

Using digital media projects that incorporate inclusive design, we can center the disability community in our

STEM classes and help more students feel welcome in paleontology. Ultimately, having more frequent dialogue about disability accessibility in paleontology can make a tangible difference in creating a more just and equitable learning experience for every one of our students.

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## **Non-avian Theropod Systematics, Biology, and Evolution**

### **LIMITED POTENTIAL FOR TRIGEMINAL-INNERVATED SENSORY BEHAVIORS AMONG DINOSAURS**

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Among vertebrates, rostral integumentary sensory systems take many forms but are similar in their trigeminal nerve innervation. All extant reptiles exhibit trigeminal nerves extending from the braincase through a series of bony canals and foramina in the face and mandibles, but size and distribution of these features is variable with ecology. For instance, species engaging in specialized tactile sensory behaviors (e.g., crocodylians, probing birds) exhibit relatively large trigeminal features and dense distributions of terminal branches and sensory receptors leading to small receptive fields. In contrast, species not engaging in specialized tactile sensory behaviors have small trigeminal features and low densities of simple nerve branches and receptors and thus large receptive fields. As such, the osteological correlates of the reptilian trigeminal system (i.e., trigeminal fossa, trigeminal foramina, mandibular canal) are useful in inferences of facial sensation and tactile sensory behaviors in extinct taxa. Of particular interest are dinosaurs, often hypothesized to have unique trigeminal-innervated sensory systems based on qualitative observations of trigeminal osteological correlates. Using linear and derived measurements (e.g., maxillomandibular foramen diameter, mandibular canal Strahler order) of fossil specimens and 3D reconstructions from CT data, we performed morphometric analyses of several trigeminal-related features from a series of extant reptiles to establish morphologies associated with enhanced sensory abilities. Following this, we quantified trigeminal ganglion-associated osteological correlates in dinosaurs from eight major clades (e.g., nodosaurids, ankylosaurids, stegosaurids, sauropods, parkosaurids, ornithopods,

theropods) and canal branching patterns in the dentaries of theropods (e.g., *Dilophosaurus*, *Majungasaurus*, *Allosaurus*, *Tyrannosaurus*, *Byronosaurus*) and compared values with extant organisms to determine potential for tactile sensory abilities in extinct species. With the exception of relatively large trigeminal osteological correlates in ornithopods, comparisons reveal an overall trend of reduced trigeminal features and branching patterns among dinosaurs, indicating limited potential for specialized trigeminal-innervated tactile sensory abilities. Therefore, the presence of previously hypothesized unique sensory structures, abilities, and behavioral adaptations are not supported for the clade by quantitative analysis.

**Funding Sources** NSF EAR 1631684, 1762458; NSF IOS 1457319; Jurassic Foundation; Missouri Research Board; Evolving Earth Foundation; Society of Vertebrate Paleontology

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## **Mammalian Skeletal Morphology**

### **COMPARATIVE ANATOMY OF INTRACRANIAL OSSEOUS CANALS AND ALVEOLAR CAVITIES PROVIDE FURTHER CLUES ON THE RELATIONSHIPS BETWEEN GLYPTODONTS AND ARMADILLOS (XENARTHRA, CINGULATA)**

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The evolutionary history of the Cingulata, as for many groups, remains a highly debated topic to this day, particularly for one of their most emblematic representatives: the glyptodonts. There is currently no consensus among morphological and molecular phylogenies relative to their position within Cingulata. Recent works have shown that the study of the internal cranial anatomy constitutes a promising path for enriching morphological matrices for the phylogenetic study of armadillos, but it remains under-studied in the Cingulata. Here we explored and compared the anatomy of intracranial osseous canals and cavities in a diverse sample of extant and extinct cingulates consisting of nine extant genera and 11 fossil species including one representative of Pleistocene glyptodonts and four earliest (i.e., early Miocene) well-preserved glyptodont crania.

Using X-ray microtomography, we virtually reconstructed in 3D the following selected canals and cavities: the nasolacrimal canal, the palatine canal, the sphenopalatine canal, the canal for the frontal diploic vein, the transverse canal, the orbitotemporal canal, the canal for the capsuloparietal emissary vein and the posttemporal canal, and alveolar cavities related to cranial vascularization, innervation or tooth insertion. Comparison of the locations, trajectories and shape of these structures allowed us to provide a wealth of new anatomical data, to discuss their potential interest for cingulate systematics, and to reconstruct evolutionary scenarios for eight selected traits on these structures.

For these traits, glyptodonts generally showed a greater resemblance to pampatheres, to the eutatine genus *Proeutatus* and/or to chlamyphorines. For instance, we demonstrate that the position of the most dorsal point of the dorsal convexity of the tooth row and the sphenopalatine and palatine canal connection exhibit similarities between dwarf and giant armadillos. Resemblance to the latter is partly congruent with recent molecular hypotheses and would thus support a close relationship between these dwarf and giant forms among cingulates. Overall, this research highlights the systematic interest in the study of endocranial canals and alveolar cavities, which remain poorly studied in mammals, especially for fossil taxa.

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## **Preparators'**

### **HARNESSING THE POWER OF COMMUNITY SCIENCE TO DIGITIZE, TRANSCRIBE, AND IMPORT PREPARATION INFORMATION INTO A COLLECTIONS MANAGEMENT DATABASE SYSTEM**

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Museums with active fossil preparation labs historically have handwritten, sometimes barely legible, fossil preparation sheets (prep sheets). The digitization initiative at the Natural History Museum of Utah (UMNH), as well as the “Stay at Home” orders of the pandemic, allowed UMNH to scan the handwritten prep sheets, put these

scans onto DIGIVOL, a platform created by the Atlas of Living Australia, and have citizen scientists from all over the world transcribe these data. Since September 2019, UMNH has digitized 12,000 pages of documents, including 3,140 pages of prep sheets. These prep sheets were transcribed by citizen scientists and validated by UMNH volunteer preparators. DIGIVOL generated an Excel spreadsheet with the transcribed prep sheet data. This spreadsheet was then analyzed, massaged, and coded in a way that could be imported into EMu, our Collection Management System (CMS). When UMNH bought EMu, our Paleontology Department knew that customizing our Conservation Module in order to best record fossil preparation data was essential. In collaboration with our Preparation Lab Manager, we determined essential data to be recorded, then created customized tabs and fields for these data. These fields included drop down menus for consolidants, adhesives, solvents, and techniques used, as well as open notes fields for comments such as preparator's remarks, specimen's condition upon receipt, handling concerns, among others. A conservation number is assigned to each Preparation Record. Each record is linked to the Catalog Record of the specimen to which it is referring, the Party Record of the preparator, as well as any Multimedia Record (i.e. scanned prep sheet, preparation photos, etc.). In moving forward with our current and future preparation records, we are creating a digital prep sheet using Sapphire, a browser-based tool for EMu. By formatting the form in Sapphire, we can add only the fields we need to create accurate preparation records. Photos can also be added directly into the form and annotated with notes. All this can happen via a mobile device. This information feeds directly into EMu and, if needed, can feed into a report to be printed. Bringing preparation records into the 21<sup>st</sup> century will create fewer human errors, more relevant details recorded, and make for easier importation into EMu.

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## Holocene & Pleistocene Mammalian Faunas

### THE ORIGIN OF NEW WORLD MAMMOTHS: MORPHOLOGY MEETS DNA

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Recent research on ancient DNA back to a million years or more has contributed significantly to our understanding of mammoth evolution. The new data confirm the model, based on morphology, that early Pleistocene mammoths from northeast Siberia, of relatively advanced morphology comparable to *Mammuthus trogontherii*, were the source of endemic North American mammoths on the one hand, and the Holarctic woolly mammoth (*M. primigenius*) on the other. The genomic data further reveal two or more introgression events in the origin of late Pleistocene Columbian mammoths (*M. columbi*), resulting from hybridization between the endemic North American form and immigrating woolly mammoth populations. Whether these events are considered to represent hybrid speciation depends on the criteria employed. The data do not, however, support the contention that early mammoths in North America were more 'primitive' morphologically than late Pleistocene Columbian mammoths (e.g., referable to the Eurasian *M. meridionalis* or a local equivalent like '*M. hayi*'). On the contrary, the DNA evidence for the origin of North American mammoths from *trogontherii*-like populations supports the observation that the mammoths that seeded North America were already of advanced type. The taxonomic implication of a speciation hypothesis, such that only post-hybridization mammoths should be named *Mammuthus columbi*, would pose significant practical issues for researchers and curators. Since there is as yet no DNA evidence from pre-hybridization North American mammoths, nor clear morphological features distinguishing them from later populations, there would be no reliable way to select a type specimen on which such an 'early species' could be based. By the same token, the only clue to the identity of any North American mammoth fossil as *columbi* or its predecessor would be its age—but many mammoth fossils are poorly dated, and the date of the hybridization event itself is only broadly constrained. This warrants a conservative approach to taxonomy, in which palaeontologists continue to employ a morphospecies concept and label all North American *columbi*-like mammoths as *M. columbi* or *M. cf. columbi* until/unless we locate consistent morphological changes at the hybridization event. Further DNA evidence from the Siberian lineage and, especially, its North American descendants, will aid the resolution of these evolutionary and taxonomic issues.

**Funding Sources** Swedish Research Council and Natural Environment Research Council (UK)

## Fishes Evolution & Distribution

### PLANKTIVORES BITE BACK: REEXAMINATION OF MAXILLAE ENDS EDENTULOUS PACHYCORMID CLADE

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Pachycormids occupy a key-position within Actinopterygii, as part of the Holostei–Teleostei Transition. Due in part to their restricted ossification, remains of suspension-feeding pachycormids are invariably frustratingly incomplete in spite of the large size of the individuals concerned, making interspecific comparisons for phylogenetic purposes as problematic as intraspecific comparisons for ecological or ontogenetic objectives. One consequence of this is that amongst the hypodigm of 70+ specimens of the Callovian (Middle Jurassic) *Leedsichthys*, there are a very limited number of common bones between specimens, which furthermore often have their fragile extremities destroyed through the vagaries of preservation and recovery, making comparisons even more difficult. The five individuals of *Leedsichthys* whose remains preserve maxillae (including three of the five individuals used in 2013 to assess the size, age, and growth in this animal) were examined. The fragility of the weakly ossified remains rendered comparison difficult, but a growth series was established amongst the five, based on commonly-preserved stretches of the maxilla, within which the largest individuals were found to exhibit the eruption and presence of maxillary dentition. Though at odds with the classification of their ‘edentulous’ clade, this observation is consistent with previous interpretations of marine trace fossils as showing *Leedsichthys* engaged in benthic feeding on shellfish, similar to the way that contemporary gray whales and Pacific walrus have been observed to do on the Bering Shelf, Alaska.

The emergence of dentition at the upper limit of the animal's recorded ontogeny illustrates an at least partial trophic shift for these planktivores in later (> 10m) adulthood and serves as further evidence of widespread paedomorphosis in the group. However, the high dependence of pachycormid datasets on cranial characters (over 75%), around a tenth of which are specifically dental characteristics, questions the safety of using dentition and/or its presumed absence as characteristics in future pachycormid phylogenies.

**Funding Sources** JJ Liston is supported by the Tyrrell Museum Cooperating Society.

## Fishes Evolution & Distribution

### PALEOCENE-EOCENE JIANGHANICHTHYIDS (TELEOST, OSTARIOPHYSI, CYPRINIFORMES) FROM SANSHUI BASIN, CHINA ARE THE OLDEST KNOWN CYPRINIFORMS

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Molecules and fossils offer conflicting inferences on the origin of cypriniform fishes, a highly speciose order of teleosts. Whereas molecular data suggest a Jurassic, East/Southeast Asian origin and divergence for the clade, the oldest cypriniform skeleton fossils are known from Eocene deposits in Asia and North America. We recovered new materials from Paleogene sediments of Sanshui Basin (Guangdong Province, China) that shed light on the first occurrence of definitive fossil cypriniforms. The new specimens represent two species that belong to the fossil-only family †Jianghanichthyidae. The first species is from the late Paleocene–early Eocene Buxin Formation, previously assigned to extant carp genus *Osteochilus* and originally described as *O. sanshuiensis*, along with two coeval species (*O. longipinnatus* and *O. laticorpus*). Based on characteristics of the anal fin, caudal peduncle/vertebrae, and neural spines, these three nominal species and our new materials from Buxin Fm. are all assignable to *Jianghanichthys sanshuiensis* in the family †Jianghanichthyidae. Our analyses also suggest that previously cited differential diagnostic characters of these species can be explained by preservational and ontogenetic variation. A second new species is reported based on new materials recovered from middle Eocene Huachong Fm. (= Huayong Fm.). It is different from *J. hubeiensis* and *J. sanshuiensis* in characteristics of the opercle and the temporal sensory canal. The morphological features shared by the above species with type species *J. hubeiensis* reaffirm the unique and basal characters of †Jianghanichthyidae, including a branched first principal ray of the anal fin,

lack of well-formed pharyngeal teeth (or as minute as gill rakers), un-ossified kinethmoid, less developed Weberian apparatus, and heavily bone-enclosed sensory canals. The occurrence of *J. sanshuiensis* from Buxin Fm. extends the unambiguous earliest occurrence of cypriniforms from the Eocene into the Paleocene in Asia, bearing very basal characters of cypriniforms. Two evolutionary scenarios stem from these new findings: (1) A Jurassic origin of cypriniforms and the retention of basal characteristics from the 100 million-year ghost lineage to jianghanichthyids, representing an exceptional case of morphological stasis, (2) True cypriniforms originated shortly before the Paleocene, and any closely related Mesozoic taxa to be discovered would represent stem otophysans rather than cypriniforms.

**Funding Sources** Open Grant of State Key Laboratory of Palaeobiology and Stratigraphy (132311KYSB20170022), NSFC (41862001), International Partnership Program of CAS (132311KYSB20170022)

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## Late Cenozoic Mammalian Evolution and Ecology

### NICHE PARTITIONING BETWEEN CONGENERIC SPECIES WITHIN A RICH MIOCENE NEOTROPICAL BAT COMMUNITY FROM COLOMBIA

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With 14 species, the La Venta bat fauna is the richest fossil community in South America. It covers a poorly-represented time span in the middle Miocene, referred to as the Laventan South American Land Mammal Age (SALMA). La Venta has yielded 14 Miocene bat species, including one of the oldest plant-visiting bats in the world, and some of the earliest fossil evidence of the extant families Phyllostomidae, Thyroptera and Noctilionidae. Genus *Notonycteris* is an early phyllostomid taxon that has been instrumental for phylogenetic and systematic analyses. It is represented by two species, *N. magdalenensis* and *N. sucharadeus*, both described as early relatives of the modern subfamily Phyllostominae, a group of Neotropical carnivorous and

omnivorous bats. Previous research has reconstructed the diet and body mass of *N. magdalenensis* as a large-bodied omnivore, revealing transitional adaptations for carnivory found in its modern relatives. However, the biology of *N. sucharadeus* remains mostly unknown. Based on 3D multivariate dental topography analysis (DTA) of lower molars, we inferred the diet and body mass of both *Notonycteris* species. A comparative DTA was performed with a sample of 110 modern noctilionoid bat species, covering the entire dietary range found in modern bats. Principal Component Analysis (PCA) revealed species with liquid diets (i.e., nectarivory and sanguivory) and carnivore species occupied unique subregions of morphospace, whereas frugivores, insectivores and omnivores showed the greatest dispersion and overlap. Both *Notonycteris* species fell within the omnivore-insectivore subregion, but distant from each other. Discriminant Function Analysis (LDA) correctly classified up to 80% of modern species, indicating robust discriminatory power. Both *Notonycteris* species were classified as omnivore species, *N. magdalenensis* clustering with larger carnivore species and *N. sucharadeus* with smaller insectivore species. Our results indicate an ecologically diverse palaeocommunity with high morphological diversity, where *Notonycteris* species partitioned their niches to exploit different dietary resources. Estimating and comparing the diet and body mass of the bats from La Venta would allow a better reconstruction of the ecological evolution of New World bats.

**Funding Sources** MTS is funded by a NSERC Discovery grant and SJH by the Australian Research Council DP170101420.

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## Late Cenozoic Mammalian Evolution and Ecology

### THE EVOLUTION OF MIOCENE CRICETIDAE (MAMMALIA, RODENTIA): BAYESIAN MORPHOLOGICAL CLOCK, DISPERSAL AND BIODIVERSITY

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The fossil record is our only resource to provide a deep-time perspective on ecosystem processes and understand

the dynamics that have shaped our current biotas. Morphological data remain the only available information to reconstruct evolutionary scenarios and reconcile the fossil record with molecular trees. Methodological challenges have prevented until recently the application of tip-dating Bayesian approaches in morphology-based fossil-only datasets. Herein, we present a morphological dataset for a group of cricetid rodents belonging to the subfamilies Democricetodontinae, Megacricetodontinae and Cricetodontinae. We compare the tree topologies obtained by traditional parsimony, Bayesian dated and undated phylogenetic approaches and calculate stratigraphic congruence indices for each. Bayesian tip-dated clock methods seem to outperform parsimony in the case of our dataset, which includes highly homoplastic morphological characters. Regardless, all three topologies support the monophyly of Megacricetodontinae, Democricetodontinae and Cricetodontinae. Cricetodontinae are the sister-group to the clade consisting of Megacricetodontinae plus Democricetodontinae.

The Miocene is marked by major climatic changes, which happen to have profoundly influenced the evolution of faunas. Dispersal and speciation events inferred through Bayesian Binary Markov chain Monte Carlo and biodiversity analyses provide evidence for a correlation between biogeographic events, climatic changes and episodes of diversification in cricetids. The cricetids arrived at different times in different areas around the Mediterranean Basin and became extinct asynchronously as well. Our results evidence that the Miocene cooling events, particularly Mi2, Mi3, Mi4 and Mi5, which took place at 16 Ma, 13.8 Ma, 12.8 Ma and 11.5 Ma, respectively, have strongly impacted the evolution of cricetids by promoting dispersal and triggering significant origination and extinction events.

**Funding Sources** Research project PGC2018-094122-B-100 (MICU/AEI/FEDER,EU) and SYNTHESYS+ project (<http://www.synthesys.info>), which is financed by the European Commission.

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## Late Cenozoic Mammalian Evolution and Ecology

### LARGE- AND SMALL-MAMMAL RICHNESS OF THE BASIN AND RANGE THROUGH CHANGING CLIMATE SINCE 36 MA

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Climate and topography have important influences on the distribution of plants and animals. The Basin and Range province in North America represents a landscape that rapidly changed over the Neogene during intervals of significant climate change. Tracking changing climate and topography through time can be useful for interpreting their effects on species distributions in the past. We evaluated trends in large- and small-mammal species and family-level richness of the Basin and Range in relation to changing climate over the past 36 Myr. Species richness of large versus small mammals differs over the 36-Myr evolution of the Basin and Range province. The number of large-mammal species per 0.5-Myr time bin exceeded that of small-mammal species until the late Miocene, and small-mammal species richness remained higher than large-species richness through to the recent. Species richness of all mammals was highest during the middle Miocene and Pliocene, coinciding with warm climate states of the Middle Miocene Climatic Optimum (MMCO; 17–14 Ma) and the Pliocene Warm Period (3–5 Ma). Large-mammal species richness peaked during the MMCO, whereas small-mammal species richness peaked during the Pliocene. Family richness of all mammals peaked during the MMCO, declined slowly through the late Miocene, and increased again during the Pliocene, reflecting the influx of immigrant taxa. Herbivorous large-mammal species peaked during the MMCO and declined through to the Pliocene when the fewest number of large herbivores occurred. Heteromyid rodents accounted for the greatest proportion (~0.5) of small-mammal species during the early MMCO, whereas cricetid rodents comprised roughly half of small-mammal species by the early Pliocene. Climate simulations for North America show overall decreasing precipitation from the MMCO to the late Miocene, with a substantial decline in precipitation in the Pliocene. East-west precipitation gradients became more gradual through the Miocene as the Basin and Range expanded and elevation decreased. These trends correspond with a decrease in net primary productivity and in heterogeneity of vegetation from the middle Miocene to the Pliocene in western North America.

**Funding Sources** This work was funded by National Science Foundation Integrated Earth Systems grant No. 1814051.

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#### **Preparators'**

### **COLLECTION AND PREPARATION OF A *TRICERATOPS PRORSUS* SKULL PROVIDES UNIQUE OPPORTUNITIES FOR SCIENCE COMMUNICATION AND EDUCATION IN MATERIALS AND METHODS IN PALEONTOLOGY**

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Science education and communication highlighting the multifaceted processes of preparing a fossil specimen for study and museum exhibition infrequently transpires in tandem with the project. However, the initial discovery (2016), excavation (2017–2018), extraction (2018) and preparation (2019–current) of a nearly complete, articulated skull of *Triceratops prorsus* from the Upper Cretaceous Hell Creek Formation of Montana presented such an opportunity. Field expeditions conducted by the North Carolina Museum of Natural Sciences (NCMNS) paleontology unit, are showcased, tweeted, and uploaded on NCMNS social media platforms, throughout the expedition, directly from the field. Additionally, live-stream interviews by field team members are broadcast directly into the Daily Planet theater in the museum's research wing and are free and open to the public. Once back at the museum, the skull was prominently placed within the publicly viewable Paleontology Research Lab allowing museum visitors to watch the progression of the preparation process. Opening of the field jacket was live streamed by NCMNS to local news agencies and was free and open to the public. Once open, K–12 students at the event were provided the opportunity to help sweep down the newly exposed matrix. Furthermore, NCMNS set up information tables where museum visitors could engage with paleontology staff and volunteers during the event. Additionally, in collaboration with the museum's Exhibits and Digital Media team, Paleontology staff set up a time-lapse camera system set to capture a still photo every five minutes to record the progress of preparation. Current preparation status is regularly reported via Twitter and other museum social media platforms and aimed at

highlighting preparation progress of the skull and the discovery of secondary fossil specimens (e.g., paleobotanical specimens and other taxa) in the entombing matrix. Preparation is ongoing and projected to continue for several years. This project and the discovery of such an iconic dinosaur species has allowed NCMNS to engage with the public in effective science education and communication more broadly regarding the materials and methods of paleontology generally and fossil preparation and conservation specifically.

**Funding Sources** Bank of America Charitable Foundation

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#### **Preparators'**

### **UTILIZING OLD AND NEW TECHNIQUES TO BRING NEW LIFE TO OLD DISPLAYS**

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Many remarkable specimens that had been on display at the Yale Peabody Museum (YPM) as much as a hundred years ago are facing a refreshed new life for the upcoming renovation. In many cases, a variety of inexplicable work had been performed on specimens showing various layers of preparation and exhibition techniques used at the time. Specimens were prepared for the YPM renovation using well-established techniques (e.g., molding and casting), as well as relatively new procedures to preparation and exhibit work like 3D printing. Specimen mount types encountered at YPM included completely prepared specimens (fossil bone), specimens in situ (fossil bone in rock), plaque mounts (fossil bone embedded in a plaster backing), and plaster body mounts (fossil bone embedded in a plaster body sculpture). Each project brought its own unique challenges due to specimens' existence through prior museum renovations; therefore, a critical eye must be given to resolve each issue on an individual basis. This case study focuses on an assortment of specimens including *Orohippus agilis* (YPM 65700), which exemplified many of these exhibit preparation techniques. This small fossil horse is a plaque mount of a composite skeleton constructed in the early 20<sup>th</sup> century. Originally used as a display piece, this specimen was loaned to another institution where several elements were removed. It was eventually returned to YPM to be displayed but was no longer in exhibit quality. Often exhibit specimens

possessed many layers of coatings and/or sculptural materials such as paint, adhesives, plaster, fabrics, putties, metal, etc. which masked real fossil material. Once the real fossil material was exposed, the specimen could then be rehabilitated and prepared for exhibit. Several of these display techniques included building stabilizing bases, creating faux matrix, molding and casting, sculpting, and painting. The traditional techniques of molding and casting are utilized whenever possible, but 3D printing has been added to YPMs skill set to add or mirror image missing portions of the specimen. Distinct methods are used to paint casts versus reconstruction; casts are painted to look like the real specimen, while sculpted reconstructions are painted a matte color to blend, but also slightly stand out from the real fossil material. The natural beauty of fossil material is brought back into view resulting in rejuvenated specimens ready for display to a modern audience.

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## **Paleohistology & Paleopathology**

### **DIFFERENTIATING BITE MARKS AND SHELL DISEASE IN MODERN AND FOSSIL TURTLES USING COMPUTED TOMOGRAPHY**

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Interpreting and differentiating types of bone damage provide insights into the paleoecology and palaeobiology of extinct groups. However, accessing these data can be complicated by equifinality, the convergence of different taphonomic processes upon similar appearances. Among turtles, this issue historically has impacted separating shell disease from feeding traces. Shallow tooth marks, such as pits and scores, are superficially similar to the pock marks associated with shell disease, which is caused by infections or irritants present between the bone of the turtle carapace or plastron and the overlying keratinous scutes. In the literature, similar terminology is even used

to describe these distinct pathologies. To better identify and differentiate these two processes in a non-destructive manner, we used computed tomography (CT) scans to generate 3D models of known examples of these pathologies on modern *Trachemys* carapace and plastron elements, as well as putative shell disease and bite marks on fossilized turtle shell fragments from the Cenomanian Woodbine Formation of north-central Texas, U.S.A. Internal morphologies of each specimen were visualized and compared using the programs SPIERS and Dragonfly. In the modern samples with known examples of each type of pathology, shell disease produced irregular, bubble-like textures within the shell bone, appearing to grow from the inside toward the external surface; these features are not always obvious or visible at the surface of the bone. Bite marks, however, produced damage that is more regular, with tooth scores that leave marks that are always wider towards the surface of the shell and taper with increased depth. Internal crushing, breakage, and compression of the shell related to impact trauma is also apparent as a result of tooth marks. Both are broadly different from abrasion, erosion, and other taphonomic processes that remove surficial cortical bone without crushing impacts or remodeling during life. Congruence between the expression of these pathologies in the modern samples and the fossil exemplars further supports the use of CT scanning and internal imaging to differentiate bite marks from shell disease in paleontological samples.

**Funding Sources** NSF IUSE:GEOPATHs Impact grant #1600376, National Geographic Society grant #C325-16, and crowdfunding through Experiment.com

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## **Taphonomy, Paleoenvironments, & Stratigraphy**

### **ELASMOBRANCHS FROM THE PEACE RIVER AND TAMIAMI FORMATIONS (MIOCENE-PLIOCENE) ON THE SUBMERGED CONTINENTAL SHELF NEAR VENICE, FLORIDA, USA**

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The submerged continental shelf near Venice, Sarasota County, Florida, USA exposes clays and hardbottom limestone scarps of the Peace River and Tamiami formations (Miocene–Pliocene). These formations occur in  $\leq 12$  m of seawater, within 3 km of the modern-day shoreline, as a result of wave- and current-driven deposition and erosion during glacioeustatic sea-level cyclicity, shifting of the ancestral shoreline, and storm activity since the Miocene. These processes have accumulated residual, fossiliferous lag deposits on the modern seafloor that contain an abundance of elasmobranch remains (primarily isolated teeth of sharks and rays) belonging to at least 30 taxa including: *Ginglymostoma cirratum*, *Carcharias taurus*, *Otodus megalodon*, *Isurus oxyrinchus*, *Carcharodon carcharias*, *C. hastalis*, *Scyliorhinus* sp., *Mustelus* sp., *Galeorhinus* sp., *Hemipristis serra*, *Galeocerdo cuvier*, *Physogaleus contortus*, *Rhizoprionodon* sp., *Negaprion brevirostris*, *Carcharhinus falciformis*, *C. leucas*, *C. obscurus*, *C. perezii*, *C. cf. C. brachyurus*, *Sphyrna* sp., *Rhynchobatus* sp., *Rhinobatos* sp., *Pristis* cf. *P. pectinata*, *P. cf. P. pristis*, *Raja* sp., *Dasyatis* cf. *D. americana*, *Rhinoptera* cf. *R. bonasus*, *Mobula* cf. *M. hypostoma*, *Aetobatus* cf. *A. narinari*, and *Myliobatis* sp. Comparison of the submerged Venice shelf elasmobranchs with those from land-based exposures in Florida and elsewhere along the Atlantic and Gulf Coastal Plains of the USA indicates that the Venice taxa and formations become progressively younger geologically to the south. Moreover, the Venice taxa provide a unique means to assess the stratigraphic distribution of many well-known and globally occurring elasmobranchs, including megatoothed sharks (*Otodus* spp.), as related to habitat shifts along the west coast of Florida since the late Cenozoic.

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## Biomechanics & Functional Morphology

### PALEOBIOLOGICAL RECONSTRUCTIONS OF ARTICULAR FUNCTION REQUIRE ALL SIX DEGREES OF FREEDOM

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Paleobiologists typically exclude impossible joint poses from reconstructions of extinct animals by estimating the

range of motion (ROM) of fossil joints. ROM-based exclusion is generally defended as a tenable—or even conservative—approach to functional reconstruction because studies have indicated that osteological manipulations tend to overpredict true ROM, and that only a subset of each joint's mobility is exploited in life. By contrast, however, other analyses have concluded that osteological manipulations might actually underpredict true ROM. If viable joint poses were to be omitted from ROM estimates, they would also erroneously be excluded from functional reconstructions. This possibility is especially concerning because ROM-based exclusion of limb configurations has played a large role in shaping not only our understanding of the stance and gait of individual animals, but also that of major transformations in locomotor evolution. In this study, we aimed to evaluate whether ROM-based exclusion is, as currently implemented, a reliable strategy for use in paleobiological reconstructions. Specifically, we tested how many degrees of freedom must be included in osteological ROM analyses to ensure that they consistently capture true joint mobility. We measured the true mobilities of five intact archosaur hindlimb joints using marker-based X-ray Reconstruction of Moving Morphology, and compared them to osteological estimates of ROM made allowing (1) only all three rotational, (2) all three rotational and one translational, and (3) all three rotational and all three translational degrees of freedom. We found that allowing combinations of motions in all six degrees of freedom is necessary to ensure that true mobility is always successfully captured. As a result, we suggest that existing paleobiological reconstructions should be re-evaluated to determine if their conclusions still hold when all six degrees of freedom are considered. We also offer an improved methodological framework for virtual ROM estimation and outline recommendations for future ROM-based exclusion studies.

**Funding Sources** This work was supported by the NSF, Bushnell Graduate Research and Education Fund, Sigma Xi, AWG/Paleo Society, and SVP.

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## Stem Tetrapod, Squamate, & Amphibian Diversity & Biology

### A FAREWELL TO ARMS: SNAKE-LIKE LIMB LOSS IN A MOLGOPHID RECUMBIROSTRAN FROM MAZON CREEK

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Among modern tetrapods, many lineages have converged on a snakelike body plan, where extreme axial elongation is accompanied by reduction or loss of paired limbs.

However, the fossil record of how and when this adaptive strategy evolved in various tetrapod groups remains poorly understood. For example, limb reduction and loss is known in a handful of early stem-group tetrapods and total-group lissamphibians, whereas the fossil record of limb reduction and loss within the amniote lineage is sparse. We here provide new insights into these questions by reporting a new molgophid recumbirostran from the Francis Creek Shale of Illinois, USA, with extreme axial elongation and corresponding limb reduction. The new molgophid, represented by two exceptionally-preserved specimens preserving complete body outlines, shows affinities with *Brachydectes* and *Infernovenator*.

However, unlike in these taxa, the forelimb and pectoral girdle is entirely absent in the new molgophid, thus representing the earliest occurrence of complete loss of a limb in a fossil amniote. The presence of a complete hindlimb and pelvic girdle contrasts with the condition seen in limb-reduced amphibians and certain limb-reduced reptiles, where there is a hindlimb-first reduction process that is characterized by the loss and/or reduction in size of hindlimb elements, are rudimentary pelvic girdle elements are often retained. Instead, the morphology of the new molgophid is consistent with a pattern of limb reduction that is seen in modern snakes, where the forelimb and pectoral girdle are lost first. In snakes the loss of the forelimb is caused by the failure to form a discrete forelimb field due to homogenous *Tbx5* expression over the entire pre-cloacal flank region, rather than a discrete *Tbx5* domain to signal forelimb bud initiation. The similar morphology between the new molgophid and snakes suggests a common limb-reduction mechanism may apply more broadly across the amniote tree.

**Funding Sources** Ontario Graduate Scholarship (OGS) awarded to Arjan Mann

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**Stem Tetrapod, Squamate, & Amphibian Diversity & Biology**

## THE ORIGIN OF AMNIOTA IN PHYLOGENETIC CONTEXT

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Ever since phylogenetic analysis was introduced to the study of early limbed vertebrates in the mid-1990s, there have been exactly two types of such analyses: those that extend from the origin of limbs to the origin of Amniota (but barely reach into Amniota or Diadectomorpha) and those that try to investigate amniote phylogeny and barely reach beyond Amniota. Yet, some questions have recently surfaced that cannot be researched if this dichotomy is upheld; whether Seymouriamorpha or a grouping of mostly “microsaurs” is closer to the amniote–diadectomorph clade, whether at least some “microsaurs” are stem-sauropsid amniotes, and the monophyly and position of Diadectomorpha (in the stem group of Pan-Amniota or that of Pan-Mammalia). Moreover, research on purely amniote-internal problems like the positions of Varanopidae and the “parareptiles” may be misdirected if too distant outgroups are used (potentially leading to misrooted, distorted trees) – and which taxa are best suited as outgroups for amniote phylogeny depends on the questions mentioned above. I have updated and enlarged a dataset of early limbed vertebrates by adding amniotes and other potentially relevant taxa as well as a large number of characters. Diadectomorpha and Amniota are, at the moment, supported as mutually exclusive; a pan-mammalian position is very weakly supported for Varanopidae, the “parareptiles” and the “captorhinomorphs” are scattered, and all “microsaurs” are found as stem-amphibians rather than stem-sauropsids. Seymouriamorpha is placed next to the amniote–diadectomorph clade with very weak support. Successively less close lie Amphibia, *Solenodonsaurus*, Chroniosuchia, Temnospondyli, a “gephyrostegid” grade, Anthracosauria, *Caerorhachis* and the “Parrsboro jaw”, and a baphetid-colosteid clade. *Westlothiana* is found as an amphibian, *Casineria* as a temnospondyl or a “gephyrostegid”. Further redescription of taxa and of character complexes will be necessary, though not sufficient, to improve our understanding of amniote origins. My results also underscore the still underestimated importance of “microsaurs” as close amniote relatives, and the closeness of the origins of Amniota and Lissamphibia – a narrow gap largely bridged by Albanerpetidae, Lysorophia and the “microsaurs”. Depending on the exact size of this gap, extant

amphibians may be better model organisms for amniotes like ourselves than used to be thought: phylogenetics is important even for biomedical research.

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## Permo-Triassic Ecosystems

### A NEW SPECIES OF CARNIVOROUS AZENDOHSAURID (ARCHOSAUMORPHA) FROM THE CHINLE FORMATION OF PETRIFIED FOREST NATIONAL PARK

Marsh, Adam<sup>1</sup>, Parker, William<sup>1</sup>, Nesbitt, Sterling<sup>2</sup>, Kligman, Ben<sup>2</sup>, Stocker, Michelle<sup>2</sup>, Patellos, Emily<sup>2</sup>

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Azendohsaurids, a group of large bodied and possibly herbivorous archosauromorphs, were thought to be restricted to the Middle Triassic and Late Triassic of Morocco, Madagascar, and India, but now include partial skeletons and isolated bones from the Late Triassic of the western United States. Many of these skeletal remains have been attributed to *Malerisaurus* or larger *Malerisaurus*-like taxa, but unambiguous associations of skeletal material remain rare. Here we present the skeletal anatomy of a new early-diverging, but late-surviving azendohsaurid from the upper part of the Blue Mesa Member (Chinle Formation) at Petrified Forest National Park. This new taxon is diagnosed by numerous autapomorphies throughout the skeleton and is closely related to *Malerisaurus robinsonae* from the Maleri Formation of India and to *Malerisaurus langstoni* from the Colorado City Formation (Dockum Group) of western Texas. The PEFO azendohsaurid comes from a monodominant bonebed that also includes chondrichthyans, actinopterygians and sarcopterygians, metoposaurid temnospondyls, and suchian and dinosauromorph archosaurs; the azendohsaurid is represented by over 900 skeletal elements with a minimum number of nine individuals of varying size. The dentigerous elements from the new taxon confirm that isolated teeth in lower Chinle Formation microvertebrate assemblages can be referred to *Malerisaurus*-like azendohsaurid taxa. Along with recent discoveries of new trilophosaurid species in and near Petrified Forest National Park, this new azendohsaurid further supports the hypothesis that non-archosauriform archosauromorphs were diverse near the end of the Norian and experienced

an extinction event prior to the end-Triassic mass extinction coincidental with the Adamanian-Revueltian boundary at the park, after which only select trilophosaurids persisted. The relatively late age of this early-diverging taxon (Norian, ~220 Ma) suggests that the diversity of azendohsaurids is underrepresented in the Middle Triassic and Late Triassic fossil record around the world.

**Funding Sources** Petrified Forest National Park; Petrified Forest Museum Association; Virginia Tech

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## Non-avian Theropod Systematics, Biology, and Evolution

### ON THE STANDING POPULATION SIZE OF *TYRANNOSAURUS REX*, THE TOTAL NUMBER THAT EVER LIVED, AND ITS ABSOLUTE PRESERVATION RATE

Marshall, Charles R.<sup>1</sup>, Latorre, Daniel<sup>1</sup>, Wilson, Connor<sup>1</sup>, Frank, Tanner M.<sup>1</sup>, Magoulick, Katherine<sup>1</sup>, Zimmt, Joshua<sup>1</sup>, Poust, Ashley<sup>2</sup>

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While much can be deduced from fossils alone, estimating abundance and preservation rates require data from living species. Here we use Damuth's relationship between population density and body mass among living species, combined with our now exceptional knowledge of *Tyrannosaurus rex*, to calculate population variables and preservation rates for post-juvenile *T. rex*. We estimate its post-juvenile abundance at any one time was ~20,000 individuals (but anywhere from 1,300 to 328,000 individuals), that it had a generation time of 19 years (but anywhere between 17.8 and 20.1 years), that it persisted for ~127,000 generations (but anywhere from 66,000 to 188,000 generations), that the total number of *T. rex* that ever lived was ~2.5 billion individuals (but anywhere from 140 million to 42 billion individuals), with a current fossil recovery rate of one diagnosable individual (housed in a public museum) per ~80 million individuals that ever lived (but anywhere from one in 4.5 million to one in 13 billion), or one in 16,000 in the Hell Creek Formation where its fossils are most abundant (but anywhere from one in 1,100 to one in 260,000). As part of our

calculations, we computed an ecological body mass for *T. rex*, the average mass of post-juveniles on the landscape, estimated to be 5,200 kg (but anywhere from 3,700 and 6,900 kg). The uncertainties in many of these values span over two orders of magnitude, largely due to the variance in the density–body mass relationship rather than due to the variance in the paleobiological variables.

Interestingly, the uncertainty in the physiology of *T. rex* is less important than the range of population densities seen among living species with the same physiology and trophic level—differences in ecology swamp differences in plausible physiologies of *T. rex*.

**Funding Sources** Partially supported by the Philip Sandford Boone Chair in Paleontology at the University of California, Berkeley

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### **Symposium - Vertebrate dental ecomorphology: Tooth traits that reflect ecology**

#### **DENTAL MORPHOLOGY OF PROCOLOPHONIDAE AND IMPLICATIONS FOR PERMO-TRIASSIC POST-EXTINCTION RECOVERY**

Martinez, Selena A., Jenkins, Kelsey M., Bhullar, Bhart-Anjan

Earth & Planetary Sciences, Yale University, New Haven, Connecticut, United States

Procolophonidae, an extinct clade of small-bodied parareptiles, persisted through the Permo-Triassic mass extinction event and radiated in the Middle and Late Triassic. Although small-bodied tetrapods are important components of modern and extinct ecosystems, the ecological role of procolophonids has not been analyzed in a systematic way. Tooth morphology is an indicator of function and diet, and in extinct organisms, dentition is used to infer ecological niche. To estimate the dietary breadth of procolophonids we analyzed the dentition of thirty-five species ( $n=35$ ). Differences in maxillary and dentary tooth dimensions suggest a variety of diets. These measurements reveal four dental morphogroups: (1) small teeth with rounded bases, (2) buccolingually widened, ovoid teeth, (3) mesiodistally -widened teeth, and (4) large, molariform teeth. Comparisons to modern and extinct tetrapods with well-attested diets indicate that our morphogroups correspond to insectivorous, omnivorous, durophagous, and herbivorous diets, implying considerable ecological diversification within

Procolophonidae. Preliminary data also indicate temporal shifts in ecomorphological diversity through time.

**Funding Sources** Department of Earth & Planetary Sciences, Yale University

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### **Mammalian Skeletal Morphology**

#### **INFLUENCE OF CONSTRAINT AND ADAPTATION ON MORPHOSPACE OCCUPATION PATTERNS OF THE CARNIVORAN APPENDICULAR SKELETON**

Martín-Serra, Alberto, Figueirido, Borja

Universidad de Malaga, Malaga, Andalucía, Spain

How phenotypic evolution is influenced by adaptation and constraints is one of the keystones of evolutionary biology. Constrained evolution can be identified using morphospace occupation indices, which can be related to ecological adaptations.

Here, we use three-dimensional landmarks of the appendicular bones of mammalian carnivores to compute their disparity, constraint (estimated by the morphological disparity index, MDI) and integration (estimated by the relative eigenvalue standard deviation). These indices of morphospace occupation are compared with locomotor ecological signal to explore the association between constraint and adaptation.

Our results show that there is not a significant relationship between morphospace occupation indices and locomotor adaptations for carnivoran limb elements. In contrast, we find that those elements with stronger ecological signal (ulna and femur) do not show the same pattern, as the femur is more constrained than the ulna. This suggests that a constrained evolution does not hinder possible adaptations. In addition, the elements with the weakest ecological signal (scapula and pelvis) show an intermediate level of constraint. Finally, the element with the least constrained pattern (the tibia) and the most integrated variability does not show a strong ecological signal, which indicates that other aspects, besides locomotor adaptations, may also be playing a role for this element. In conclusion, the carnivoran appendicular skeleton demonstrates that the interactions between constraints and adaptation in phenotypic evolution are more complex than previously expected.

**Funding Sources** CP18-FR3193 (Junta de Andalucía) to BF  
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### **Colbert Poster Prize**

#### **TOOTH BE TOLD: THE ADVANTAGES OF DIGITAL MEASUREMENTS FOR THE MORPHOMETRIC ANALYSIS OF THREE RANCHO LA BREA CARNIVORES**

Mata, Kendall<sup>1</sup>, Shiinoki, Aaron<sup>1</sup>, Noriega, Nicolas<sup>1</sup>, Cohen, Joshua<sup>2</sup>, Binder, Wendy<sup>1</sup>

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Technological advancements in paleontology have allowed for 3D renderings of specimens to become accessible to researchers worldwide. Dentary measurements in particular are of great interest due to their ability to serve as proxies for function and behavior in mammals, including carnivores. Traditionally, these measurements are conducted in-person using digital calipers and previously determined landmarks. Today, landmark-based measurements from scans enable researchers to gather measurements remotely, allowing for an unprecedented degree of collaboration amongst the paleontological community. However, it is essential to understand if data gathered via landmark-based measurements from 3D scanned fossils are comparable with traditional caliper-based measurements from physical specimens. In this study, the similarity between morphological measurement techniques were tested by comparing landmark-based measurements taken from 3D scans with comparable caliper measurements taken directly from fossil specimens of three taxa from Rancho La Brea deposits: *Canis dirus* (n = 73), *Canis latrans* (n = 111), and *Smilodon fatalis* (n = 72). Overall, the measurements were similar, with less than a five percent error in all three taxa, with some exceptions. However, measurements with high percent error between techniques were likely due to differences in measurement protocols between methodologies, rather than a lack of congruence or inaccuracies in measurements. Therefore, this study indicates that comparable data can be collected from in-person caliper-based measurements of physical specimens and remote landmark-based measurements from 3D scans, as long as measurement protocols are the same

between techniques. Museums that are able to scan their specimens and make them publicly available will grant any researcher and academic institutions of all levels, access to museum collections without the need to travel, thereby promoting the expansion of fossil related studies and scientific collaboration. This further supports existing recommendations that collections worldwide be digitized to further advance the accessibility of specimens and safeguard from any potential damages associated with handling physical specimens. Future studies may focus on expanding the validity of digital measurements to other specimens, such as herbivore dentaries, and utilize advanced statistical analyses.

**Funding Sources** National Science Foundation (Award #1758117) awarded to Wendy Binder.

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### **Fishes Evolution & Distribution**

#### **MAMMALIAN-LIKE TOOTH REPLACEMENT IN A PYCNODONT FISH JAW**

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Vertebrates acquired the first tooth replacement mechanism 424-million-year ago, which has enhanced complex prey-predator relationships. From that time to the present, they have diversified various patterns of tooth replacement and attachment mechanisms. In general, fishes, amphibians, and reptiles replace teeth in many generations in their lifetime, and mammals are shed one time or less in their lifetime. Teeth are implanted on the lingual side or on the margin of the mandible in fishes, amphibians, and squamates, whereas mammals and archosaur reptiles have ankylothecondont dentition, in which tooth roots are enclosed in sockets of bones. An enigmatic pycnodont fish, *Serrasalmimus secans*, was reported from the Paleocene of Morocco and was placed in an extinct family, Serrasalmimidae. The evolution of the Serrasalmimidae is characterized by the reduction of tooth rows in their ankylothecondont-like dentitions, with the most derived species, *S. secans*, possessing a piranha-like dentition. The compressed mammiform teeth of *S. secans* show vertical wear facets created by shearing on the labial and the lingual side of the prearticular dentition, which resembles carnassial teeth of mammals. Although,

in a reverse contact, and crown morphology of *S. secans* superficially resembles some lizards. Here, we characterize a unique combination of a tooth replacement pattern and implantation in *S. secans* based on CT-scan data of tooth germs in an additional specimen and propose that serrasalmimids independently acquired true vertical replacement and a thecodont dentition, which is usually seen in tooth replacement of mammals. The internal structures of *S. secans* shows thecodont-like implantation in ankylosis attachment to the vomer bone. The 3D reconstruction visualizes the tooth replacement system. There is a pulp cavity containing a tooth germ in the center of each functional tooth, in contrast to common fishes, in which their tooth germs are formed on the lingual side of the functional teeth. *S. secans* lacks any trace of bone resorption on the buccal or lingual side of the bone unlike common fishes with tooth germs under the functional teeth, where replacement teeth erupt from replacement pores on the bone. We interpret that replacement teeth in *S. secans* develop between tubular root structures of the functional teeth and erupt from their position directly below the teeth, which closely resembles the vertical mode of tooth development in mammals.

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## Non-avian Theropod Systematics, Biology, and Evolution

### NEW DATA ON THE TYRANNOSAURID DINOSAUR *DYNAMOTERROR*, INCLUDING A MORE COMPLETE SKELETON, FROM THE MENELEE FORMATION (MIDDLE CAMPANIAN) OF NEW MEXICO, USA: IMPLICATIONS FOR TYRANNOSAURID EVOLUTION IN SOUTHERN LARAMIDIA

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*Dynamoterror dynastes* was based on UMNH VP 28348, a fragmentary skeleton from the upper Allison Member of the Menefee Formation (middle Campanian), New Mexico. It was diagnosed by two autapomorphies on the

frontals and placed among large-bodied tyrannosaurines, but its exact phylogenetic relationships have been unresolved. We report WSC 1027, a more complete skeleton recently collected geographically and stratigraphically close to the holotype and of similar size. WSC 1027 includes many skull bones, including both frontals, allowing direct comparison with UMNH VP 28348. WSC 1027, as well as recent independent work questioning the original autapomorphies, prompted a new look at the holotype and further comparisons with other tyrannosaurids.

UMNH VP 28348 can be distinguished by a unique combination of frontal features: (1) small, tab-like prefrontonasal process (PNP); (2) prefrontolacrimal process (PLP) is a rugose prominence separated from PNP by a striated notch; (3) PNP, PLP, and notch are situated on a mediolaterally-broad, dorsoventrally-thick shelf that roofs the dorsal end of the vertical prefrontal contact; and (4) medial wall of prefrontal contact does not merge with ventral surface of PNP, such that the ventral surface of PNP is free and a deep cleft separates it from the medial wall of the prefrontal contact. This same unique suite of features is present in WSC 1027.

Together, these observations show that *Dynamoterror dynastes* is a valid taxon and WSC 1027 is referable to it. The frontals of both specimens and the jugal, quadrate, and dentary of WSC 1027 share several features with *Lythronax* and *Teratophoneus* from the Wahweap and Kaiparowits formations of Utah. Phylogenetic analysis recovers a clade of (*Lythronax*+(*Dynamoterror*+*Teratophoneus*)), which in turn is sister to a clade of more derived large-bodied tyrannosaurines from Laramidia and Asia. One of the synapomorphies of *Dynamoterror*+*Teratophoneus* (protuberance on jugal at rostral end of quadratojugal contact) was previously considered an autapomorphy of the latter, and is present in WSC 1027. The phylogeny, geography (spanning ~300 km), and chronostratigraphy of *Lythronax* (80.6–79.9 Ma), *Dynamoterror* (>78 Ma), and *Teratophoneus* (76.46–75.51 Ma) are consistent with anagenesis. Precise dating of *Dynamoterror*, identification of sequential changes, and further material that fills remaining stratigraphic gaps will help explore this hypothesis.

**Funding Sources** David B. Jones Foundation

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## Quantitative Paleontological Methods

## SUBSAMPLING VERTEBRATE FOSSILS AS DIGITAL FRAGMENTS CAN ASSESS COLLECTIONS FOR BIASES AGAINST TAPHONOMIC DATA

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Fossil collections are often built by many individuals and teams with disparate priorities, resulting in non-uniform field protocols that can skew collections in species richness, size, completeness, taphonomic condition, and aesthetic value. To test the effects of sampling biases on paleoecological data, we analyzed a large dataset of bone surface modifications (BSMs) on vertebrate remains from the Mygatt-Moore Quarry (MMQ) in Colorado (Morrison Formation). We focused on BSMs, as they can provide critical taphonomic and paleoecologic data, and the widespread practice of preferentially collecting more complete, better-preserved fossils potentially creates a bias against these data. This is compounded by a lack of research quantifying sampling biases affecting taphonomic data quality in vertebrate paleontological collections.

A shift from selective sampling to bulk collection at the MMQ gave us the opportunity to examine collection bias. Frequencies of BSMs were recently reported for the MMQ in an explicit site-wide survey. We divided that dataset into the two collection modes at the quarry (1984–2015 and 2016–2019) and took a 10% random subsample of elements from each. To assess fidelity between collection protocols, we had to account for the disparity in sampling. Because fragments recovered in bulk collection are not a 1:1 comparison to larger identifiable bones, we reduced both datasets to digitally created fragments by overlaying images of specimens with a 2.0 cm<sup>2</sup> grid to create new sets of digital fragments. Grid squares were assigned unique values and randomly subsampled to pull new 10% subsets of the digital fragments. This was repeated 25 times with frequencies calculated for BSMs present in grids for each subsample. Results show the bulk collection subset returned a higher frequency of BSMs than selective sampling, and thus should be incorporated into field collection protocols. However, though subsampling can test the quality of data among disparate collection protocols, it should not be employed as a substitute for rigorous, site-wide surveys. The initial

element-level subsampling proved insufficient to replicate modified bone frequencies reported in the full site survey, recovering an order of magnitude lower frequencies of BSMs, suggesting these traces are not randomly distributed. These results suggest that BSM frequency data in the absence of bulk collection may not realistically reflect the real diversity of these taphonomic alterations.

**Funding Sources** David B. Jones Foundation

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## Colbert Poster Prize

### A COMMON AND SEVERE BONE INFECTION IN THE DROUGHT-RIDDEN POPULATION OF THE AUSTRALIAN PLEISTOCENE GIANT, *GENYORNIS NEWTONI* (AVES, DROMORNITHIDAE)

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Lake Callabonna is one of Australia's most highly regarded Pleistocene fossil sites with near complete, well-preserved, articulated fossils. Among the taxa preserved is an extinct giant flightless bird, *Genyornis newtoni*, the last surviving species in a once abundant, unique avian radiation, the Dromornithidae. Several fossils of *G. newtoni*, from minimally four individuals, have been discovered with evidence of osteomyelitis, a severe bone infection. Major distortion of the bone is present both externally and internally, with the type, and appearance of the pathologies allowing for identification of osteomyelitis as the diagnosis. The high prevalence of osteomyelitis in this single population of *G. newtoni* at Lake Callabonna is unusual; most studies of pathologies in birds show large populations of birds to have much lower general infection rates, and even lower rates of osteomyelitis infection. Novel dating of Lake Callabonna shows the fossil site to have accumulated during an extended period of severe drought, a factor which we suggest might have played a large role. It is well known that the susceptibility of a host to a pathogen can be increased by predisposing environmental factors. For example, drought conditions can lead to high stress levels due primarily to limited resources and initiated stress responses can be negatively impactful if maintained for long periods of time. Thus, we suggest that the drought experienced by this population of *G. newtoni* could ultimately be a primary contributor in increasing

susceptibility to infection, resulting in the high prevalence of osteomyelitis.

**Funding Sources** This research was supported by the Australian Research Council grant DP180101913 (Extricating extinction histories at Lake Callabonna's megafauna necropolis).

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## Fishes Evolution & Distribution

### USING GEOMETRIC MORPHOMETRICS AND OUTLINE ANALYSIS TO DELINEATE ONTOGENETIC HETERODONTY IN RECENT AND FOSSIL WHITE SHARK (*C. CARCHARIAS*) TEETH.

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Earth and Environmental Sciences, Michigan State University, East Lansing, Michigan, United States

Many sharks exhibit ontogenetic heterodonty, in which they develop different dental morphologies at different life stages. Accurately identifying these patterns would allow for age estimates based on isolated teeth, whether they be fossil or recent, and also aid in weeding out some dubiously erected fossil shark taxa. Sharks in the Family Lamnidae exhibit strong ontogenetic heterodonty, which has usually been described qualitatively. This is particularly evident in *Carcharodon carcharias*, the Great White Shark. One such feature in *C. carcharias* is the presence of lateral cusplets – enameloid-covered projections on the mesial and lateral sides of a tooth – in juveniles. Lateral cusplets can be a useful tool in determining age in these sharks, but this is complicated by several factors. Lamnids as a whole can exhibit various other forms of heterodonty, including anterior–lateral and monognathic heterodonty, that must be accounted for when examining dental morphology. In addition to this, lateral cusplets may not always be present due to inconsistent expression, pathologies, or damage. To address these issues that arise when using qualitative techniques, we have turned to more quantitative techniques to capture the degree of ontogenetic heterodonty expressed by white sharks. We have used geometric morphometrics and outline analysis to assist in quantifying ontogenetic changes and variation in tooth shape in both extant and fossil white shark teeth. We used a combination of landmark-based geometric morphometrics and Elliptical Fourier Analysis to capture the range of tooth shapes expressed by a series of white

shark jaws ranging from neonate to adult individuals. We then applied these same techniques to a sample of isolated fossil white shark teeth. We found that the fossil sample set largely reflected the same degree of ontogenetic shape variation as the series of recent jaws. Some tooth shapes observed in the recent jaw series were relatively sparse or absent from the fossil dataset, which may be due to collection bias for particular tooth sizes or shapes.

**Funding Sources** Michigan State University, Department of Earth and Environmental Sciences, Aural T. Cross Endowed Graduate Fellowship.

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## Macroecology & Macroevolution

### HOW HAS THE BIOGEOGRAPHY OF GONDWANAN MAMMALIAN CLADES VARIED OVER DEEP TIME?

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The prominence of marsupials differs across the Gondwanan continents; marsupials in Australasia have adopted a variety of body sizes and ecological niches, while the group is restricted to small-bodied omnivores and herbivores in South America. By contrast, placentals have proliferated in South America, yet were largely excluded from Australasia until the Quaternary. This discrepancy in distribution is obvious in both the present and the geological past, but its causal factors remain obscure and controversial, in part due to a limited fossil record.

One possible method of resolving this is ecological niche modelling (ENM). South America and Australasia were both adjacent to Antarctica until the Eocene, with many clades continuously dispersing between the three continents; it is unlikely that significant physical barriers prevented marsupials and placentals from establishing a homogenous distribution across South America, Antarctica and Australasia. Mammalian dispersal across Gondwana in the Mesozoic and early Cenozoic was thus probably dictated by the limitations of and interactions among the ecological niches of different groups, establishing a baseline from which the present-day distributions of marsupials and placentals originated. By applying ENM to extinct groups (either by extracting paleo-environmental data from an appropriately filtered



dataset of fossil occurrences, or by adapting the niches of seemingly equivalent extant taxa), we can predict habitat suitability across Gondwana over deep time. This in turn can be used to extrapolate potential dispersal patterns, as well as the apparent niche conservatism and niche breadth of both extant and extinct mammalian groups. ENM then has the potential to elucidate at least some aspects of the evolutionary ‘conflict’ between marsupials and placentals, as well as the wider biogeographical history of Gondwana.

**Funding Sources** NERC, St Cross College Oxford

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### Romer Prize

#### **DOES SIMILAR MORPHOLOGIES MEAN THE SAME MOVEMENT CAPABILITIES? MORPHOFUNCTIONAL SPACES FOR *CARAGUATYPOTHERIUM MUNOZI* (NOTOUNGULATA; MESOTHERIIDAE) AND *NOTOSTYLOPS MURINUS* (NOTOUNGULATA; NOTOSTYLOPIDAE)**

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The functional inferences in paleontology are based on *ex vivo* morphological and behavioral databases obtained from living animals compared to the fossil record corresponding plotting place. However, a morphology may produce a variety of functions, hence usually there is no a single response. The MorphoFunctional Space (MFS) approach intends to tackle this problem by identifying movement extreme ranges. In addition, the complement of *in vivo* database (*i.e.* kinematics parameters in current mammals), would allow estimating angular movement capabilities during locomotion. *C. munozi* and *N. murinus* are examples of midsize, plantigrade, terrestrial mammals, with no modern relatives nor functional homologues. But, will the movement capabilities be different when applying the MFS approach to compare two apparently similar Notoungulata species? Our aims was to construct an MFS to evaluate biological factors (BF) of i) posture (*i.e.* plantigrade, digitigrade, unguligrade), ii) maximum speed (*i.e.* slow, medium, fast) and iii) locomotor habits (*i.e.* arboreal, scansorial, cursorial, terrestrial) and infer the joint amplitude (JA) during the support phase of locomotion in *C. munozi* and *N. murinus*. To evaluate the

BF, a database of astragalus (9 order; n=57) and calcaneus (6 order; n=69) of modern mammals was used, in addition to the fossil record of *C. munozi* (astragalus, LabPaleo UACH) and *N. murinus* (astragalus and calcaneus, MPEF-PV 1115). To infer angular movement capabilities, 187 species (15 orders) of land mammals were evaluated during the support phase of the gait cycle. JA (degrees) was determined for the forelimb and hindlimb joints through the range obtained between the minimum and maximum values (touchdown, mid-stance and toe-off phases). *C. munozi* has a plantigrade posture; slow speed and terrestrial-scansorial locomotor habit. *N. murinus* has a plantigrade posture with facultative digitigrady; slow-medium speed and a terrestrial-scansorial locomotor habit. The JA is higher for *N. murinus* in elbow (+18°), wrist (+71°), hip (+9°), knee (+21°) and ankle (+17°). In *C. munozi* it is greatest at shoulder (+13°). Although both species of notoungulate have comparable overall morphological characteristics, the MFS allows us to infer a different JA profile, which is related to a greater range of biological faculties and movement capabilities in *N. murinus* than in *C. munozi*.

**Funding Sources** Agencia Nacional para la Investigación y Desarrollo [2017–21171271].

This work is part of a Doctoral Thesis in Veterinary Sciences at the Universidad Austral de Chile.

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### Dinosaur Systematics, Diversity, & Biology

#### **EXCEPTIONALLY SIMPLE, RAPIDLY REPLACED TEETH IN SAUROPOD DINOSAURS DEMONSTRATE A NOVEL APPROACH TO HERBIVORY IN LATE JURASSIC ECOSYSTEMS**

Melstrom, Keegan, Chiappe, Luis, Smith, Nathan

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Dinosaurs that lived during the Late Jurassic exhibit a wide range of dental shapes. In particular, the long-necked sauropods are characterized by two distinct single-cusped morphotypes: the narrow, peg-like teeth of diplodocoids and the broad-crowned morphology observed in many macronarians. These morphologies contrast with the multicusped teeth that typify other herbivores, both living and extinct. In previously sampled amniotes, dental complexity, a quantitative representation of morphology, displays a clear relationship with diet: carnivores possess simple teeth whereas herbivores have

complex, multicusp dentitions. Here, we use the orientation patch count rotated method to test for this relationship between diet and dental complexity in 13 Late Jurassic dinosaur genera and ten additional theropod dental morphotypes, which capture much of the total shape variation during this time period. We find that dinosaurs exhibited dental complexity disparity on par with that of modern saurians. Ornithischians, which are inferred to be herbivorous, possess complex teeth, whereas carnivorous theropods have simple teeth, supporting previously documented patterns. The dentition of herbivorous sauropods, however, departs from these trends. Diplodocoids, in contrast to nearly all known herbivores (living or extinct), possess remarkably simple teeth. Thus, we find that high dental complexities are not correlated with an herbivorous diet in sauropods. Instead, we document that complexity is associated with tooth replacement rate even when phylogenetic relationships are taken into account. Diplodocoids with rapid dental replacement rates possess exceptionally simple teeth, whereas sauropods that have slower rates exhibit more complex dentitions. This pattern represents a novel approach to herbivory and may have permitted multiple genera of large-bodied herbivores to inhabit the same environment. Additionally, the consumption of a highly abrasive, silica-rich diet coupled with elongate necks may have been a primary driver of the evolution of simple, light weight, rapidly replaced teeth. Ultimately, the decoupling of herbivory and tooth complexity combined with a correlation between complexity and replacement rate demonstrates a novel evolutionary strategy for herbivory in sauropod dinosaurs.

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### **Symposium - Vertebrate dental ecomorphology: Tooth traits that reflect ecology**

#### **HIGH INTRASPECIFIC MOLAR VARIATION IN NORTH AMERICAN EOCENE–OLIGOCENE RODENTS**

Messec, Rose<sup>1</sup>, Keller, Jonathan S.<sup>2</sup>, Moore, Jason<sup>1</sup>

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Under the inhibitory cascade (IC) model, the ratio of activator and inhibitor signals during dental development determines the relative size of mammalian molars and

gives rise to several common dental phenotypes (e.g.,  $m1 > m2 > m3$ ). Discovered in in vivo rodent developmental models, putative patterns of IC-driven variation have been documented across many mammalian orders and linked to both dietary ecology and evolutionary history. Modern rodent species span a range of dental phenotypes consistent with the IC model, and recent studies report low intraspecific variation in molar area ratios of modern rodent populations. However, IC position and molar variation of fossil rodents remain understudied. In this study, we used ImageJ to collect molar outline areas from published images to assess molar ratio variation and position in IC morphospace for early North American rodents (including *Ischyromys*, *Eumys*, and *Paradjidaumo*). Preliminary results for 44 species showed almost all species plotting consistently within regions of IC morphospace occupied by modern rodents. This is consistent with the ecological and evolutionary interpretations of the IC model, although the dietary ecology of the extinct taxa is unknown so the hypothesis cannot be tested conclusively.

Of the 44 studied species, we characterized intraspecific molar ratio variation for the seven species with sufficiently complete tooth rows and sample sizes. Intraspecific variation in these extinct taxa was significantly greater than that of modern rodent populations. This pattern is supported by the relatively high intraspecific variation in cusp and loph morphology seen in some of the studied fossil species relative to observed conservatism of dental morphology in modern rodent populations. Higher intraspecific variation among the Eocene–Oligocene taxa could be tied to one of three causes: that the taxonomy of extinct rodents is significantly more lumped than that of modern or recent fossil rodent counterparts; that greater molar variation may be explained by greater time-averaging of these older specimens; or that these early North American rodents were more morphologically plastic than recent rodents. The latter case could suggest that rodent lineages have become more dietarily canalized since the Eocene.

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### **Symposium - Vertebrate dental ecomorphology: Tooth traits that reflect ecology**

#### **EFFECTS OF DEMOGRAPHY AND MORPHOLOGY ON VOLE (*MICROTUS* SPP.) MESOWEAR: IMPLICATIONS FOR PALEOECOLOGICAL RECONSTRUCTIONS**

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A key component in paleoecological reconstruction is the determination of diet. Mesowear, dental wear developed over the last months of an animal's life, is an indicator of diet and environment. Mesowear, initially developed for selenodont and trilophodont ungulates, has since been applied more broadly, including vole teeth.

Modern vole species have been used as a model for extinct congeners. However, differences in dental morphology between modern and extinct species may affect mesowear values, and fossil samples may include left and right teeth obscuring differences in mesowear due to laterality. Moreover, in fossil teeth, we often do not know the specimen's sex and ontogenetic age. Thus, paleontological mesowear results may be confounded by demographic and morphological variables rather than diet or environment.

We measured mesowear in two skeletal samples of laboratory raised vole species (*Microtus ochrogaster* [M = 16 and F = 22] and *M. pennsylvanicus* [M = 34 and F = 16] with an age range of 5 days to 1262 days (70% aged 0–299 days). All individuals were fed a diet of 10% sunflower seeds and 90% alfalfa rabbit pellets. Mesowear was measured in situ at 10X magnification by the angle between the occlusal surface and the most anterior edge of the anterior cup observed from the buccal side on the lower first molars and analyzed using LASX imaging software. Age was binned into three categories <198 days, 198–795, and > 795 using Jenks Natural Breaks to determine age cutoffs.

A Standard Least Square Regression was calculated to correlate mesowear with age, sex, species, and side and all interactions. A significant regression equation was found ( $F [14,79] = 2.2053$ ,  $p\text{-value} = 0.0144$ ) with an  $R^2$  of 0.28. However, none of the post hoc pairwise correlations were significant when corrected for multiple comparisons.

Results suggest that the application of mesowear to fossil voles is not dependent on age, sex, side, or species. Using modern species to explore how diet affects mesowear provides a robust model for fossil congeners. Mesowear on fossil specimens from both left and right teeth can be combined into a single sample, and mesowear recorded on fossil teeth that cannot be ascribed to sex or age can be used to evaluate paleodiets and paleoecological reconstructions. However, we acknowledge that these results do not remove the need for region-specific calibration of herbivore ecometrics as proxies to evaluate fine-scale habitat changes in the fossil record.

**Funding Sources** National Science Foundation grant number 1851613 and The University of Tulsa Student Research Grant

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## Stem Tetrapod, Squamate, & Amphibian Diversity & Biology

### COMPUTED TOMOGRAPHY REVEALS A JURASSIC STEM-GEKKOTAN FROM THE MORRISON FORMATION

Meyer, Dalton, Brownstein, Chase D., Gauthier, Jacques  
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Squamates, with more than 11,000 species, are a major portion of extant tetrapod biodiversity. However, their phylogenetic relationships remain highly contested between hypotheses generated from morphological versus molecular data. This may be due in part to poor sampling of stem members of disparate crown clades, particularly from the Jurassic, when most of the crown ‘backbone’ clades are estimated to have originated. Here, we identify a stem gekkotan from the Kimmeridgian Brushy Basin member of the Morrison Formation. This new species replaces the Tithonian *Eichstaettisaurus* as the oldest stem gekkotan currently known.

This identification is based on a reexamination of specimen DINO 19514. It consists of a disarticulated partial skull including the maxillae, prefrontals, frontals, parietal, left jugal, right postfrontal and squamosal, partial braincase, both dentaries, and the fused left postdentary bones. Previous examination of DINO 19514 assigned it to the scincomorph *Paramacellodus*. We utilize  $\mu$ CT to re-examine the morphology of DINO 19514 in previously inaccessible detail and find it to be a new taxon that is neither *Paramacellodus* nor a scincomorph. This new taxon is diagnosed by an enlarged pineal foramen, a relatively wide inter-orbital portion of the frontals (more than 50% of the width of the frontoparietal suture), a postfrontal fused to the postorbital, and a wide parietal nuchal fossa.

We incorporated DINO 19514 into a large squamate dataset (165 out of 791 characters x 169 species). Unconstrained maximum- and implied-weights ( $K=12$ ) parsimony infer it as the earliest-diverging stem gekkotan, sister to a clade containing *Eichstaettisaurus*, *Norellius* and crown gekkotans. DINO 19514 grants insight into the condition at the base of *Pan-Gekkota*. As in other stem

gekkotans, it has paired frontals, in contrast to the fused condition of the crown. While incomplete, it is apparent that the subolfactory frontal processes are like those of other stem gekkotans in being intermediate between the ancestral squamate condition and the crown gekkotan condition in which they meet and fuse on the ventral midline. Likewise, the elevated marginal tooth count of DINO 19514 is intermediate between the low ancestral count and the high count of crown gekkotans. A lack of palatal dentition unites it with stem and crown gekkotans, pushing this loss to the Jurassic. The posterior teeth are unicuspid, a feature that it shares with other stem and basal crown-gekkotans.

**Funding Sources** Yale University; James Dwight Dana Fellowship; Yale Institute for Biospheric Studies

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

### **USING EBSD FOR THE IDENTIFICATION OF A FOSSILIZED EGG FOUND IN THE MIDDLE JURASSIC TIOURAREN FORMATION OF NIGER, AFRICA**

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In the country of Niger, Africa a fossilized egg of an unknown origin has been found in the Tiouraren Formation which dates to the Middle Jurassic. The discovery of this fossil is significant because fossil eggs are extremely rare in Africa. Our goal was to identify the taxonomic species that this egg might belong to. The identification of this egg is of great importance because it will help give a better understanding of the prehistoric ecosystem at this location during the Jurassic period. Additionally, it has the potential for being the oldest and one of the only known eggs of a turtle, dinosaur, crocodile, gecko, or even bird found in Africa. The only known turtle eggs in Africa are from the Hadar Formation dating to the Pliocene. The only other eggs that have been reported from Africa are from the Middle to Late Jurassic and Late Cretaceous dinosaur eggs. To find the identification of this egg an Electron backscatter diffraction (EBSD) was used. This was necessary in order to be able to answer the question of what kind of animal species this egg came from. Based on the small size, spherical shape, and small pores of the egg we predict that this egg belonged to a turtle. Based on these results, our

study will focus our observations and comparisons with other turtle eggshells.

**Funding Sources** USP (Undergraduate Scholars Program) funded for this project

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## **Colbert Poster Prize**

### **THE DIET OF FOSSIL BIRDS AND A NEW FRAMEWORK FOR ITS RECONSTRUCTION**

Miller, Case V., Pittman, Michael

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Birds are some of the most ecologically diverse organisms on Earth, with species filling a huge swath of niches across every major biome. As such, birds are vital to the study of extant ecosystems. Our understanding of the evolutionary history of extant ecosystems, thus, is hampered by gaps in our knowledge of the origin of bird diversity and ecosystem ecology. A critical part of addressing these shortcomings is a better understanding of the earliest birds, the non-avian avialans (i.e. non-crown birds), particularly of their diet. The diet of non-avian avialans has been a matter of much debate because of the ambiguous, qualitative approaches that have been used to reconstruct it. After reviewing methods for determining diet in extant and extinct avians (i.e. crown birds) as well as non-avian theropods, we propose a set of comparable, quantitative approaches to ascertain fossil bird diet. Using this and direct evidence, we summarize what is currently known about fossil bird diet. While no single approach can precisely predict diet in birds, each can narrow the dietary possibilities and reach precision in concert. We recommend combining: (1) dental microwear, (2) landmark-based muscular reconstruction, (3) stable isotope geochemistry, (4) body mass estimations, (5) traditional and/or geometric morphometric analysis, (6) lever modelling, and (7) finite element analysis to accurately determine possible fossil bird diets. We note current applications of dental mesowear, skull traditional morphometrics, geometric morphometrics, and certain stable isotope systems have yet to be proven effective at discerning fossil bird diet. With this in mind, we know little about the diet of non-avian avialans. The ancestral dietary condition in non-avian avialans remains unclear due to scarce data from early-diverging avialans and contradictory evidence in *Archaeopteryx*. Due to a scarcity quantitative studies of bird diet leading to a

dearth of robust dietary assignments, trends in non-avian avialan dietary evolution are also unclear. We expect dietary knowledge and evolutionary trends of bird diet to become much clearer in the coming years with this new framework as a roadmap. This will allow for a better understanding of the role birds played in Mesozoic ecosystems and how this developed into their pivotal role in extant ecosystems.

**Funding Sources** The University of Hong Kong PGS Research Grant Council of Hong Kong's General Research Fund (17120920; 17103315) RAE Improvement Fund of the Faculty of Science, HKU

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## Holocene & Pleistocene Mammalian Faunas

### CARNIVORES PREFERRED HORSE IN LATE PLEISTOCENE YUKON

Miller, Joshua H.<sup>1</sup>, Wright, William<sup>1</sup>, Kelly, Abigail<sup>1</sup>, Neale, Bianca<sup>1</sup>, Gaetano, Madison Q.<sup>1</sup>, DeSantis, Larisa<sup>4</sup>, Zazula, Grant<sup>3</sup>, Wooller, Matthew<sup>2</sup>

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How do predator-prey interactions adapt to significant ecological change? During late Pleistocene environmental perturbations, the abundances of many mammals changed dramatically and individualistically; sometimes shifting a community's dominant species. Such changes can alter predator-prey relationships, but fossil records rarely have the temporal completeness to study these dynamics. Taking advantage of highly fossiliferous permafrost deposits of the Klondike (Yukon Territory, Canada), we used the occurrences of carnivore modifications on bones to evaluate changes in prey utilization through time. Specifically, we tested whether the carnivore guild (e.g., *Canis*, *Arctodus*) was consistently biased towards particular prey species, or alternatively targeted prey as a function of their relative abundances. We used AMS radiocarbon (<sup>14</sup>C) dating to establish timeseries of the Klondike's two dominant ungulates: bison (*Bison priscus*)

and horses (*Equus* sp.). We taphonomically standardized the timeseries by using only mandibles ( $n_{\text{bison}} = 84$ ,  $n_{\text{horse}} = 59$ ). All specimens were visually evaluated for punctures, scores, and furrows consistent with carnivore modification. To reduce bias, taphonomic analysis was done blind to <sup>14</sup>C dates. While tooth marks alone cannot discriminate predation from scavenging, such data provide metrics of prey utilization. To estimate species' abundances through time, we synthesized <sup>14</sup>C dates using KDE\_model (OxCal). We found that bison and horse had population maxima both prior to and following the Last Glacial Maximum. However, the timing of peak abundances was offset; establishing two shifts in dominance. We identified carnivore modification on mandibles of 11 bison (13%) and 20 horse (34%), revealing a strong horse bias ( $p < 0.05$ ). Further, while horse were modified across their timeseries, bison were modified only prior to ~40 kyr BP and during the terminal Pleistocene; periods of low horse abundances. While modified bison mandibles only dated to intervals when horse abundances were low, horse were modified regardless of bison population size. In fact, during peak bison abundance (when horse abundance was increasing, but not yet peaked), only horse mandibles exhibited carnivore modification. While identification of bone-modifying agent(s) requires further study, our results indicate a strong preference for horse among late Pleistocene Yukon carnivores, with bison utilized when horse abundances were below an accessibility threshold.

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## Romer Prize

### THE FEEDING ECOLOGY OF MESOZOIC MAMMALS: A BIOMECHANICAL APPROACH

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Mammals not only originated during the Mesozoic, but also experienced most of their evolutionary history (over 150 million years) during this era; as such, Mesozoic mammals can provide invaluable insights into the early functional evolution and ecological diversification of one of the most successful vertebrate clades on the planet today. In particular, diet is one of the most important and oft-studied traits of mammals, as it helps us understand the ecological structure of terrestrial communities and prevailing environmental conditions. Jaws are one of the

most commonly preserved fossils of Mesozoic mammals and are generally used as indicators of diet. In this talk, I set out to investigate the relationship between jaw shape, functional performance and diet of small modern mammals to later infer diet in Mesozoic mammals. I take two different approaches. Firstly, I use a combination of 2D form and function analyses. I evaluate the variation in jaw shape among small extant mammals of known diets and the mechanical advantage of the two main adductor muscles of their jaws: the masseter and the temporalis. The combination of these data reveal differences in form and function between herbivores, carnivores, and insectivores. I find a very good correspondence between independently inferred diets of Mesozoic mammals (based on body size, dental morphology and wear) and the results of my analyses. Secondly, I use finite element models to study jaw functional performance in modern small mammals. I find broad differences in stress distribution between insectivores, hypercarnivores, mesocarnivores, and herbivores: most Mesozoic mammals resembled insectivores, and a few resembled hypercarnivores. Put together, modern small mammals of different diets can be distinguished using jaw shape, mechanical advantage values, and stress distribution patterns. We can use this information to infer diet in Mesozoic mammals. Jaw functional performance corroborates the hypothesis that most Mesozoic mammals were insectivores, and a few taxa were carnivores.

**Funding Sources** Funded by a PhD scholarship (#689870) by CONACYT (National Council of Science and Technology), Mexico

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## Avialan Evolution & Biology

### SMALL RAILS (AVES: GRUIFORMES: RALLIDAE) FROM THE LATE PLEISTOCENE AND EARLY HOLOCENE OF THE SOUTHERN HIGH PLAINS OF TEXAS.

Moretti, John A., Johnson, Eileen

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Quaternary birds in North America are understudied relative to mammals and herpetofauna. This situation is particularly the case in the Great Plains where the depauperate fossil avifauna fails to document past avian diversity. Recent research on avian samples from the Southern High Plains (SHP) of Texas has begun to

expand the regional record of Quaternary birds. Among this material are the remains of multiple small rallids recovered from late Pleistocene (Macy Locality 100) and early Holocene (Lubbock Lake, Paul site) deposits spanning from ~11,550 to ~9,905 <sup>14</sup>C yrs BP within regional drainages. The rallid specimens have been identified taxonomically based on analysis of morphological variation in 100 modern skeletons from 16 species in nine genera. *Porzana carolina* and *Rallus limicola* occur in the late Pleistocene samples. *Porzana carolina* is also present in early Holocene samples from Paul site. Both species are known previously from early Holocene deposits at Lubbock Lake. Due to the lack of distinguishable characters for some of the Lubbock Lake specimens in the present sample, those elements are assigned only to the category of *P. carolina* or *R. limicola*. *Laterallus jamaicensis* is identified for the first time on the SHP based on two elements from the early Holocene of Lubbock Lake. A single coracoid from ~8,600 <sup>14</sup>C yrs BP at Lubbock Lake has been referred to the Central and South American form *L. exilis*. The older material (~9,905 <sup>14</sup>C yrs BP) assigned here to *L. jamaicensis* is clearly distinct from *L. exilis*. These fossils suggest a past non-analog distribution for *L. exilis* and the presence of two *Laterallus* species on the SHP. Modern *Laterallus* skeletons, however, are few and these identifications are based on only three individuals of each species. An improved understanding of the extent of morphological variation within *Laterallus*, therefore, is critical to clarifying these species occurrences. The present samples contribute to documenting the evolution of migratory and biogeographic patterns of relevant taxa. The distribution of suitable marsh habitats decreases across the SHP during the late Quaternary. These small rails appear to have been present throughout regional drainages during the late Pleistocene and early Holocene. Today, however, these species occur primarily as migrants and are confined to the few remaining isolated wetlands as well as reservoirs and other anthropogenic habitats.

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## Dinosaur Systematics, Diversity, & Biology

### A MORPHOMETRIC ANALYSIS OF DENTAL VARIATION THROUGHOUT ONTOGENY IN *JEHOLOSaurus SHANGYUANENSIS* (DINOSAURIA, ORNITHISCHIA) AND IDENTIFICATION OF TEETH FROM MICROSITES

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*Jeholosaurus shangyuanensis* was a small, herbivorous thescelosaurid that lived in the Early Cretaceous of northeastern China. Unusually for a thescelosaurid, several well-preserved skulls of this taxon have been collected, including ontogenetically immature specimens. Feeding strategy and dietary preferences may have changed over the course of ontogeny, and any such changes should be reflected in the morphology of the teeth. We use twelve linear measurements to document morphometric variation among ontogenetically immature and mature *J. shangyuanensis* individuals based on their unworn, heterodont teeth. In a principal components analysis (PCA) of the measurements, PC1 and PC2 accounted for 64% and 21% of the variation, respectively. In a canonical variates analysis (CVA), CV1 and CV2 accounted for 96% and 3% of the separation among groups, respectively, and an associated confusion matrix correctly classified 91% of the teeth. This accurate confusion matrix holds promise for assigning isolated *J. shangyuanensis* teeth to particular ontogenetic stages, although a PERMANOVA revealed no statistically significant separation among ontogenetic stages ( $F=1.247$ ,  $p(a)>0.05$ ). In both the PCA and the CVA, the premaxillary teeth of mature and immature individuals form one cluster with significant overlap, while the maxillary and dentary teeth form a second cluster, albeit with less overlap. This suggests that the feeding strategy and dietary preferences of *J. shangyuanensis* remained constant throughout life, although the distinctive morphology of the premaxillary teeth may indicate that they differed in function from the maxillary and dentary teeth. This morphometric analysis should facilitate the referral of isolated *J. shangyuanensis* teeth to specific ontogenetic stages and should serve as a basis for testing hypotheses regarding changes in diet and feeding strategy throughout ontogeny in basal neornithischians.

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**Symposium - Vertebrate dental ecomorphology: Tooth traits that reflect ecology**

**WHERE'S THE POINT? DENTAL SURFACE SHARPNESS ARISING FROM CONVEX VERSUS**

## **CONCAVE OCCLUSAL MORPHOLOGY AND IMPLICATIONS FOR INTERPRETATION OF FOSSIL PRIMATE DIET**

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Primates from the early Oligocene of North Africa include taxa that have been characterized as basal or stem catarrhines. Prior efforts to interpret their dietary ecology have consistently concluded that well-represented Egyptian Fayum taxa such as *Apidium phiomense* and *Aegyptopithecus zeuxis* from the Jebel Qatrani Fm. most likely shared a frugivorous diet on the basis of their bunodont cheek teeth, despite disparities in estimated body size and relative enamel thickness.

An increasingly popular tool for analogically interpreting fossil primate diet is Dirichlet normal energy (DNE), a measure of dental sharpness which successfully sorts prosimian and monkey molars by heuristic dietary category. Yet DNE has produced confounding results when applied to ape teeth, which are characterized by thick enamel and deep sulci between cusps. The DNE calculation does not distinguish convex crests from concave sulci, with the latter potentially drastically inflating DNE despite having little direct role in food breakdown. Here we modify DNE to sort between convex and concave contributions to total occlusal sharpness. We apply this altered metric to unworn m2s of the Fayum anthropoids *Aegyptopithecus* (N = 5) and *Apidium* (N = 6), and compare these results to a broad sample of extant primates.

Total surface DNE is significantly different between the two Fayum taxa ( $p = 0.006$ ), with *Aegyptopithecus* DNE similar to that of extant frugivores, and *Apidium* DNE similar to that of folivores. When only convex DNE is considered, the two taxa are indistinguishable ( $p = 0.5$ ), and both exhibit values similar to the convex DNE of extant frugivores. While convex parts of the dental surface account for the majority of the DNE signal among extant prosimians and monkeys, there is a much greater relative contribution from concave DNE among apes and Fayum anthropoids, with *Apidium* exhibiting the lowest average convex:concave ratio among all taxa. These findings support previous reconstructions of frugivory among Fayum anthropoids, but also highlight the importance of distinguishing surface curvature orientation

when interpreting molar sharpness. Concave DNE makes an outsized contribution to total molar sharpness in both thickly-enameled, large-bodied extant apes and the small-bodied fossil anthropoid *Apidium*, suggesting this is not purely an allometric effect, but potentially a morphological byproduct of relatively thick enamel.

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

### **FIVE STEPS OF MARINE ADAPTATION IN NON-AVIAN MARINE TETRAPODS**

Motani, Ryosuke

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Were plesiosaurs better adapted to marine life than mosasaurs? It is difficult to answer this question because there is no scale to uniformly measure the degree of marine adaptations across clades. Marine adaptation is largely a combination of two factors, aquatic and haline adaptations. Aquatic adaptation allows animals to efficiently forage in water at the cost of terrestrial locomotion, whereas haline adaptation ultimately allows animals to do without drinking fresh water. I hypothesize that marine tetrapods share the sequence in which they acquire such ecophysiological characteristics as they adapt to marine life.

I tested the hypothesis based on a literature survey of marine adaptations in 34 extant lineages of non-avian marine tetrapods. The results suggest that there is a common sequence of five steps in which aquatic and haline adaptations are acquired in combination. The steps are: (1) incipient use of marine resources; (2) direct feeding in the saline sea; (3) water balance maintenance without terrestrial fresh water; (4) minimized terrestrial travel and loss of terrestrial feeding; and (5) loss of terrestrial thermoregulation and fur maintenance. These steps do not involve evolution of viviparity since there is no example known of viviparity evolving after marine adaptation. Steps in snakes are slightly different because haline adaptation lags behind aquatic adaptation, probably due to limitations in space availability for salt glands. Osteological data for extant species suggest that the humerus is longer than the femur in those at steps 4 and 5,

whereas the forearm pronation and supination are disabled at step 5. Also, habitat data suggest that non-marine habitats are expected only in steps 1 and 2, with exceptions of some step 5 species such as river dolphins. These three pieces of information can be inferred from fossils and their geological settings, allowing us to estimate marine adaptation steps in extinct non-avian tetrapods to a large extent. Application of this principle to fossil marine tetrapods revealed, for example, that step 5 was achieved by at least four extinct lineages, namely Sauropterygia, Ichthyosauromorpha, Mosasauroida, and Thalattosuchia. Also, mapping of the estimated adaptation steps on phylogeny revealed some interesting historical patterns—lineages reaching steps 4 or 5 tend to last longer and have a high diversity, and the evolution of these steps seems to always occur early in the history of a lineage.

**Funding Sources** University of California, Davis

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## **Holocene & Pleistocene Mammalian Faunas**

### **NICHE CONSERVATISM AND DIETARY ECOLOGY OF *DASYURUS* ACROSS SPACE AND TIME**

Mueller, Elsa, Abdelmalak, Mark, DeSantis, Larisa

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The northern quoll, *Dasyurus hallucatus*, is a carnivorous marsupial that is found throughout northern Australia and has recently become endangered. Some factors believed to be involved in this include changes in fire regimes, predation, human interference, and the introduction of the invasive cane toad in the 1930s. Determining if there are variations in diet due to factors such as location or time can be useful in developing a conservation plan for the future. Diet is able to be inferred from dental microwear texture analysis, the assessment of microscopic wear patterns on teeth. Casts of tooth molds of northern quolls were analyzed using a confocal microscope and compared across space, time, and to other species of quolls. Results demonstrate that there were no significant differences in diet between quolls in the Northern Territory versus Queensland, over time, or over latitude/longitude. This supports the idea that northern quolls display 'niche conservatism' in regards to the textures of food they consume, meaning they are retaining their dietary habits over time and in disparate locations. While there are no



significant relationships between the body size of *Dasyurus hallucatus* and any DMTA attribute examined (Asfc, epLsar, Tfv), *Dasyurus hallucatus* eats softer foods than other quolls including *Dasyurus maculatus*. Further, larger quolls of the genus *Dasyurus* do eat significantly harder foods (higher Asfc values with larger body size) than smaller quolls, when examining all *Dasyurus* specimens. Thus, body size does seem to constrain hard-food eating in quolls. Collectively, these data provide insight into the dietary ecology of the smallest carnivorous quoll in Australia while also indicating conserved diets across space and time.

**Funding Sources** Funding was provided by the National Science Foundation of the USA (1053839, 1455198) and Vanderbilt University.

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### **Paleohistology & Paleopathology**

#### **ENAMEL HISTOLOGY AND DENTAL GROWTH IN THE EXTINCT CAPE ZEBRA**

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*Equus capensis*, also known as the extinct Cape zebra, was a large equid that lived in different parts of Africa from the early to the late Pleistocene. It was closely related to the extant Plains zebra (*Equus quagga*), but it had more robust limbs and taller teeth. To date, studies on *E. capensis* have mainly focused on disentangling its taxonomic position and reconstructing its diet, but little is known about other aspects of its biology. In this regard, the histological analysis of its mineralized tissues presents an opportunity to obtain information about its growth and development. Specifically, the microscopic study of dental enamel is key to understanding the pattern of dental growth and formation, which can ultimately shed light on the palaeoecology and life history of extinct animals. Here, we studied the enamel histology of four first lower molars and three third lower molars of *E. capensis* to reconstruct their rates of formation. The material studied was recovered from the middle Pleistocene palaeontological site of Elandsfontein, located in South Africa. From each tooth, we prepared longitudinal thin sections at the level of the protoconid following standard procedures. All samples were studied and analyzed under polarized light to calculate several enamel growth parameters such as daily secretion rate and

extension rate. Our preliminary results revealed similar values of enamel growth parameters for the molars of the Cape zebra and that of the extant *E. quagga*. These findings suggest that the higher degree of hypsodonty observed in the extinct African zebra likely resulted from longer teeth formation time rather than from higher rates of dental development, as described in other extant and extinct equids. Future research will focus on the precise estimation of the crown formation time of both molars, as well as on the reconstruction of their eruption time through an analysis of their enamel histology. These studies will enable a better appreciation of the paleobiology of this iconic giant zebra by providing an estimation of important life history traits of the species, such as its age at weaning and its age at skeletal maturity.

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### **Mammalian Skeletal Morphology**

#### **BARBOUROFELIS FRICKI—THE HEAD BONE IS CONNECTED TO THE NECK BONE OR HOW TO REBUILD A UNIQUE CAT**

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The sabertooth adaptation has appeared at least five times (twice in true felids, twice in pseudofelids and once in synapsids) in the evolution of carnivorans. Many hypotheses have been advanced to explain the iterative appearance of this extremely specialized adaptation. Each sabertooth taxon that is discovered in the fossil record shows unique aspects of morphology that reflect different biomechanical considerations for the use of these canines. Among the most specialized sabertooths is *Barbourofelis fricki*, the largest bodied and most recently evolved taxon belonging to the pseudocat barbourofelin lineage. Our work is focused on explaining these anatomical differences and why they are important. This lion-sized sabertooth had the longest upper canines in absolute and relative terms among all taxa so far discovered with exaggerated upper canines. *Barbourofelis fricki* is distinguished by its elongated canines that are the most slender and highly recurved upper canines among sabertooths. Although strong and sharp-edged, the narrow

shape and tapering anterior and poster edges of these canines renders them brittle, therefore requiring the highest possible precision in biting behavior to avoid breakage. This priority is reflected in many other cranial anatomical features, including a foreshortened rostrum, increased skull depth, in combination with a vertical occiput and a mandible with a reduced coronoid process and robust dependent flange. Concomitant with these cranial features is a reorientation of the masticatory muscles reflecting an increase in the dorsoventral component and the reduction of mediolateral mandibular movements. Reconstruction of the cranium of this predator demonstrated that this animal had a larger head than would have been predicted, and that modifications of the anterior cervical vertebrae also contribute to enhanced dorsoventral movements of the head on the neck in *B. fricki*. Our work demonstrates that this animal probably showed body proportions that differed significantly from previous reconstructions as well as from other sabertooths.

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## Macroecology & Macroevolution

### THE MISSING DIVERSITY OF THE DINOSAUR FOSSIL RECORD

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A large suite of research is predicated upon the assumption that the incomplete fossil record is representative of the actual diversity that existed in the past. Based on several lines of evidence, I argue that this assumption is unjustifiable. Approximately 1,300 species of non-avian dinosaurs are known from the entire Mesozoic Era. This diversity pales in comparison to that of modern diverse amniote clades. The mean species richness of diverse, disparate amniote clades in the present is  $\sim 10^4$ , while an average of only 7 non-avian dinosaurs are known from any 1 Ma interval in the Mesozoic. Controlling for body size, global non-avian dinosaur species richness at any time should be no less than  $10^3$ , indicating that our total knowledge of dinosaur diversity comprises at most 1% of their actual diversity, which was on the order of 100,000 total species. This diversity is asymmetrically distributed in time and space, with 20% of the Mesozoic Era containing over 50% of known dinosaur species, and each time interval

represented by regional localities rather than a global sample. Even the most productive strata and localities preserve clear size bias, usually (but not exclusively) favoring the preservation of large taxa. The fossil records of non-avian dinosaurs and extant amniote clades show a linear relationship between the number of species recognized and the number of fossils sampled per geologic stage, indicating that even putatively well-sampled intervals do not approach an adequate summary of regional or global biodiversity. This and coupled diversity trends among amniote clades suggest the recognized species diversity in any geological stage is purely a function of sampling. The vast quantity of missing species in the fossil record is problematic for macroevolutionary and paleoecological research, as the influence of unknown taxa is unquantifiable and consistent with an infinite number of scenarios. Field exploration and the discovery of new fossils remain critical components of paleontological research. As methods for morphological species delimitation improve, it is likely that collections of individuals currently referred to a single species will prove to represent assemblages of multiple taxa, especially when the specimens come from a wide spatial or temporal distribution. As species are continually discovered, phylogenetic topologies will likely change considerably, particularly within clades that comprise mostly small taxa such as Paraves.

**Funding Sources** This work was supported by the Newt and Calista Gingrich fund and a Richard Gilder Graduate School student fellowship.

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## Holocene & Pleistocene Mammalian Faunas

### NEW LOCALITY OF PLEISTOCENE FOSSIL VERTEBRATES FROM THE MUNICIPALITY OF JULIMES, CHIHUAHUA, MEXICO

Nava-Rodríguez, Rosalba L.<sup>2</sup>, Sylva, Hector R.<sup>1</sup>, Guzmán-Gutierrez, José Rubén<sup>1</sup>, Sánchez-Urbe, Ivan E.<sup>2</sup>, López-Díaz de León, Vanessa G.<sup>2</sup>, López-Palma, César A.<sup>2</sup>

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In 2013, a field team from the Chihuahuense Desert Museum located fossils of vertebrates in a new locality near the town of Julimes, in the State of Chihuahua, Mexico, which was assigned a late Pleistocene age

(Rancholabrean Land Mammal Age). The material was found embedded in a caliche matrix, on the banks of an intermittent stream, possibly due to a storm drainage system. To date, 22 bone elements have been rescued, prepared and identified and have been preliminarily determined as belonging to proboscidians, equids, rodents, bovids and xenarthrans.

These records provide valuable information that will allow us to make inferences about the paleoenvironments present in this region of the Chihuahuan Desert during the last stage of the ice age, and in addition increase the probability of discovering new megafaunal fossil deposits in the surrounding area.

**Funding Sources** The financial and material resources to carry out the field work during 2013 were covered by the Chihuahuense Desert Museum.

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### Colbert Poster Prize

#### A NEW CROCODYLIFORM FROM THE MID-CRETACEOUS KEM KEM GROUP OF MOROCCO DEMONSTRATES HEIGHTENED DIVERSITY IN THE PEIROSAURID LINEAGE

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Notosuchians are an extinct, speciose clade of terrestrial crocodyliforms noted for their strange, morphologically disparate bauplans, as well as their preference for a terrestrial mode of life in hot, semi-arid environments. The group has its highest apparent diversity in the middle to Late Cretaceous of Gondwana, produced largely by an abundance of South American taxa. However, despite severe and pervasive under-sampling of fossiliferous localities relative to most other continents, diverse assemblages of extinct crocodyliforms have also been discovered from several spatiotemporal intervals in Africa and Indo-Madagascar. Three notosuchian species are currently recognised from the early Late Cretaceous Kem Kem Group of Morocco: the small-bodied uruguaysuchid *Araripesuchus rattoides*, the candidodontid *Lavocatchampsia sigogneaurussellae*, and the peirosaurid *Hamadasuchus rebouli*. Here, we describe two new specimens that demonstrate the presence of a fourth

notosuchian species in this fauna. The new material is incorporated into one of the largest notosuchian-focused character-taxon matrices yet to be compiled. Comprising 443 characters and 63 notosuchian species, the matrix emphasizes increased sampling of African and peirosaurid species. Parsimony analyses run under equal and extended implied weighting ( $k=8$  and 12) consistently recover the newly identified species as a peirosaurid notosuchian. This position is supported by the presence of two distinct waves on the dorsal dentary surface, a surangular which overlaps the dentary above the mandibular fenestra, and a relatively broad mandibular symphysis. Within Peirosauridae, a rugose enamel tooth surface, a distinct concavity adjacent to the 5<sup>th</sup>–10<sup>th</sup> dentary teeth for the reception of the enlarged maxillary tooth, and an elongate contribution of the splenial to the mandibular symphysis, indicate close affinities with *Hamadasuchus rebouli*, with is recovered as the sister taxon to the newly identified species. The new specimens differ from *Hamadasuchus rebouli* with respect to the ornamentation of the lateral mandibular surface, the angle of divergence of the mandibular rami, and the texture of tooth enamel. Combined with a review of Kem Kem crocodyliform material, including several specimens previously referred to *Hamadasuchus rebouli*, we suggest the existence of at least three peirosaurid lineages within this fauna, indicating a higher Cretaceous African crocodyliform diversity than previously recognised.

**Funding Sources** Royal Society research grant (RGF\R1\180020); Palaeontological Association Undergraduate Research Bursary (PA-UB201804)

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### Non-avian Theropod Systematics, Biology, and Evolution

#### MORPHOMETRIC ANALYSIS OF NORTH AMERICAN ORNITHOMIMID MANUAL AND PEDAL UNGUALS: CAN UNGUAL SHAPE BE USED TO DISTINGUISH BETWEEN TAXA?

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Ornithomimids from the Late Cretaceous of North America have been primarily distinguished by differences in manus morphology using metacarpal ratios, the degree of ungual curvature, and general robusticity. Characters in the manual unguals are used to diagnose the two most

common genera with the manual unguals of *Ornithomimus* being relatively short and straight with weakly-developed flexor tubercles, and *Struthiomimus* manual unguals being long and strongly curved with well-developed flexor tubercles. However, pedal ungual characters such as the distinct arrowhead-shaped ventral surface appear to be shared among ornithomimids and therefore have not been considered diagnostic of any one taxon. Recently, a combined qualitative analysis of ungual shape and quantitative analysis of ungual ratios contributed to the validation of *Dromiceiomimus* as a distinct taxon in North America. This approach suggests that the quantification of ungual shape has the potential to differentiate ornithomimid taxa. There is a relative abundance of preserved manual and pedal unguals from North America and this provides an opportunity to quantify their shape in order to identify the range of morphologies and determine if shape can be used to diagnose taxa. Two-dimensional geometric morphometrics quantified manual and pedal ungual shape using a series of landmarks and sliding semi-landmarks. Landmark data was superimposed through a Generalized Procrustes Analysis and a Principal Components (PC) Analysis determined which aspects of shape contribute the greatest variation in ungual shape. PC1 (~60%) for manual unguals differentiated short and heavily curved claws versus elongate, straight, and narrow claws. When shape differences were quantified using a Procrustes ANOVA, *Ornithomimus* and *Struthiomimus* manual ungual shape was found to be significantly different. PC1 (~35%) for pedal unguals differentiated left- versus right-turning at the distal tip, and PC2 (~25%) differentiated elongate and narrow claws versus short and broader claws. No significant differences were found between genera when shape differences were quantified with a Procrustes ANOVA. These findings suggest that quantified manual ungual shape can be used to distinguish ornithomimid taxa, which may reflect functional differences in the forelimb. In contrast, pedal ungual shape may not be as useful in distinguishing between ornithomimid taxa due to the conserved cursorial pattern of the ornithomimid hindlimb.

**Funding Sources** NSERC PGS-D, QEII Doctoral Scholarship, Alberta Historical Resources Foundation Roger Soderstrom Scholarship

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## Holocene & Pleistocene Mammalian Faunas

## HIGH-ELEVATION CENSUS OF MONTANE ECOSYSTEMS: ECOLOGICAL IMPLICATIONS FOR QUATERNARY VERTEBRATES FROM BOOMERANG CAVE, UTAH, U.S.A.

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Deposits of vertebrate remains are increasingly recognized as a powerful tool for censusing wildlife populations, supplementing traditional zoological survey techniques (e.g., trapping, camera traps, aerial census) by providing observations spanning larger temporal scales. We describe a Quaternary paleontological assemblage from Boomerang Cave in the Bear River Range of Cache County, northern Utah, U.S.A., at an elevation of 2231 m. The site is a limestone cave with a >40 m vertical entrance forming a natural trap alongside multiple other vertical chambers, each containing vertebrate fossils. Local habitats range from forested mountains dominated by fir, Douglas-fir, spruce, and aspen at the cave elevation, to lower elevation semiarid foothills and valleys dominated by pinyon-juniper woodland and sagebrush. Vegetation is supported largely by snowmelt and via perennial streams hosting an array of resident and summer migrant species.

We analyze 1245 surface-collected specimens from four main chambers within the cave: a single *Ursus americanus* ulna is fully lithified and likely dates to the Pleistocene, whereas most specimens are recent (late Holocene). Many are well-preserved due to the stable, cool cave environment, low disturbance, and protective coatings of calcite. We identified a minimum of 23 non-overlapping taxa (22 mammals, one bird), with 16 mammals identified to species. These comprise seven of the eight functional groups of mammals in the region: terrestrial herbivores, terrestrial omnivores, terrestrial carnivores, arboreal herbivores, arboreal omnivores, volant carnivores, and semiaquatic carnivores, with only semiaquatic herbivores missing. Of particular importance is the cave's diverse carnivoran assemblage, preserving at least nine taxa.

Our dataset was then compared to mammalian museum specimen data from VertNet from the Bear River Range.

We find that the traditional census methods under-sample taxonomic and functional diversity. This is particularly apparent for Carnivora, which are rare in zoological assemblages but well-sampled in the cave assemblage. We attribute this to the more random nature of natural trap cave deposition removing accumulation biases due to size and/or diet. This supports the importance of skeletal deposits for censusing of terrestrial ecosystems.

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## Avialan Evolution & Biology

### FIRST AVIAN SKULLS FROM THE LOWER CRETACEOUS XIAGOU FORMATION, GANSU, CHINA

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We describe six specimens consisting of cranial remains with associated presacral vertebrae belonging to ornithuromorph birds from the Changma locality of the Lower Cretaceous (Aptian) Xiagou Formation of northwestern Gansu Province, China, four of which were preliminarily reported at SVP in 2009. Comparison between specimens is limited by the paucity of overlapping elements, their differing exposed views, and, in some specimens, poor preservation. Of previously described Changma ornithuromorph taxa, only *Gansus yumenensis* can be compared to any of the new specimens, specifically the three that preserve the caudal-most cervical and cranial thoracic vertebrae. Despite the fact that *G. yumenensis* is numerically dominant at Changma, whereas all other ornithuromorph taxa from the site are known from single specimens, the six fossils described here clearly pertain to at least three taxa as evidenced by differences in the dentary dentition. Namely, the dentary of one specimen is edentulous, another has sharp, closely spaced, fairly high-crowned and peg-like teeth, and a third preserves blunt, relatively low-crowned teeth placed in a communal groove, a

morphology previously reported only in Hesperornithiformes among adult birds. The high-crowned specimen is tentatively referred to *G. yumenensis* based on similarities to the closely related *Iteravis huchzermeyeri*, including closely comparable dentition and an edentulous premaxilla with elongate, unfused frontal processes and no palatal processes. The variation in dental morphology observed among the new Xiagou Formation ornithuromorph specimens hints at a trophic diversity similar to that observed in ornithuromorphs from the penecontemporaneous Jehol Group of northeastern China.

**Funding Sources** Strategic Priority Research Program CAS; National Natural Science Foundation; Chinese National Natural Science Foundation.

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## Marine Mammals

### THE RELATIONSHIP BETWEEN THE POSTURE OF FLIPPERS AND THE PRESENCE OF DORSAL FINS LEADING TO THE RECONSTRUCTION OF THE DORSAL FIN IN SMALL CETACEANS: THE CONTRIBUTION OF FINS TO LATERAL/DIHEDRAL INHERENT STABILITY

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The morphology of the dorsal fin in small cetaceans varies widely, and several lineages lack dorsal fins. The reconstruction of the dorsal fin is important for understanding the evolution of ecology and behavior of extinct cetaceans because the fin is related to postural stability in water. However, the dorsal fin of cetaceans is extremely difficult to reconstruct from fossils because it is composed of soft tissue. In this study, we investigated the relationship between the posture of the pectoral fins and the presence of dorsal fins based on the dihedral angle effect, which contributes to lateral/directional inherent stability. We measured the dihedral angle of flippers during straight-line swimming in five captive species, including two species lacking dorsal fins, in two aquariums. According to the results, all measured species maintained their flippers at a specific negative dihedral

angle during straight-line swimming, and species without dorsal fins swam with the dihedral angle of their fins more horizontal to the lateral axis than species with dorsal fins. The rolling moment generated by the dihedral angle effect of flippers and dorsal fins was roughly the same small roll-promoting moment for all species. Small cetaceans are assumed to have either left and right flippers with dihedral angles close to parallel to the lateral axis or dorsal fin features in order to reduce the roll-promoting moment. The differences in the posture of flippers in small cetaceans are also reflected in the morphology of the humerus and shoulder joint. Therefore, the relationship between the posture of flippers and the presence of a dorsal fin could be an extremely powerful tool to reconstruct the dorsal fins of extinct cetaceans in terms of lateral/directional inherent stability.

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## Mesozoic & Paleogene Mammals

### A NEW MAMMAL FOSSIL FROM THE UPPER CRETACEOUS BAYNSHIRE FORMATION, GOBI DESERT, MONGOLIA

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Numerous exquisitely preserved mammal fossils recovered from Upper Cretaceous strata in the Gobi Desert of Mongolia have played a key role in understanding Mesozoic mammalian evolution. These splendid mammal fossils have been recovered from the Barungoyot, Djadokhta, and Nemegt formations, but only one fragmentary dentary of a metatherian mammal has been collected from the underlying Baynshire Formation. Here we report a new mammal specimen recently discovered from the Baynshire Formation at the Bayn Shire locality.

The new specimen is a partial but well-preserved right dentary that possesses the distal portion of a premolar and three complete molars, suggesting it belongs to Eutheria. The following molar characters show zhelestid affinity: protoconid height is subequal to the metaconid, and the hypoconulid is located close to the entoconid. The phylogenetic analyses were performed based on multiple published data matrices, and this new specimen is consistently recovered as a member of Zhelestidae. Furthermore, the new specimen was included in Zhelestinae in some iterations. The phylogenetic analyses also revealed that this specimen has a unique character combination (e.g., morphology of the hypoconulid and proportion of molar sizes) that is not observed in other zhelestid specimens, suggesting that this dentary represents a new taxon.

Zhelestidae was widely distributed from Eurasia to North America in the Late Cretaceous but has not previously been recovered in the abundant Mesozoic mammalian fauna of Mongolia. Previous studies hypothesized that the lack of zhelestids in Mongolian Upper Cretaceous strata was caused by environmental factors (i.e., more arid and inland setting compared to other zhelestid localities) and/or competition with multituberculates, which are abundant in these strata. The new zhelestid from the Baynshire Formation indicates that this clade was also distributed in the arid and inland region, but the hypothesis of competition between zhelestid and multituberculates remains to be tested.

**Funding Sources** Grants-in-Aid for Scientific Research by JSPS; Private University Research Branding Project by MEXT, Japan

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## Holocene & Pleistocene Mammalian Faunas

### PATTERNS OF RELATIVE ABUNDANCE AMONG LARGE CARNIVORANS IN WESTERN EURASIA DURING THE PLIO-PLEISTOCENE

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The present-day large carnivoran metacommunity in western Eurasia is functionally impoverished of large hypercarnivores due to late Pleistocene megafaunal extinctions and Holocene range contractions. However, major taxonomic changes in regional large carnivoran faunas also occurred earlier between the Pliocene and the

beginning of the late Pleistocene. The roles of climate change and interspecific competition in these earlier changes are not well understood.

I estimated relative abundances for large (<7 kg) carnivorans in western Eurasia belonging in the families Canidae, Felidae, Hyaenidae and Ursidae using relative locality coverage (occupancy). The fossil localities were sampled within six temporal intervals, spanning from the early Pliocene until the beginning of the late Pleistocene. The aims of this study were twofold. First, to infer competitive relationships within the different carnivoran families that include hypercarnivores (Canidae, Felidae and Hyaenidae) based on their occupancy trajectories. Second, to examine how the family-level patterns influenced the proportion of hypercarnivores at the metacommunity level over time.

The results indicate differences in coexistence potential between different types of hypercarnivores. Large felids, including both sabre-toothed and conical-toothed forms, generally have broadly overlapping occupancy trajectories. This suggests that while many of the felid taxa responded individually to climate change, they were ecologically buffered against competitive exclusion. In contrast to the felids, the occupancy trajectories of bone-cracking hyaenids overlap less extensively, suggesting limited coexistence potential with each other. The occupancy trajectories in the Canidae in turn seem almost independent from each other. At the community level, both the number of common carnivorans and the proportion of hypercarnivores among them increased from the Pliocene to the early Pleistocene. This trend reversed again during the middle Pleistocene. The most common middle Pleistocene carnivorans mainly belonged in different families, emphasizing different survival strategies in seasonally cold environments.

The results highlight an interplay of climate change and interspecific competition as regulators of large carnivoran community structure over time.

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## Holocene & Pleistocene Mammalian Faunas

### ONTOGENETIC GROWTH IN THE PLEISTOCENE PRONGHORN *STOCKOCEROS* FROM SAN JOSECITO CAVE, MEXICO

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In 1943, Furlong first described large samples of adult and juvenile limbs of the Pleistocene pronghorn *Stockoceros conklingi* from San Josecito Cave, Nuevo Leon Province, Mexico (now in the collections of the Natural History Museum of Los Angeles County). The abundance of juvenile specimens allows the determination of growth trends in ontogeny, and the comparison of growth trends in other pronghorns. We measured the four main limb bones (humerus, radius-ulna, femur, tibia), taking both the length of the bone (minus epiphyses in juveniles) and the midshaft circumference (following the conventions of Kilbourne and Makovicky from 2012). Sample sizes were as follows: 105 humeri, 122 radius-ulnae, 64 femora, 60 tibiae. The Reduced Major Axis (RMA) fit was then calculated for all four limbs using both R and PAST software (RMA is more appropriate than a Least Squares Correlation, because there is no dependent or independent variable). All four limb bones showed slopes that were less than 1.0, suggesting that their growth is negatively allometric, growing thicker as they mature, rather than more gracile or growing isometrically (humerus slope = 0.82; radius-ulna = 0.73; femur = 0.88; tibia = 0.89). The RMA run in R software determined that all four limbs were significantly more robust, but in the PAST software, only the radius-ulna was significantly distinct from the isometric slope of 1.0, using 95% bootstrapped confidence intervals. This might be because the  $r^2$  value for some of these slopes was low (0.5), although others were quite high (0.8 to 0.9 for most of them). This is very similar to the modern *Antilocapra americana*, which was significantly more robust in three limbs, and only isometric in the radius, according to Prothero and colleagues. Similar studies should be undertaken on extinct pronghorns with abundant juvenile limb elements to see if there is an overall pattern in antilocaprids.

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## Paleohistology & Paleopathology

## **OSTEOHISTOLOGICAL DESCRIPTION OF OSTRICH AND EMU LONG BONES, WITH COMMENTS ON POTENTIAL GROWTH MARKS**

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Ostriches and emus are the largest extant birds, and are frequently used as a modern analog for the growth dynamics of non-avian theropod dinosaurs. These raptines reach adult size in less than one year, and as such do not typically exhibit annually-deposited growth marks. Growth marks, delineated into annuli or lines of arrested growth, represent the reduction and outright cessation of osteogenesis rates, respectively. Growth marks have not yet been reported from ostriches and emus, prompting authors to suggest that they lack the developmental plasticity required to deposit them. Here we describe the complete hind limb bone histology of three captive juvenile emus and one captive adult ostrich. Two of three juvenile emus exhibit unremarkable bone histology but are summarized for comparison. The third emu, a 4.5 month old juvenile, exhibits a tibia with a regional arc of avascular tissue, which we interpret as a localized growth mark. As this mark co-occurs with a contralateral broken fibula, we suggest variable biomechanical load as a potential cause. The ostrich exhibits a complete ring of avascular, hypermineralized bone with sparse, flattened osteocyte lacunae. We identify this as an annulus and interpret it as a skeleton-wide slowing of growth. These findings demonstrate that both taxa retain the developmental plasticity required to temporarily slow growth. We propose physiological stress, late hatching seasons, or protracted growth as potential causes for the deposition of these structures. We also discuss potential challenges of identifying growth marks using captive populations, incomplete population data sets and partial cortical sampling.

**Funding Sources** Oklahoma State University

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### **Paleohistology & Paleopathology**

## **THE HISTOLOGY OF ORNAMENTED TRIONYCHOID SHELLS FROM THE KAIPAROWITS FORMATION OF UTAH**

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In the Late Cretaceous Kaiparowits Formation of Utah, upwards of 14 species of turtles can be found. Because specimens are often fragmentary, surficial ornamentation is frequently used to generically identify shell material. Despite this, ontogenetic and phylogenetic variation is still poorly understood on a histological level, especially in the Kaiparowits Formation. To remedy this, five Kaiparowits turtle genera from multiple ontogenetic stages have been described herein to understand how the shell grows, and how this process varies taxonomically. Across ontogeny, sampled trionychids exhibit relatively consistent histological anatomy. The Upper External Cortex (UECO) shows a highly vascularized basal ornament overlain by fibrolamellar bone that is sparsely remodeled by radial primary vascularization and Sharpey's Fibers (SF). The Lower External Cortex (LECO) consists of structural collagen fiber bundles in alternating layers that resemble plywood. The morphological and distributional regularity of the Medullary Cavity (MC) canals vary with ontogeny. The Internal Cortex (ICO) shows some radially-decreasing primary vascularization, but is otherwise laminar. Ornament migration, vascularization and resorption are more apparent with taxa that exhibit distinct external ornamental morphology (*Basilemys*), but more subtly ornamented taxa (*Adocus*) display similar, albeit subtle features. Consistent with previous studies, the relative thickness and vascularization of cortices appear heavily influenced by ecology. Genera that are inferred to be terrestrial (*Basilemys*) exhibit relatively thick and avascular cortices, whereas aquatic (*Adocus*) and semiaquatic (trionychid) genera exhibit relatively thin, vascularized cortices. The trionychid plywood-like structure expands externally, with additional layers being added along the distal margins of the shell. In contrast, the adocusian lower external cortex consists of a dense mat of secondary osteons that frames the medullary cavity. All examined taxa exhibit externally-expanding MCs with canals that preferentially remodel ISF bundles between denser LAGs. The ICO grows radially outward at a slow and consistent rate. In summation, the external ornament morphology is alpha-taxonomically diagnostic, but the histological processes that create it are not. Ecology is the primary determinant of relative zonal thickness and can



be used to supplement taxonomic classifications based exclusively on external ornament morphology.

**Funding Sources** University of Utah Office of Undergraduate Research, The Natural History Museum of Utah, The College of Mines and Earth Sciences, and Oklahoma State University

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## Education & Outreach

### IMPACT OF EXPERIENTIAL VIRTUAL DINOSAUR EXCAVATION ASSIGNMENTS ON EXAM PERFORMANCE IN AN INTRODUCTORY, UNIVERSITY-LEVEL COURSE ON DINOSAURS

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Advocates assert that experiential/applicational learning facilitates deep understanding. Nevertheless, there is a dearth of empirical research testing the effectiveness of experiential learning in university geology and paleontology courses. Although previous workers documented applicational assignments within such courses, these studies were based solely on instructor opinion and informal student comments. To evaluate the effectiveness of experiential assignments we designed a study that utilizes empirical data from control and test groups in each of two semesters of a general education course on dinosaurs. Pretests showed no significant difference in prior knowledge between test and control groups. Control groups completed traditional research papers. The papers were replaced in the test groups by experiential assignments: virtual dinosaur quarry excavations consisting of stylized quarry maps and field notes students studied to answer questions pertaining to taphonomy, taxonomy, phylogeny, paleoenvironment, etc. In the first semester, there was no statistical difference in exam scores between the control and test groups. For the second semester, the experiential assignment was redesigned for clarity and the test group scored 4.8% better on average on exams than the control group. Post-exam questionnaires revealed that the test groups in both semesters of the study felt the experiential assignments provided significant exam preparation, an opinion not shared by the control groups' experience with term papers.

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## Stem Tetrapod, Squamate, & Amphibian Diversity & Biology

### OLD THINGS ARE NEW AGAIN: *WHATCHEERIA*, *AYTONERPETON*, AND A TOURNAISIAN TETRAPOD CROWN

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Since its initial description, *Whatcheeria* has become the poster child of post-Devonian stem tetrapods. But this consensus is matched by uncertainty about the broader membership of the apical stretch of the stem lineage: *Whatcheeria*, in general, is the 'safe' pick while other genera and families flip in and out of the crown. Here, we take advantage of the new postcranial redescription of *Whatcheeria* to re-examine these relationships and explore patterns of tetrapod clades and characters close to the crown node.

A new dataset assembled around *Whatcheeria* provides strong corroboration of the sister group relationship with *Pederpes*, and that this clade, the Whatcheeriidae, is, in turn, the sister group to all post-Devonian tetrapods (excluding finned relatives). However, the Viséan genus *Ossinodus*, although often presented as a whatcheeriid, is likely not a member of the same group and instead provides a glimpse of an as-yet undersampled Mississippian- or earlier- tetrapod radiation. Further to this, we find no close links between *Whatcheeria* and another group of putative close relatives, the anthracosaurs. Anthracosaurs (whole or in part), 'lepospondyls' (whole or in part), and colosteids are clustered with early members of the amniote and amphibian total groups. In summary, our results increase crown membership at the expense of the stem, and the baphetids remain as the only limbed clade other than the whatcheeriids excluded from the tetrapod crown. In these trees, support for the tetrapod crown node remains weak and the branching structure throughout much of the tree is unstable. In our estimates, *Caerorhachis* and the colosteids might not be far removed from conditions at the crown node. Their current placement implies fewer steps between the basal-branching members of the crown group and the most crownward stem members. Of particular interest, in results of reweighted analyses, colosteids are joined by

*Aytonerpeton*, previously mooted as a colosteid, and these are coupled with the temnospondyls. The Tournaisian age of *Aytonerpeton* suggests that this more inclusive crown group is older than previous Visean dates, pegged by the diversity of tetrapod clades known from East Kirkton. Correspondingly, this earlier, albeit tentative, minimum date implies a much greater range of Tournaisian tetrapods than currently recognized.

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## Fishes Evolution & Distribution

### A MASS DEATH ASSEMBLAGE OF JUVENILE SEMIONOTIFORM FISHES (NEOPTERYGII: HOLOSTEI) FROM THE REDONDA FORMATION, DOCKUM GROUP, NEW MEXICO

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Ray-finned fishes from the order Semionotiformes are a group with a global distribution and range in age from the Early Triassic to Early Cretaceous. In North America, notable geologic formations preserving semionotiform fishes include the Upper Triassic–Lower Jurassic Newark Supergroup of the eastern United States and Canada, and the Upper Triassic Chinle Formation of the southwestern United States. Specimens are also reported from the Upper Triassic Dockum Group of New Mexico and Texas, but many remain undescribed or are incomplete specimens. In this study we describe a set of large blocks of fine-grained sandstone that contain hundreds of semionotiform fishes from the Redonda Formation, Dockum Group (221–206 Ma) from northeastern New Mexico. The specimens are all small (~5 cm), and most are preserved in lateral view. The size of the specimens compared to other known semionotiforms from the Chinle Formation and Dockum Group, as well as the preserved thickness of the ganoid enamel suggests that these fishes represent juveniles. We describe the anatomy and morphology of the specimens present on these blocks and identify them to a putative new species. We hypothesize that these blocks represent a mass death assemblage of juvenile semionotids, and they provide important information regarding the reproductive behaviors and ecological niches of semionotiforms in the early

Mesozoic. We examine and describe the paleoecology of the site.

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## Stem Tetrapod, Squamate, & Amphibian Diversity & Biology

### NEW BOOID SNAKES FROM THE MIDDLE EOCENE (LUTETIAN) FOSSIL KONSERVAT LAGERSTÄTTE GEISELTAL, SAXONY-ANHALT, GERMANY

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Articulated remains of fossil snakes are extremely rare and known from only a handful of localities globally. One such locality is the middle Eocene fossil lagerstätte of Geiseltal, located about 300 km northeast of the more famous locality of Messel, in the state of Saxony-Anhalt, Germany. Here, coal deposits (lignite) yielded a great quantity of exceptionally well-preserved fossils. We studied two of the best-preserved fossil snakes from Geiseltal, GMH-LIX-3-1992 and GMH-XXXVIII-20-1964, curated in the Geiseltal Museum (GMH) (Halle, Saxony-Anhalt, Germany). The fossils were examined, photographed and microCT scanned using a Tomoscope HV 500-Werth at the Fraunhofer-Entwicklungszentrum Röntgentechnik EZRT of the Fraunhofer-Institut für Integrierte Schaltungen IIS in Deggendorf, Bavaria, Germany. The CT data were analysed in Avizo Lite 9.0, where the individual bones were digitally isolated via segmentation for anatomical description and comparative analyses. The snakes could be confidently identified as booids based on general morphology, and were thus compared to other geographically and/or temporally close fossil snakes in this group. We found that GMH-LIX-3-1992 is morphologically very similar to *Eoconstrictor*

*fischeri*, from the middle Eocene of Messel (47 Mya), but differs in the number of labial foramina in the maxilla (3 vs. 1) and in the position of the mental foramen (below 5<sup>th</sup> tooth alveolus in *E. fischeri* vs. below the 4<sup>th</sup> in GMH-LIX-3-1992). We believe that these differences indicate a new species in the genus *Eoconstrictor*. GMH-XXXVIII-20-1964 is very similar to GMH-LIX-3-1992, and differs from the latter only in features that can potentially be attributed to ontogeny (the former is ~30% larger). We performed phylogenetic analyses using maximum parsimony and Bayesian inference on datasets inclusive of both morphological and molecular data for all major lineages of snakes. The results support a close affinity of these two specimens to *Eoconstrictor fischeri*, and place both fossils at the base of the evolutionary radiation of a clade inclusive of Central American, South American, and Malagasy boids, suggesting the potential importance of the northern hemisphere for the early evolution of boids.

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## **Taphonomy, Paleoenvironments, & Stratigraphy**

### **VERTEBRATE PALEONTOLOGICAL RECORD OF THE NON-MARINE CENOMANIAN-SANTONIAN FRONTIER FORMATION OF SOUTHWESTERN MONTANA**

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The iconic Cretaceous terrestrial fauna of North America has primarily been described from Lower and uppermost (Campanian–Maastrichtian) Cretaceous deposits, whereas that of the Cenomanian through Santonian remains only partially documented. Recent studies have suggested that this interval may represent the key to understanding the evolutionary transition from Lower to the uppermost Cretaceous terrestrial faunas. Novel discoveries from the mid Cenomanian–early Santonian deposits of the non-marine Frontier Formation in southwestern Montana have revealed a rich fossil record consisting of dinosaur eggshells, dinosaurian and non-dinosaurian remains, and an abundant dinosaur track assemblage. Dinosaur eggshells consist of at least three morphotypes: smooth, bumpy, and reticularly ornamented. Morphotypes with

bumpy (dispersituberculate) ornamentation may be assigned to oviraptorosaurs; those with a more reticular pattern may be tentatively assigned to dromaeosaurids. Dinosaur remains include fragmentary material assigned to hadrosauroid and theropod dinosaurs. Non-dinosaurian specimens consist of undetermined crocodylian teeth and partial shells assigned to the freshwater baenid turtle *Neurankylus* sp. Dinosaur tracks represent ornithopods, theropods and thyreophorans. Eggshell sites occur in the lower Frontier Formation, but a specific age is still uncertain. Bone localities and the dinosaur tracks record from the middle Frontier Formation have been assigned to the Coniacian based on lithological, palynological, and absolute age dating. The Frontier Formation paleontological record reflects similarities with temporally equivalent formations of the North American Western Interior. The eggshell material reported in the lower Frontier Formation is akin to that reported in older Albian–Cenomanian Wayan and Cedar Mountain formations. Presence of hadrosauroid and thyreophoran dinosaurs also indicate affinity with equivalent Turonian and Coniacian formations. Occurrence of the family Baenidae may reflect increasing endemism, as the genus *Neurankylus* is characteristic of North American uppermost Cretaceous formations. The Frontier Formation represents about 10 myr of non-marine sedimentation in a rapidly subsiding foreland basin. Its paleontological record could represent a critical source of data to understand the evolution of terrestrial ecosystems across the Upper Cretaceous.

**Funding Sources** This research was supported by the Montana Geological Society

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## **Macroecology & Macroevolution**

### **LONG-TERM STABILITY OF INDIVIDUAL DIETARY SPECIALIZATION IN HERBIVOROUS MAMMALS**

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Diet is a fundamental aspect of the ecological niche. Although the niche is classically conceptualized at the species level, the dietary breadth of a generalist species comes down to whether individuals are generalists (high intra-individual/low inter-individual variation) or if individuals are specialists (low intra-individual/high inter-individual variation). Food selection at the individual scale impacts biotic interactions from within populations to landscapes. Degree of individual specialization has implications for inter/intraspecific competition, carrying capacity, and population stability, and thus impacts evolutionary outcomes. The existence of species with, overall, generalized diets that are composed of dietarily specialized individuals has been demonstrated in some modern species, notably humans. But, the generality of this phenomenon is unknown. We explore individual specialization among herbivorous mammals (Artiodactyls, Perissodactyls, and Proboscideans) through the analysis of serially sampled stable carbon isotopes ( $\delta^{13}\text{C}$ ) from tooth enamel. We sampled new individuals and gathered published values from the Miocene to the present (318 individuals summarized, 4,134 serial samples) to examine how dietary strategy affects individual isotopic variation. Almost all herbivore species, regardless of their overall dietary strategy, are composed of individual specialists. This finding holds through time, even within taxa exhibiting high intraspecific dietary breadth. For example, *Cormohipparion emsliei* (Equidae) from the Pliocene of Florida (~5 Ma) exhibits an overall  $\delta^{13}\text{C}$  enamel range of 13.4‰, but sampled individuals have  $\delta^{13}\text{C}$  enamel ranges of  $\leq 2\%$  (mean = 1.1‰). This pattern also holds globally, with almost all individuals (>80%) exhibiting narrow  $\delta^{13}\text{C}$  enamel ranges ( $\leq 3\%$ ), demonstrating that diets of individuals are typically specialized and not representative of the overall dietary breadth of a species. Less than 6% of individuals have dietary breadths >5‰, and these are all from grazing species. Although mixed-feeding species tend to have diets that are isotopically generalized, there are no significant differences between mixed-feeding and browsing individuals regarding  $\delta^{13}\text{C}$  breadth. Our study demonstrates that almost all herbivore individuals specialize on a narrow range of food types throughout their lives and this common ecological phenomenon has been shaping interactions and

evolutionary processes across the globe for millions of years.

**Funding Sources** This work was supported by the National Science Foundation (EAR1725154).

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## Dinosaur Systematics, Diversity, & Biology

### A NEW SPECIMEN OF *TARCHIA GIGANTEUS* FROM THE UPPER CRETACEOUS NEMEGT FORMATION OF MONGOLIA, WITH EVIDENCE OF AGNOSTIC BEHAVIOR AND NICHE SHIFTS IN ARMORED DINOSAURS

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A new specimen of the ankylosaurid dinosaur *Tarchia giganteus* (MPC-D 100/1353) was collected from the Upper Cretaceous Nemegt Formation in Hermin Tsav, southern Gobi Desert, Mongolia, during the Korea-Mongolia International Dinosaur Expedition (KID) in 2008. The specimen includes a well-preserved skull, dorsal, sacral, caudal vertebrae, sixteen dorsal ribs, ilia, free osteoderms, and a tail club. Evidence of fracture healing is preserved on both sides of the first dorsosacral rib, the anterolateral part of the pelvic area. Localized injuries on the pelvis in ankylosaurids were suggested to have been caused by intraspecific combat, possibly inflicted by the tail club knob. A poorly healed ossified tendon on the tail knob handle in MPC-D 100/1353 suggests another possible injury due to active tail use during combat. Based on beak morphology, *T. giganteus* is considered a mixed feeder, switching between grazing and browsing. Mongolian ankylosaurids specialized in grazing were present before the Nemegt and the

Baruungoyot “time” (middle Campanian–lower Maastrichtian). However, all ankylosaurines from the Nemegt and the Baruungoyot formations are adapted for browsing or mix feeding. This niche shift in ankylosaurines might have been a response to habitat change, from semi-arid and arid to more humid environments, which caused intense competition among other grazing dinosaurs.

**Funding Sources** National Research Foundation of Korea (grant number 2019R1A2B5B02070240) to Yuong-Nam Lee

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### **Colbert Poster Prize**

#### **REPTILE BODY SIZE HISTORIES IN THE TURKANA BASIN: INFLUENCES OF LOCAL HABITAT CHANGE**

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The vertebrate fossil record of East Africa has been intensely studied due to interest in hominid evolution, but few studies have examined its reptile records, which are abundant at sites from the Miocene, Pliocene, and Pleistocene. Reptiles differ from mammals in their ecologies and, as body size is important for thermoregulation in poikilotherms, potentially exhibit stronger relationships between their body size and climate. We investigated the utility of this reptile record for reconstruction of paleohabitats, focusing on crocodylians and turtles from the Turkana Basin in Kenya and Ethiopia. We measured specimens during fieldwork in the Shungura Formation and West Turkana, as well as from the collections at the National Museum of Ethiopia and the Nairobi National Museum, to estimate body sizes from over 30 sites and compared this size record to published isotope records and reconstructions of climate and lake levels in Lake Turkana.

Notable giant specimens include Pleistocene tortoises with carapaces up to 1.6 m in length, and Pliocene *Euthecodon*, an extremely longirostrine crocodylian, with 1.6 m skull lengths, corresponding to a total body length upwards of 10 m. We examined maximum crocodylian and turtle body size through time and found no long-term trends in size change from the Miocene through the Pleistocene; shifts towards a more arid climate in East Africa over this period do not seem to have affected size

in these reptiles. In the Shungura Formation (southwest Ethiopia), local habitat conditions do correspond with changes in reptile body size. The largest Shungura aquatic reptiles come from members where reconstructed lake levels are higher, with the largest-bodied *Euthecodon* present during the Lorenyang lake highstand. Testudinid size at the start of this lake highstand is less than half that of the largest Shungura specimens, despite high turtle sampling in those members. Comparison to  $\delta^{13}\text{C}$  isotope records from paleosols in the formation shows that this drop in testudinid size occurred as wooded vegetation cover was spreading in the Omo Valley. This indicates that growth to large sizes in terrestrial tortoises depended on the availability of open habitats, while crocodylian size increased when larger lake areas were present. Reptile body size is linked to available habitats in this local section. The lack of regional size trends suggests that this influence of local conditions overwhelms that of potential regional to global environmental drivers.

**Funding Sources** AKP PhD funding: Harvard Herchel Smith Scholarship. Fieldwork funding: Emmanuel College Panton Trust Grant and University of Cambridge Worts Travelling Scholars Award.

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### **Romer Prize**

#### **CEREBRAL REORGANIZATION IN OLD WORLD MONKEYS (CERCOPITHECOIDEA): NEW APPROACHES QUANTIFYING TEMPORAL LOBE EVOLUTION**

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In paleobiology, differences in cerebral proportions can indicate cerebral reorganization. Extant Old-World Monkeys (Cercopithecoidea) have larger brain sizes (absolutely) compared to fossil catarrhines; however, whether there is a relative increase or decrease in temporal lobe size is uncertain. The temporal lobes of the brain are in close spatial proximity to the middle cranial fossa (MCF) of the basicranium allowing prediction of temporal lobe volume (TLV). Computed Tomography (CT) and Micro-Computed Tomography ( $\mu\text{CT}$ ) cranial scans were generated into 3D virtual crania and 6 MCF metrics used to predict TLV. A multivariate regression of 11 extant anthropoid species (N=135) examined the

correlation between TLV and MCF metrics confirming prediction was reasonable. Predicted body mass (BM) from maxillary M<sup>2</sup> crown surface, predicted TLV and hemisphere volume (HV) from extant cercopithecines (n=20) *Macaca mulatta*, *Cercocebus atys*, *Papio anubis*, fossil African Early Oligocene anthropoids (n=7), *Apidium phiomense*, *Parapithecus grangeri*, *Aegyptopithecus zeuxis*, Miocene catarrhine (n=1) *Victoriapithecus macinnesi* and Pleistocene cercopithecines (n=3) *Dinopithecus ingens* and *Papio angusticeps* were natural log-transformed. A multivariate regression examined the association between predicted TLV and HV, and predicted TLV, HV and predicted BM in fossil and extant taxa. Results indicated *P. anubis* had a smaller TLV and HV for body size, *M. mulatta* and *C. atys* had a larger TLV and HV for body size, and all extant cercopithecines had proportionally smaller TLV for brain size. In fossil taxa, *Ap. phiomense* had a larger TLV and HV for body size, *Pa. grangeri* had a smaller TLV and HV for body size, *D. ingens* had a larger HV for body size, *V. macinnesi* had a smaller TLV but larger HV for body size, while *A. zeuxis* had a smaller HV for body size with variable TLV relative to body size, and similar intraspecific variation in TLV and HV relative to body size in *P. angusticeps*. Most fossil taxa had proportionally smaller TLV for brain size except *P. angusticeps* and *A. zeuxis* where intraspecific variation was noted, potentially influenced by size-related sexual dimorphism. The temporal lobes in extant and fossil taxa were relatively smaller for brain size, but relative temporal lobe size to body size was variable across extant and fossil species. This study provides the first quantification of relative changes to temporal lobe size in the Cercopithecoidea.

**Funding Sources** Australian Government Research Training Program Scholarship (2016-Present)

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## Permo-Triassic Ecosystems

### RHYNCHOSAUR RELATIVITY: NEW STENAUORHYNCHINES FROM THE MID-LUANGWA BASIN, ZAMBIA, AND THE EVOLVING BIOSTRATIGRAPHY OF VERTEBRATE ASSEMBLAGES AT THE MIDDLE-LATE TRIASSIC BOUNDARY

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The Triassic Period was a time of critical importance: ecosystems recovered from the largest mass extinction and established patterns of Mesozoic biodiversity. The utility of the Triassic fossil record for testing hypotheses related to ecosystem recovery, the radiation of major clades, or macroevolutionary patterns is severely hampered by a paucity of radiometric ages for important fossil-bearing formations. Instead, vertebrate fossil assemblages, particularly in southern Pangea, are linked to one another via biostratigraphic correlations that are becoming increasingly refined. Dates from South American formations temporally calibrate some of these links and strongly imply that the traditional Anisian (early Middle Triassic) assemblages of Africa are much younger, and at least partly Late Triassic in age. The Luangwa Basin in Zambia is a rich source of terrestrial and freshwater vertebrates from Lopingian and Triassic times. Triassic fossils were first identified in the northern reaches of the basin, and two assemblages have been delineated: a lower assemblage; and an upper assemblage with traversodontid cynodonts, stahleckeriid dicynodonts, and diverse archosaurs. The middle portion of the basin contains more expansive exposures of fossiliferous sediments and to date only the upper Triassic assemblage had been found there, low in section and near the unconformable contact with the underlying Permian strata .

In 2018 and 2019, our team collected fossils and stratigraphic information from the Triassic of the mid-Luangwa Basin. Notably, 15 km west from the known upper assemblage and stratigraphically higher we found the first rhynchosaurs from Zambia. Several partial dentaries possess the following character states that refer them to Stenaulorhynchinae: two parallel rows of teeth on the dentary, with a crowded field of teeth expanding posteriorly in the lingual row. Previously, the absence of rhynchosaurs in Zambia challenged correlations with the mid-upper Lifua Member of the Manda Beds in Tanzania, where the stenaulorhynchine *Stenaulorhynchus* makes up ~20% of the assemblage. Additionally, the presence of

these rhynchosaurs high in the Zambian section reinforces biostratigraphic links with Ladinian–Carnian stenaurohynchine-bearing assemblages in South America established via cynodont and dicynodont taxa: *Tarjadia* Assemblage Zone (AZ) of the Chañares Formation (*Elorhynchus*); *Dinodontosaurus* AZ of the Santa Maria Supersequence (*Brasinorhynchus*).

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### Colbert Poster Prize

#### MORPHOLOGICAL AND ECOLOGICAL EVOLUTION IN ASIAN RODENTIA

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Rodents are the most species-rich order of modern mammals. Today, over half of this diversity can be found in Asia, where the order is thought to have originated. The Asian continent also possesses a rich and well-studied Cenozoic fossil mammal record, which offers the opportunity to examine the patterns of Asian rodent biodiversity through the Cenozoic. In particular, an understanding of the relationship between morphological evolution and species diversity is crucial for a holistic perspective of biodiversity. These measures are of particular interest in Asia given its position as a biogeographic crossroads among all the continents for much of the Cenozoic, and may also inform about the processes that govern continental-scale immigration patterns and their effects on mammalian evolution and ecology. In this study, we present an investigation of morphological and ecological diversity in rodents on the Asian continent through the Cenozoic as compared to species diversity. We contextualized these findings in light of various immigration events and continental interchanges. We obtained data from the New and Old Worlds (NOW) database supplemented by the primary literature. We examined a suite of morphologically- and ecologically-informative measures, including body mass and dental diversity through this time period. We also explored changes in taxonomic diversity and morphological disparity in this context and considered various biotic and abiotic drivers. We found that the proportion of taxa with low-crowned cheek teeth steadily

decreased through the Cenozoic in line with what has been recorded on other continents, with a departure from this trend in the present day. Average body masses also underwent several fluctuations, with maximum masses being reached at 19 Ma and 8 Ma. Overall, rodent species diversity appears to have steadily increased in Asia over the past 25 million years, whereas morphological diversity fluctuated significantly during this same period. We compared these findings to dynamics in North America, and find that despite distinct faunal assemblages, these continents shared similar patterns of morphological diversity through time. This suggests that drivers of morphological evolution in rodents may have operated on a global scale, with fundamental linkages even between continents over geologic time. In turn, this can inform us about the diversity and distribution of rodents that we observe today.

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### Mesozoic & Paleogene Mammals

#### WHAT DID THE PALAEOOTHERIID *PLAGIOLOPHUS* FEED FROM?—A STUDY ON ITS EVOLUTIONARY ECOLOGY AND PALEODIET THROUGH TIME AND SPACE

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The genus *Plagiolophus* is one of the most abundant components of the extinct European Eocene family Palaeotheriidae, with seventeen species described from the middle Eocene (Lutetian) to middle Oligocene (Chattian). The study of the paleodiet of extant and extinct mammals has improved our knowledge of the ecology of past communities and its relationship with environmental changes. Due to the wide chrono-spatial distribution of *Plagiolophus* representatives, this taxon is useful to assess environmental variations through time and space, including paleodiet, and can provide important paleobiological information. Despite all the paleodiet studies done on Neogene mammals, studies on Paleogene species are very scarce, especially for the Palaeotheriidae. Due to increasing heterodonty and hypsodonty index (HI)

through time, it has long been suggested that the different *Plagiolophus* species may have had different dietary preferences. These dietary changes could be the result of the slow degradation of the tropical and subtropical ecosystems during the early and middle Eocene, with the presence of more arid or/and more open landscapes during the latest Eocene and earliest Oligocene driven by climate cooling. However, neither of these dietary ecological and evolutionary hypotheses have been tested until now.

Here, we study for the first time the combination of three dietary proxies (HI, mesowear and microwear) in *Plagiolophus* to test the hypothesis that dietary changes were the main drivers of the evolutionary history of this palaeotheriid through time and space. Study populations include the endemic species *Plagiolophus mazateronensis* from the middle Eocene of western Iberia, two late Eocene populations of *Plagiolophus annectens* (one from north-eastern Iberia and the other from Central Europe), and *Plagiolophus minor* (latest Eocene) and *Plagiolophus ministri* (early Oligocene) of Central Europe. As none of the species of *Plagiolophus* shows high HI, or high mesowear score, this clearly excludes the dominance of abrasive food stuff and silica-bearing and dust-laden food. Dental microwear textural analysis suggests browsing of tough foliage and exclusion of hard items in their diet. In summary, *Plagiolophus* was a highly selective and invariable feeder that fed on few plants with the same features despite chronology or location, so it would have ate tough foliages of monocots or dicots and avoided lignified tissue or hard materials, without seasonal variations in its diet.

**Funding Sources** Spanish Ministry-ERDF (CGL2017-85038-P), Basque Gov. (IT418-19), UPV/EHU (LPG), Ramon y Cajal fellowship (AGO) and ANR TRIDENT (ANR-13-JSV7-0008-01, PI: GM)

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## Holocene & Pleistocene Mammalian Faunas

### DIETARY BEHAVIOR OF *EQUUS CONVERSIDENS* AND *HARINGTONHIPPIUS FRANCISCI* FROM THE VALSEQUILLO BASIN, LATE PLEISTOCENE OF PUEBLA, MEXICO

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An important sample of fossil mammalian remains belonging to medium- and large-sized herbivores and carnivores was recovered from the Valsequillo Basin, late Pleistocene of Puebla. Among the herbivores, horses are the most abundant, including medium-sized *Equus conversidens* and small-sized *Haringtonhippus francisci*. We assayed a microwear analysis of those species to evaluate their dietary behavior. The microwear pattern of *Equus conversidens* is characterized by a higher number of scratches than pits, a high frequency of cross and fine scratches, a high frequency of small pits, and uncommon gouges. This pattern is related to a mixed dietary behavior that includes abrasive and succulent resources with a tendency for browsing. On the other hand, the microwear pattern of *Haringtonhippus francisci* is characterized by double the number of scratches than pits, a high frequency of fine scratches and small pits, and uncommon gouges, indicating a variable diet but with emphasis on abrasive resources or exogenous grit. The different dietary behavior between these horses could be related to their body size, home range, and/or migration patterns, allowing resource partitioning of these species in the Valsequillo Basin during the Pleistocene.

**Funding Sources** PAPIIT– UNAM for financial support (grants #IA104017 and #IN101321) and CONACYT (grant # 132620) for this study.

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## Biomechanics & Functional Morphology

### A PRELIMINARY STUDY ON THE EFFICIENCY IN LARGE LIVING CATS USING COMPUTATIONAL FLUID DYNAMICS (CFD)

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In this study, computational fluid dynamics (CFD) analysis has been used to investigate the association between nasal air-flow (inspired air) and ecological adaptations in big cats. Our main aim is to investigate its potential to decipher different ecological aspects in extinct big cats from well-preserved, CT-scanned skulls. For this, the skull of three frozen cadavers belonging to the genus *Panthera* with different biogeographic ranges were CT-scanned: *Panthera pardus*, *Panthera onca*, and *Panthera tigris sumatrae*. We virtually developed models of the nasal, nasomaxillary, paranasal and nasopharyngeal tract, and we applied dynamic computational fluid dynamics, using the software Flowgy. We modeled the efficiency of the nasal air-flow in three different environmental scenarios: temperate forest region, warm desert region and cold or high mountain region varying the temperature and relative humidity parameters. The results obtained indicate that *Panthera pardus* is the species that obtains the best acclimatization of the inspired air (air flow) as a function of temperature and relative humidity. This degree of efficiency is followed by *Panthera onca* and, finally, by *Panthera tigris sumatrae*, which is the felid that least efficiently adapts to the three environmental scenarios of modeled habitats. These preliminary results suggest an association between our models of air-flow efficiency and the ecological data in the three species of felids, and we can verify that the modeled data are accurate, although the inclusion of more taxa will confirm or refute our preliminary results. This opens new avenues for future research on the ecomorphological adaptations related to climatic variables such as temperature and relative humidity in extinct taxa.

**Funding Sources** CP18-FR3193 Junta de Andalucía PID2019-111185GB-I00

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## Biomechanics & Functional Morphology

### FUNCTIONAL TRADE-OFFS IN MULTITUBERCULATE THEORETICAL JAW MORPHOLOGY BETWEEN STRESS RESPONSE AND JAW SPEED

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The question of how function constrains morphology has long been interrogated by paleontologists. For example, multituberculates, an extinct mammal group that first arose in the Mesozoic, are defined by their unique tooth morphology, which has led to questions about why their teeth and, in combination, jaws take the shape that they do. Here, I attempt to examine this particular relationship between form and function by examining the breadth of potential theoretical morphologies of multituberculate jaws, and determining the functional optima among these morphologies for stress response and rotational efficiency. I first constructed a dataset of 2D multituberculate jaw images from the available literature, consisting of approximately 70 species across the order Multituberculata, ranging from the ancestral family Paulchoffatiidae to the derived clade Cimolodontia, with an even temporal distribution among the taxa, including specimens from the Late Jurassic, Late Cretaceous, and early Paleogene periods. and then used Elliptical Fourier Analysis to take the outlines of each jaw and produce a grid of theoretical morphologies for multituberculate jaws. Using this theoretical shape data, two performance landscape tests were conducted. The first test used Finite Element Analysis to determine stress response, and the second used rotational inertia calculations to determine rotational efficiency among jaw shapes. Our results indicate that multituberculate jaw morphology primarily differentiates based on the prominence of the coronoid process and the height of the dentary. Additionally, Cimolodonts appear to exhibit a greater stress response than other multituberculates, while rotational efficiency is evenly distributed across the order. Our results also suggest that higher jaw speeds in multituberculates are correlated with thinner jaws, while higher jaw strength is associated with mid-size coronoid processes. These results suggest a presence of potential trade-offs between stress response and jaw speed. I hope to follow this research by constructing a phylomorphospace and using it to estimate hypothetical ancestral jaw morphologies, which in turn may be able to be mapped to diet. Additionally, this data can be directly compared to that of rodents, providing potential insight into the long-standing hypothesis of ecological similarity between rodents and multituberculates.

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**Symposium - Vertebrate dental ecomorphology: Tooth traits that reflect ecology**

## **DIETARY GENERALISM AND ITS IMPLICATIONS TO PALEOECOLOGY, DENTAL MORPHOLOGY AND WEAR**

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Dietary proxies used in paleoecology, such as dental morphology and microwear, can often yield incongruent dietary reconstructions. Such contradictions could be the product of dietary generalism. In this talk, we present a framework for categorizing dietary generalists. By generalist, we mean a species where no single food type (meat, bone, insects, nuts, fruit, leaves, etc.) constitutes more than 50% of its diet. We observe that some species are generalist by virtue of opportunism and others by changing their diet at one of several temporal scales. We propose that generalists can fall into at least four types: constant generalists (or opportunists), seasonal generalists, ontogenetic generalists, and geographic generalists. Some but not all of these categories may have diagnostic dental traits.

Constant generalists have individuals that eat anything palatable whenever they can. Some species have diets that may be more targeted but change seasonally. For example, herbivore animals living in seasonal habitats display dental morphologies that are only beneficial for feeding on back-up food resources during short periods of scarcity. Similarly, many canids have diets that are more meat heavy in the spring and summer and vegetable heavy in the winter, and a combination of shearing teeth and more bunodont ones. Other species alter their diet and dental morphology with ontogeny. For example, proboscideans may switch from grazing to browsing as their teeth wear down. Similarly, rainforest primates are known to change their diet with dental senescence as function changes due to wear. Finally, species with large geographic ranges may have different diets in different regions. For example, grizzly bears in Alaskan fjords feed on salmon seasonally, a food resource that is less prevalent to grizzly bears living at higher altitudes. Importantly, a single species could belong to more than one of these generalist types.

These dietary variations may have important implications for paleoecological studies. First, they may explain observed incongruences between dietary proxies (i.e., dental morphology and microwear and isotope analyses). Second, they can help identify seasonal or unstable paleo-environments and even animal behavior in fossil species. Finally, a species with a stable diet throughout its lifetime occupies fewer ecological niches than one with

ontogenetic generalism, which should also be considered when studying community dynamics in fossil ecosystems.

**Funding Sources** Department of Earth and Atmospheric Sciences, Indiana University, Bloomington, Indiana

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### **Preparators'**

#### **FOSSIL PREPARATION CONTINUES AT THE SMITHSONIAN INSTITUTION NATIONAL MUSEUM OF NATURAL HISTORY DURING COVID-19 PANDEMIC**

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Fossil preparation at the National Museum of Natural History (NMNH) has been impacted by workplace changes in response to the SARS-CoV-2 COVID-19 pandemic, but has continued owing to its designation as time-sensitive and a priority for continuing scientific work at NMNH.

COVID-19 response at the Smithsonian Institution (SI) is managed in a tiered system, with primary policy being set by a central task force. A phased reopening plan for SI units was developed, with phases benchmarked by public health metrics. Led by unit-level Directors, unit-specific policies affected COVID-19 response at individual facilities. At NMNH, research department Chairs and other program leads managed staff in coordination with Facilities and Security personnel.

Fossil preparation staff at NMNH were restricted to telework from the time Smithsonian buildings closed on March 13<sup>th</sup>, 2020, until limited building access was granted in early July 2020, during the first of four reopening phases. In Phase 1, three staff performed laboratory work for a combined four days per week. NMNH shifted to Phase 2 operations in September 2020, continuing through the spring of 2021. Phase 2 increased access to 6 days combined between 3 preparators per week. In addition to preparation, staff responded to concerns including the moving collections, water leaks, maintaining safety equipment, monitoring exhibits, and assisting department staff unable to access the building. When not on site, tasks done via telework included digitization of records, outreach, attending conferences, and communicating with volunteers.

Preparation staff have implemented workplace changes in response to COVID-19. Multilayered fabric masks were

required to be worn on Smithsonian property. Occupancy limits were set at one person per room, with two fossil preparation ‘rooms’ including the laboratory in the Deep Time exhibit space, and all preparation facilities on the ground floor of the East Wing. Online training regarding COVID-19 safety was required prior to initial building access, and daily personal health checks required before leaving home. Staff were required to sanitize shared lab surfaces and to maintain a daily contact tracing log. For a time during late 2020 into early 2021, a halt was ordered for work requiring two people to be within 3 meters of one another. Field work has been restricted to Director-approved expeditions, and fossil preparation staff did not participate in field collecting activities during 2020.

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### Biomechanics & Functional Morphology

#### PTEROSAURS IMPROVED FLIGHT PERFORMANCE BY EVOLVING ADVANCED AERODYNAMIC SMOOTHING OF THE WING-BODY JUNCTION AND SOPHISTICATED WING BASE CONTROL

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Pterosaurs lived for over 160 million years and were the first vertebrate flyers. However, facets of their flight anatomy and performance remain unclear. Using Laser-Stimulated Fluorescence, we observe the first direct evidence of a wing root fairing in a pterosaur. This feature smooths out its aerodynamic profile and reduces drag of the wing-body junction, as in modern aircraft and flying animals. Unlike bats and birds, the pterosaur wing root fairing was unique in being primarily composed of soft tissues rather than fur or feathers. As a soft tissue feature, it appears that pterosaurs used their fairing to access further flight performance benefits through sophisticated control of their wing base. Our study underscores the value of using new instrumentation to fill knowledge gaps in pterosaur flight anatomy and evolution.

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### Non-avian Theropod Systematics, Biology, and Evolution

#### EXAMINATION OF MORPHOLOGICAL VARIATION ACROSS *VELOCIRAPTOR MONGOLIENSIS* SPECIMENS REVEALS A NEW SPECIES WITH POSSIBLE ECOMORPHOLOGICAL VARIATION IN SNOUT DIMENSIONS

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Eudromaeosauria is a sub-clade within Dromaeosauridae (small to medium sized theropods) made up of medium- to large-bodied members, which were most diverse during the Late Cretaceous. This group is recognized for its striking carnivorous adaptations (including a hypertrophied sickle claw on pedal digit II). Like small predators today, they would have played important roles in their respective ecosystems. However, relationships within the clade are poorly understood because of the paucity of skeletal material for the group, and some diagnoses using fragmentary remains. The maxilla—a tooth-bearing bone with a complex paranasal sinus system—is a frequently used element to diagnose species. Although this element can be diagnostic, intraspecific variation has not been examined, largely because most species are represented only by their holotypes. *Velociraptor mongoliensis*, however, is represented by nearly a dozen specimens, five of which possess nearly complete maxillae. To examine intraspecific variation of velociraptorine maxilla, 14 linear measurements relevant to diagnostic features were analysed with Principal Component Analysis (PCA). Results show tight clustering of maxillae referred to any particular species with a linear spread indicative of allometric shifts towards dorsoventral deepening of the maxillae, and elongation of the anterior rami. *Velociraptor osmolskae* plots close to the *V. mongoliensis* cluster but more positively along PC 1 towards *Linheraptor* and *Tsaagan*. One specimen previously referred to *V. mongoliensis* (MPC-D 100/982)

plots away from the *V. mongoliensis* cluster (negatively) to a degree much greater than that of the accepted species *V. osmolskae*. Regressions of taxonomically informative maxillary features show little variation within *V. mongoliensis* specimens and demonstrate MPC-D 100/982 to be a clear outlier. Examination of the skeleton of MPC-D 100/982 reveals more features of the cranium and hindlimbs that suggest it is distinct from *V. mongoliensis* at the species level. MPC-D 100/982 was discovered at the Flaming Cliffs of Mongolia near the discovery site of the holotype for *V. mongoliensis*. However, most *V. mongoliensis* specimens have been recovered from Tögrögiin Shiree, about 35 kms farther west. Although the stratigraphy in the region is poorly understood, differences in the snout morphology of MPC-D 100/982 and *V. mongoliensis* may indicate ecological differences of two closely related species living in the same region.

**Funding Sources** Dinosaur Research Institute - Student Project Grants; Natural Sciences and Engineering Research Council of Canada (NSERC) - Canadian Graduate Scholarship - Master's (CGS-M)

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## Holocene & Pleistocene Mammalian Faunas

### NEW FINDINGS AND TEMPORAL-RANGE EXPANSION OF *FERINESTRIX VORAX* (MUSTELIDAE, MELINAE) AT HAGERMAN FOSSIL BEDS NATIONAL MONUMENT, NATIONAL PARK SERVICE

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*Ferinestrix* is a wolverine-sized mellinae badger. Its confirmed distribution is restricted to Hagerman Fossil Beds National Monument (Glenns Ferry Formation, Idaho, USA) and Udunga (Chikoi Formation, Western Transbaikal, Russia). Hagerman's genoholotype *Ferinestrix vorax* is a right dentary described by P. Bjork in 1970. It retains the p3 alveoli, p4, partial m1, and m2 with an age estimate of 3.4 to 3.0 Ma. Bjork also attributed a femur, found 16 meters lower stratigraphically in a different area of the monument, to *F. vorax* based on its length and robusticity which exceeds that of the largest extant (wolverine *Gulo gulo* and giant

otter *Pteronura brasiliensis*) and extinct (giant otter *Satherium piscinarium* and giant badger-otter *Mionictis* spp.) New World mustelids. The femur is younger than 3.44 Ma and is the only postcranial material tentatively attributed to the genus. These age estimates overlap with Udunga's 80 cranial and dental specimens of *Ferinestrix rapax* (3.6 to 3.1 Ma).

It has taken 50 years of paleontological monitoring at Hagerman to recover additional material. A left and right dentary, both retaining the p2–m2, were discovered during the 2020 field season. The estimated age for this new material is ca. 4.1 to 3.8 Ma. The mandibular corpus is less robust than *F. rapax* with a shorter arcade, narrower premolars, paraconid tapered and more strongly directed lingually, narrower talonid, and a distinct entoconid immediately transverse to the hypoconid. It confirms retention of the p2 in *F. vorax* as seen in *F. rapax*. The two mental foramina are positioned more rostral and directly below the p2 and p3, while in *F. rapax* they are positioned below the caudal end of the p2 and between the p3 and p4. These older specimens differ from *F. rapax* and the genoholotype in their slightly smaller size and the presence of slight diastemata between the p3–p4 and p4–m1. Differences in size between these new specimens and Bjork's dentary fall within the variance expected in a sexually dimorphic mustelid and are similar to those observed in *F. rapax*.

Relative dates for Hagerman come from a monument-wide tephrochronologic study by the Hagerman Paleontology, Environments, and Tephrochronology (PET) Project and suggest an earlier divergence and introduction into North America for this genus than previously thought. This study confirms a sustained presence of this otherwise rare paleospecies at Hagerman and validates the need for continued paleontological monitoring.

**Funding Sources** A 3-year USGS-NRPP Interagency project grant

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## Dinosaur Systematics, Diversity, & Biology

### FIRST REMAINS OF THE CRANIAL CREST OF A LAMBEOSAURINE DINOSAUR FROM THE LATEST CRETACEOUS OF EUROPE, AND AN EVALUATION OF TSINTAOSAURINI

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Hadrosaurid dinosaurs were among the most diverse and abundant terrestrial vertebrates of the Late Cretaceous, and ranged over Eurasia, both Americas, Antarctica, and possibly northern Africa. The latest Cretaceous hadrosaurid fauna of Europe consists of morphologically exuberant lambeosaurine ('hollow-crested') hadrosaurids. Members of the 'bushy crown' of lambeosaurines co-occur with members of 'basal' lineages of the clade in the Ibero-Armorican domain. This might support the hypothesis that the diversification of European lambeosaurines was strongly influenced by patterns of insular endemism. However, some studies have supported grouping of many of the 'basal' lambeosaurines in two poorly known clades, Aralosaurini and Tsintaosaurini, shrinking the number of 'basal' lineages and changing the interpretation of the evolution and biogeography of the group.

In order to test the relationships of putative tsintaosaurins we re-analyzed the hypodigms of the three previously hypothesized members of the tribe, *Tsintaosaurus spinorhinus* from the late Campanian of China, and *Adynomosaurus arcanus* and *Pararhabdodon isonensis* from the Maastrichtian of Spain. We extended our comparison to the species from the richest hadrosaurid locality in Europe, the Basturs Poble bonebed, stratigraphically equivalent (lower Maastrichtian Conques Formation of the eastern Tremp syncline) to the type locality of *A. arcanus*. The Basturs Poble lambeosaurine is not referable to *A. arcanus* and shares apomorphies with *Pararhabdodon* and *Tsintaosaurus*, including characters of the maxillary jugal facet previously believed to be diagnostic of Tsintaosaurini. A crest fragment was recently recovered from Basturs Poble, corresponding to the comparable portion of the premaxilla at the summit of the crest in *T. spinorhinus*, and shares with that species an extensive emarginated facet for the reception of the dorsal expansion of the nasal.

Our phylogenetic results are strictly inconclusive, with the base of the lambeosaurine tree unresolved as a large polytomy. However, the most inclusive agreement subtrees of the optimal trees prune wildcard *A. arcanus*, revealing an underlying classic Hennegian comb of serial successive outgroups to the 'bushy crown' within Lambeosaurinae. This suggests that some 'tsintaosaurin' characters may be ancestral for lambeosaurines as a group.

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## Permo-Triassic Ecosystems

### REVISED PHYLOGENETIC ANALYSIS OF PERMO-TRIASSIC DIAPSID SUPPORTS KUEHNEOSAURIDS AS BASAL ARCHOSAUFOMORPHS

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Kuehneosaurids are a clade of rare, superficially lizard-like Triassic diapsids characterized by elongated ribs that are thought to support a patagium. Since their discovery, kuehneosaurids have been considered close relatives of Lepidosauria owing to a suite of morphological characters including an incomplete lower temporal bar, a laterally bowed quadrate with a prominent lateral crest, and a subcircular thyroid fenestra in the puboischiadic plate. Early cladistic analyses of Diapsida supported this close relationship, such that kuehneosaurids hold an important role in discussions of lepidosaur origins. Discoveries over the past two decades have expanded the anatomical diversity of non-archosauroid archosauromorphs and non-saurian diapsids. Recent phylogenetic studies have supported various alternative positions for kuehneosaurids as non-saurian diapsids, the sister taxon of Drepanosauromorpha, and as archosauromorphs close to Allokotosauria. Herein, I present a revised phylogenetic analysis focused on early Sauria (339 characters, 61 taxa). Parsimony and Bayesian analyses both support the hypothesis that kuehneosaurids are not lepidosauromorphs, but in fact non-archosauroid archosauromorphs. The kuehneosaurid sample includes the North American *Icarosaurus siefkeri* and the European *Kuehneosaurus latus* and *Kuehneosuchus latissimus*.

The morphological characters that once supported a lepidosauromorph affinity for Kuehneosauridae are distributed among multiple early archosauromorph and non-saurian taxa. Characters supporting the position of kuehneosaurids within Archosauromorpha include a postnarial process of the premaxilla, pendulous basal tubera of the basioccipital, a long and upturned retroarticular process, vertebral centra without a

notochordal canal/pit, cervical vertebrae with prominent spine tables and epiphyses, a prominent post-glenoid process of the coracoid, and a horizontally oriented iliac blade with a prominent postacetabular process.

This hypothesis removes a key outgroup to crown-group lepidosaurs, reduces the known diversity of non-lepidosaurian lepidosauromorphs, and obscures morphological transitions at the base of Lepidosauria. It also adds a clade with rib-mediated gliding adaptations to the rapidly expanding ecomorphological diversity of non-archosaurian archosauromorphs during the Triassic Period.

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## Permo-Triassic Ecosystems

### **MULTIPLE SUPERNUMERARY CARINAE IN REVUELTIAN (TRIASSIC: MID-LATE NORIAN) PHYTOSAUR TEETH FROM THE BULL CANYON FORMATION OF EAST-CENTRAL NEW MEXICO, U.S.A.**

Pugh, Isaac, Heckert, Andrew B.

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Supernumerary carinae are extra ridges, often bearing a series of denticles (“serrations”) known from the teeth of diverse fossil reptiles, including lepidosauromorphs, multiple crocodylomorphs, and theropod dinosaurs. Current hypotheses regard these as pathological, specifically genetic in nature. Here we describe supernumerary carinae on two teeth hypothesized to be from the upper left jaws of Late Triassic phytosaurs from the Bull Canyon Formation of New Mexico. The first tooth (SD1) contains a resorption pit indicating that the tooth was shed during life and possesses two converging, poorly to moderately developed, mesiolingual supernumerary carinae, one 15.4 mm long and the second only 2.8 mm. Denticle densities of the long (12/5mm) and short (17/5mm) supernumerary carinae vary from those of the primary carina (15/5mm). The second tooth (SD2) is preserved as two fragments separated by a small gap. The basal fragment includes much of the root, indicating that the tooth was in use up until the death of the animal. A

single mesiolingual supernumerary carina on SD2 begins alongside the mesial carina near the base of the crown and is 11.5 mm long. The supernumerary carina has a slightly higher denticle density (17.5-21/5mm) than the primary carina (15-20/5mm) and does not extend onto the tip fragment, apparently terminating in the gap between fragments. The carinae of these teeth offer a glimpse into the mechanics of tooth formation in Archosauriformes, especially in the formation and relation of dentine and enamel layers naturally crosscut in SD2. Because the tooth is broken, observing the dentine and enamel is straightforward, revealing that the dentine is involved in the point of origin of all carinae on SD2, but does not determine denticle form. As only the second report of Triassic supernumerary carinae, these teeth are important new data points on pathologic carinae not only from their time period but the phytosaur clade generally. Phytosaurs presumably exhibited carina formation similar to that of other Archosauriformes, so understanding their tooth formation opens a window to understanding tooth formation in later-branching members of the clade. Without such fossils, carina formation, especially abnormal development, in the clade is extremely difficult to interpret, because the only living archosaurs either lack serrated carinae (crocodilians), or teeth entirely (birds).

**Funding Sources** Appalachian State University Department of Geological and Environmental Sciences

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## Non-avian Theropod Systematics, Biology, and Evolution

### **SYNCHROTRON $\mu$ CT SCANNING REVEALS NOVEL CRANIAL ANATOMY OF THE ENIGMATIC EARLY CRETACEOUS SOUTH AFRICAN COELUROSAUR, *NQWEBASAURUS THWAZI***

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Phase-contrast synchrotron  $\mu$ CT scans of Africa’s only coelurosaurian theropod, *Nqwebasaurus thwazi*, have revealed a host of new cranial anatomy including the

jugal, lacrimal, postorbital, squamosal, quadrate, pterygoid, palatine, prootic, parabasisphenoid, surangular, angular, prearticular, articular; as well as finer details of the already-known dentition, maxilla, prefrontal, frontal, and parietal. We paired these new anatomical data with virtual comparisons of closely related taxa and analysed them using a broadly sampled phylogenetic tree tailored to address major theropod relationships. We find support, albeit reduced relative to prior work, for an ornithomimosaurian affinity for this taxon. However, when investigated under various implied weighting analyses, a sister relationship between Ornithomimosauria and Alvarezsauridae is recovered, echoing earlier hypotheses. Furthermore, 3D investigation of various craniodental features offer some evidence for a potential filter-feeding habit in *Nqwebasaurus*, consequently expanding the breadth of niches exploited by Maniraptoriformes.

**Funding Sources** VJR, KEJC: DST-NRF Centre of Excellence in Palaeosciences (CoE-Pal); VJR: Palaeontological Scientific Trust (PaST); JNC: DST-NRF African Origins Platform (grant number 98800)

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## Dinosaur Systematics, Diversity, & Biology

### EVALUATION OF THE MORPHOLOGICAL DIVERSITY OF '*PLATEOSAURUS*' FROM THE TROSSINGEN BEDS, GERMANY

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Morphometric analyses of the last 200 years revealed that all Central European sauropodomorphs could represent a coherent lineage of '*Plateosaurus*'. It was proposed that all known morphotypes represented cases of either anagenesis, one species evolving in the same place and replacing the previous one, or phenotypic plasticity, with the morphotypes originating in response to climate changes. The earliest morphometric studies on '*Plateosaurus*' focused heavily on femoral and sacral structures. More recent studies on other early-diverging sauropodomorphs from Argentina and South Africa have assessed other characters that show species-specific variation, such as the morphology of ulnae, cervical vertebrae, metatarsals, and humeral shaft circumference. Nevertheless, morphometric and phylogenetic analyses tend to focus on complete '*Plateosaurus*' specimens only,

disregarding the great variation in about 30 individuals with more incomplete or scarce material stored in Tübingen Paleontology Collection (GPIT). Through character mapping and phylogenetic analyses, we found that several massopodan characters are present in most specimens of the collection, potentially increasing the diversity of early-diverging sauropodomorphs attributed to Central Europe. Such a diverse sauropodomorph fauna would be consistent with what is seen in other Late Triassic localities, e.g. Lower Elliot Formation, South Africa, where several morphotypes and recognized species are known to have coexisted. Furthermore, some characters seem to have appeared earlier in sauropodomorph evolution than previously thought. The morphological disparity may be due to speciation processes, and the use of *Plateosaurus* as an Operational Taxonomic Unit (OTU) in phylogenetic analyses containing any Central European '*Plateosaurus*' is playing a key role in the disagreements between the sauropodomorph relationships proposed in the literature.

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## Romer Prize

### UNPACKING MAMMALIAN OMNIVORE MACROECOLOGY AND MACROEVOLUTION WITH APPLICATIONS TO THE FOSSIL RECORD

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Mammalian omnivores are a broad and diverse group of mammals that are often lumped together in ecological studies. As a result, few studies have investigated the influence of omnivore dietary differences on mammalian macroevolution and macroecology. This lack of information poses problems for paleontologists that use comparative methods to investigate the diet of extinct mammals. In this study, I address this concern and look at the frequency which vertebrate prey, invertebrate prey, fibrous plant material, and non-fibrous plant material are eaten together in 1437 extant mammals. In addition, I examine the body size distributions and the phylogenetic signal of different omnivorous diets. I also assess the evolutionary transition rates between mammalian diet strategies on the mammalian phylogenetic tree using multistate reversible jump MCMC methods. I found that most omnivorous mammals consume invertebrate prey and non-fibrous plants while very few consume fibrous

plants as their only plant source. Omnivores grouped by prey type have similar body mass ranges but very different distributions. My phylogenetic ANOVA results show that the mean body mass of insectivorous omnivores is significantly smaller than that of omnivores that incorporate vertebrate prey. Omnivores grouped by plant material consumed had more similar body mass distributions and were not significantly different from one another. When investigating phylogenetic signal, I found that omnivores and mixed feeding diets are phylogenetically overdispersed, exceeding phylogenetic dispersion expected under a threshold model of Brownian motion. My transition rate models suggest that two main evolutionary pathways dominated the mammalian tree, one from vertebrate predation to increasingly insectivorous omnivory and ultimately herbivory, and one from vertebrate predation to prey mixing and ultimately insectivory. I propose that mixed feeding ecology and evolution are heavily influenced by prey type with many mammalian lineages increasing in insectivory because of access and ease of morphological adaptation. My study highlights that prey type is an important variable when investigating mammalian omnivore ecology and evolution and I suggest ways to move forward when studying extinct communities.

**Funding Sources** NSF grant (DEB-1256897) to SAP and SSBH

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### Colbert Poster Prize

#### PALEONEUROANATOMY OF THE OTISCHALKIAN STAGONOLEPIDOID AETOSAUR *LONGOSUCHUS MEADEI* (ARCHOSAURIA: PSEUDOSUCHIA) FROM THE UPPER TRIASSIC DOCKUM GROUP OF WEST TEXAS

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The Aetosauria is one of the most taxonomically diverse vertebrate clades of the Late Triassic. Historically, most of our understanding about the evolution of this clade was based primarily on their postcrania, particularly their osteoderms. In recent years new skull material for a variety of aetosaur taxa have been described including *Aetosaurus ferratus*, *Aetosauroides scagliai*,

*Coahomasuchus chathamensis*, *Neoaetosauroides engaeus*, *Paratypothorax andressorum*, *Stagonolepis olenkae*, *Stenomylus huangae*, *Scutarx deltatylus*, and *Typothorax coccinarum*. This has allowed for studies focused on the interspecific variation of the cranium and mandible, shedding light on the morphological evolution of the Aetosauria. Despite this new availability of cranial material, not much is known about the neuroanatomy of aetosaurs. More generally, the neuroanatomy of Triassic pseudosuchian archosaurs is poorly understood. Only the brain endocast of two species of aetosaur (i.e., *Desmotosuchus spurensis*, *Neoaetosauroides engaeus*) are formally described. The lectotype skull of the aetosaur *Longosuchus meadei* (TMM 31185-98) from the Dockum Group of West Texas was CT-scanned to study the endocranial anatomy. Although the skull is deformed, the brain endocast shows that the cerebral hemispheres expand by nearly a third anteroposteriorly; the olfactory tracts are elongated and the olfactory bulbs are elliptical; the forebrain–midbrain flexure is ~130°; and the hypophysis is vertically oriented. The olfactory region of *L. meadei* does not exhibit round bulbs and short tracts, which are typically associated to archosaurs with herbivorous diets. This supports more recent hypotheses suggesting that aetosaurs were not strictly herbivorous. Overall, the neuroanatomy of *L. meadei* is more similar to that of *N. engaeus* than to *D. spurensis*.

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National Science Foundation grant (NSF-EAR-1762458)

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### Mammalian Skeletal Morphology

#### MORPHOLOGICAL DIVERSIFICATION ALONG AN ALLOMETRIC LINE OF LEAST RESISTANCE IN THE RUMINANT SKULL

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Phenotypic variation is the raw material for natural selection, but developmental systems determine the range of phenotypes that can evolve. Developmental biases constrain morphological evolution by limiting the amount of intraspecific phenotypic variation, but they can greatly facilitate adaptive morphological evolution when the



direction of selection is aligned with lines of least resistance, the most easily evolvable directions. The relationship between the adaptive landscape and developmental bias is less clear at macroevolutionary scales because their interaction operates at the microevolutionary level and because developmental systems (and their biases) evolve. In the mammalian skull, however, a highly conserved pattern of intraspecific, ontogenetic, and evolutionary allometry exists (CREA), where larger (and older) mammals have relatively longer faces. This allometric axis may act as a line of least resistance because skull shape can adaptively evolve by ‘piggybacking’ onto size. Here, we compare patterns of developmental bias at the species level with patterns of interspecific variation in Ruminantia to ask if this allometric axis is exploited as an evolutionary line of least resistance. Using a previously published landmark dataset of 2857 skulls representing 131 species, we quantify the magnitude of integration, disparity, and alignment between the axis of allometry and each species’ shape PC1. We find that there is no relationship between these metrics in Cervidae (deer), but in Bovidae (bison, sheep, goats, antelopes) more disparate species are both more integrated and have allometric axes more closely aligned with their respective PC1s. This indicates that allometry acts as a strong bias on the realized phenotypic variation of the bovid skull. Further, the intraspecific allometries are largely congruent with the interspecific PC1 in Bovidae, implying that this highly conserved developmental bias has been exploited to produce the greater morphological disparity of bovids compared to cervids. Future work incorporating fossil specimens, such as the Irish Elk (*Megaloceros giganteus*), will clarify whether cervids achieved a greater morphological disparity in the past by exploiting this developmental bias, as hinted by the shape of the extant moose skull. Given the ubiquity of CREA in mammals, an important question to consider is why closely related taxa can vary strongly in the degree to which they deploy it during evolutionary radiations.

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## Biomechanics & Functional Morphology

### RECONSTRUCTION OF FORELIMB POSTURE AND FUNCTION IN A GIANT EXTINCT MARSUPIAL VIA COMPARATIVE RANGE OF MOTION MAPPING AND HELICAL AXIS ANALYSIS OF THE ELBOW JOINT

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Joint mobility is an essential component of the functional capacity of tetrapod limbs, and its estimation is important in palaeobiological reconstructions of extinct animals. Recent advances in quantification and visualization of osteological joint mobility via virtual computational methods have expanded our understanding of its complex three-dimensional nature. However, the focus has generally been on proximal limb joints and these new approaches have seldom been applied to fossil mammals. *Palorchestes azael* is an enigmatic, extinct ~1000 kg marsupial with no close living relatives, whose palaeoecological niche in Pleistocene Australia has been subject to much speculation. Its flattened elbow morphology has led to assumptions of very low mobility at this important joint, so we applied virtual range of motion (ROM) mapping and helical axis analyses to quantitatively explore the limits of *Palorchestes*’ elbow movement. Compared with the forelimbs of their living and extinct relatives, as well as extant mammals that may be functionally analogous, we found *Palorchestes* had the lowest elbow mobility among sampled taxa, even when afforded joint translations as well as rotational degrees of freedom. *Palorchestes* appears to have been limited to crouched forelimb postures highly unusual for mammals of its size. Coupled flexion and abduction caused a skew in the primary axis of elbow movement, suggesting *Palorchestes* walked with an abducted forelimb and may have used a humeral rotation gait. We show that *Palorchestes*’ forelimb function was unlike its contemporaneous relatives and lacks clear analogues among living mammals. We speculate that their apparent specialization and functional trade-offs may underpin their ultimate demise, and highlight the extent of the marsupial ecomorphological diversity that was lost during the late Quaternary extinctions in Australia.

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## Macroecology & Macroevolution

### MORPHOMETRICS AND EVOLUTIONARY MODELING REVEAL THE COMPLEX

## EVOLUTIONARY HISTORY OF AXIAL SKELETAL REGIONALIZATION ACROSS ARCHOSAURIA

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The axial skeleton is the central body frame of all vertebrates, and is variably regionalized into discrete morphological and functional units across clades. The evolutionary-developmental underpinnings of regionalization in the mammal total clade are well understood, and regionalization is known to influence locomotory and respiratory functions in mammals. Among reptiles, archosaurs encompass a diversity of body form, function, and ecology equivalent to mammals, but axial skeletal regionalization and heterogeneity has not previously been examined in phylogenetic or ecological contexts.

To examine the history of regionalization in archosaurs, we conducted 3D geometric morphometric analysis of vertebral morphology to calculate the intracolumnar shape variance of the presacral vertebral columns of 110 taxa, including extant and extinct members of all major clades. We also included representatives of the lepidosaur, mammal, and amphibian total clades as outgroups. We combined morphometric shape variables with segmented linear regression and Maximum Likelihood model selection to determine the most likely number and arrangement of regions in each taxon. Additionally, we use mean Procrustes distances as a measure of intracolumnar heterogeneity in each vertebral column. We place these results in a phylogenetic context with data on body size, body form and ecology, and use stochastic character mapping to reconstruct ancestral states. Our results elucidate a highly complex evolutionary history of regionalization across Archosauria, including regionalization and heterogeneity equivalent to mammals. Crocodylia is highly regionalized with little intra-clade variation. Conservation of regionalization across Crocodylia may be associated with respiratory specializations and locomotory capabilities, including aquatic and terrestrial modes adopting lateral bending and parasagittal motion. Conversely, Dinosauria possesses marked variability, including a decrease in regionalization during the evolution of birds. This loss of regions is likely driven by shortening of the axial skeleton during the evolution of powered flight. In comparison to mammals where regionalization increases in stem synapsids and is then conserved in crown mammals, within Archosauria we uncover increases and decreases in regionalization.

This variability has been influential on the diversity of form and function amongst archosaurs.

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## Mammalian Skeletal Morphology

### MORPHOLOGICAL VARIATION IN THE PETROSAL OF SOME EXTINCT AND EXTANT CAMELIDS

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Camelidae, the only living family of the suborder Tylopoda, originated in North America during the middle Eocene. Camelids were endemic to North America for most of their evolutionary history, only dispersing to other continents in the late Miocene and Pliocene. Thus, North American camelids are crucial for studying the evolutionary history of camelids and tylopods. Endocranial characters, particularly petrosal characters, are often incorporated into phylogenetic analyses of artiodactyls. The basal camelid *Poebrotherium* is the most commonly included taxon, but it is not the only extinct camelid with preserved in situ petrosals. Descriptions of additional taxa, and a broader comparison of extinct and extant camelids, can illuminate the morphological variation present in the petrosals of camelids. We describe the petrosal morphologies of two additional extinct taxa, *Stenomylus gracilis* and *Oxydactylus longipes*, and compare them to the petrosals of *Poebrotherium* and the extant camelids *Camelus dromedarius*, *Camelus bactrianus*, *Lama guanaco*, and *Vicugna vicugna*. *Stenomylus gracilis* and *O. longipes* are both early Miocene camelids, but they are inferred to have had very different ecologies and phylogenetic positions; *S. gracilis* belongs to an early radiation of diminutive 'gazelle camels' whereas *O. longipes* belongs to one of the radiations of long-necked 'giraffe camels'. The morphologies of their petrosals show a combination of conserved 'camelid' features and some convergent features previously undocumented in camelids. A notable conserved feature is the presence of a large subarcuate fossa containing a mastoid fossa, a morphology that is also present in *Poebrotherium* and most extant camelids. *Camelus dromedarius* is known to have a shallow

subarcuate fossa, but its sister taxon *C. bactrianus* retains the ancestral condition. The petrosal of *O. longipes* unexpectedly has a pronounced endocranial ridge that divides the cerebral and cerebellar portions of the endocranial space. The absence of this ridge in camelids has been used as an argument against a close relationship among camelids, protoceratids, and ruminants. The presence of such a ridge in *O. longipes* (but not *Poebrotherium* or *S. gracilis*) is likely convergent. A more thorough examination of these petrosals, and eventual reconstructions of the associated bony labyrinths, will continue to reveal the endocranial variation present in Camelidae.

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## Education & Outreach

### DEMOGRAPHIC PROFILE OF BRAZILIAN VERTEBRATE PALEONTOLOGISTS

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Quantitative data on minorities in STEM is paramount to demonstrate these groups' needs and to guide existing DEI initiatives. For that purpose, we gathered demographic data on paleontologists from or working in Brazil through an online survey. Here we present preliminary results on the vertebrate paleontologists. Answers were collected between 02/24/2021 and 04/22/2021 from 191 respondents, whose ages varied from 20 to 71 (average: 34.8).

57% identified as cisgender men, 37% as cisgender

women, 4% as transgender, non-binary, or agender, and 2% gave other answers. The Brazilian Institute of Geography and Statistics (IBGE) latest census data, though only partially comparable to our survey because it uses sex (feminine/masculine) instead of gender, show that men comprise 48% of the country's population, and women, 52%, so even considering only cisgender respondents, the number is highly skewed towards men. Regarding sexual orientation, 78% of the respondents were heterosexual and 21% bisexual, gay, pansexual, lesbian, or asexual; 1% gave other answers. IBGE does not gather data on this demographic, but estimates suggest that at least 10% of the Brazilian population is not heterosexual.

6.8% of our respondents informed they had a disability (vision, hearing, or physical impairments), a number similar to the general population (6.7%) according to IBGE. Open answers in our survey also included olfactory disabilities and neurodiversity.

To survey for data on race and color, our respondents were presented with IBGE's five unique options. 71% declared they were white, 16% *pardos* (mixed-race with black ancestors), 6% black, < 3% yellow, and < 2% indigenous; 3 respondents did not answer. These results are in stark contrast to the Brazilian population of 46.8% *pardos*, 42.7% white, 9.4% black, and 1.1% yellow and indigenous. The lack of representation of black, *pardos*, and indigenous minorities in higher education has only begun to be addressed in the last decade by a nationwide policy of racial and social quotas in public universities.

16% of our respondents declared they benefited from the quotas system, all of them under the age of 40.

Although many projects have been developed to promote the inclusion of women in paleontology, considering only the demographics, the elephant in the room is the centuries-long exclusion of racial and ethnic minorities, even in a racially mixed country like Brazil.

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## Holocene & Pleistocene Mammalian Faunas

### ISOTOPIC BIOGEOCHEMISTRY OF CARBON, NITROGEN AND OXYGEN IN *URSUS SPELAEUS* FROM CUEVA DE GUANTES (SANTIBÁÑEZ DE LA PEÑA, PALENCIA, SPAIN)

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Isotopic analysis of carbon and oxygen in tooth enamel and of carbon and nitrogen in bone collagen of juvenile and adult cave bears (*Ursus spelaeus*) were carried out. The fossils, older than 50,000 BP, were found in the Gallery 1 site from Cueva de Guantes (Palencia, Spain). The results obtained suggest that the bears probably inhabited areas near this cave, which was probably used as a refuge during hibernation. This was consistent with: (1) previous taphonomic studies which interpret this stratigraphic level as a very frequented bear's den; (2) the values of  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  of dental enamel, which indicate a diet with similar sources of carbon for all individuals, and little spatial displacement; (3) the values of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in bone collagen, which in the case of the carbon isotopic values indicate similar food sources, whilst the wide interval in the nitrogen isotopic values could be a consequence of the metabolic processes occurred during hibernation; and finally, (4) the calculated  $\delta^{18}\text{O}$  values of ingested water, which suggest similar sources of water for all the bears.

**Funding Sources** For financial support: Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica (PAPIIT-UNAM) (grants # IA104017 and # IA102719), CONACyT (grant # 920655).

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## Marine Mammals

### EVIDENCE FOR OLIGOCENE CETACEAN DIVERSITY IN THE SOOKE FORMATION (CARMANAH GROUP) OF VANCOUVER ISLAND, BRITISH COLUMBIA, CANADA

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The Oligocene was a time of key anatomical innovations in cetaceans as mysticetes and odontocetes diverged and diversified from ancestral whale lineages. We assessed previously unpublished fossils from the Sooke Formation (late Oligocene) of Vancouver Island, British Columbia, Canada, in the Royal BC Museum collections. Vancouver Island is the only location in Canada to preserve Oligocene cetacean fossils, and as such has the potential to contribute new data to understanding Oligocene whale evolution. The specimens included numerous vertebrae and ribs, potential hyoid pieces, a scapula, and cranial fragments. At least three cetacean clades are represented by this material. An atlas vertebra is referable to Squalodelphinidae (Platanistoidea) based on the presence of reduced ventral transverse processes. A scapula found nearby within the same horizon as the atlas may also be referable to Squalodelphinidae. These represent a new record of the Platanistoidea clade in the Oligocene of the North Pacific. A basioccipital with inflated basioccipital crests may be a squaloziphiid dolphin, an odontocete recently discovered in the North Pacific. An exoccipital compares well to the holotype of *Chonecetus sookensis*, an aetiocetid mysticete and the only named cetacean from Vancouver Island to date. Although the postcrania of aetiocetids is poorly documented, many vertebrae from the Sooke Formation compare well to the endemic aetiocetids based on their size. However, the comparable body size between aetiocetids themselves and odontocetes indicate a need for further aetiocetid postcrania analysis. A partial lumbar vertebra is proportionally similar to those of basilosaurid archaeocetes, who were facing extinction near the Eocene–Oligocene boundary; this specimen could be from a late-surviving individual of this family. Alternatively, this specimen could belong to a large mysticete. As this is an isolated vertebra, further identification is difficult. Although most cetacean fossils from the eastern North Pacific have been found in the United States, we show that Vancouver Island preserves a rich diversity of early cetaceans including possible aetiocetids, some of the earliest platanistoids from the eastern North Pacific, and a possible basilosaurid. Future exploration is needed to expand the cetacean assemblage from the Sooke Formation, which will undoubtedly reveal cetacean taxonomic diversity within this region during the late Oligocene.

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## Dinosaur Systematics, Diversity, & Biology

## **TRICERATOPS FROM THE UPPERMOST MAASTRICHTIAN FRENCHMAN FORMATION OF SOUTHERN SASKATCHEWAN, AND IMPLICATIONS FOR THE ANAGENESIS HYPOTHESIS**

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Previous work regarding the upper Maastrichtian Hell Creek Formation of Montana hypothesized that two temporally separated species of *Triceratops* were anagenetically related, with the older *T. horridus* having directly given rise to the younger *T. prorsus*. However, this work was necessarily limited in geographic scope, and only briefly considered the many skulls of *Triceratops* known from outside the formation. Several such skulls of varying completeness have been found in the uppermost Maastrichtian Frenchman Formation of southern Saskatchewan over the last century, and provide a crucial test of the anagenesis hypothesis. Given that the Frenchman Formation was deposited contemporaneously with the upper Hell Creek Formation, the anagenesis hypothesis predicts that only *T. prorsus* should occur within the Frenchman Formation.

We tested this hypothesis with reference to the available *Triceratops* skull material from the Frenchman Formation, which had not been systematically studied prior to our investigation. Using qualitative comparisons and canonical variates analysis, we found that all Saskatchewan material compares most closely to *T. prorsus*. In particular, the nasal horn cores are generally larger, accompanied by a wide, vertically oriented, nasal process of the premaxilla and a shorter sagittal frill length. Our results concur with the predictions made by the anagenesis hypothesis.

**Funding Sources** Canadian Museum of Nature, Carleton University, the Dinosaur Research Institute, and the Natural Sciences and Engineering Research Council

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**Late Cenozoic Mammalian Evolution and Ecology**

## **NEW FOSSIL APE MATERIAL FROM THE LOTHIDOK FORMATION, NORTHERN KENYA**

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The Lothidok Range is located west of Lake Turkana in northern Kenya and is best known for its Miocene fossil apes—*Afropithecus turkanensis*, *Turkanapithecus kalakolensis*, and *Simiolus enjiessi*. All three species are unique to the Lothidok Range and are found at the early Miocene localities of Moruorot and the Kalodirr Site Complex (~17 Ma). There are also two known middle Miocene sites, Esha and Atirr (~13 Ma), but these have been only minimally prospected to date.

The West Turkana Miocene Project (WTMP) began in 2008 with the goal to explore the Miocene deposits of the Lothidok Range. Our work to date has included paleontological survey, efforts to refine the geochronology of the Lothidok sequence, study of mammalian fossils collected by our team and previous teams, and paleoclimate and paleoenvironmental reconstruction. Of particular importance has been the recovery of new ape fossils. Since 2008, we have found new craniodental and postcranial material of each of the three species of fossil apes at Kalodirr and Moruorot. To date, all of our new specimens can be comfortably assigned to the existing species, but further document metric and morphological variation in each. Re-evaluation of specimens curated in the National Museums of Kenya has led us to identify dental material of *Turkanapithecus* previously collected from Moruorot, which demonstrates that this species is found at both early Miocene localities, and not just at Kalodirr. Furthermore, our new material of *Turkanapithecus* and *Simiolus* at Kalodirr comes from the same collecting locality, suggesting that these taxa are contemporaneous and not time-successive. The new material of *Turkanapithecus* displays features reminiscent of other nyanzapithecines, and potentially informs the proposed relationship between that clade and the European *Oreopithecus*. New material of *Afropithecus turkanensis* reveals an odd variant of its premolar morphology.

**Funding Sources** Funded by NSF award BCS 1241817 to JBR, the Leakey Foundation (to JBR and SMC) and the Natural Sciences and Engineering Council of Canada to SMC.

## Taphonomy, Paleoenvironments, & Stratigraphy

### SKELETONS AND STONES: BIOLOGICAL CONCRETIONS IN THE FOSSIL RECORD

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The role of skeletons as sources of biological, physiological, and behavioral insights to life and health are supplemented by trace fossils, some of which provide unique perspectives. Among these are concretions, some of geologic and some of biologic derivation. As confidently distinguishing among them is sometimes challenging, time-consuming, and may not be feasible when large numbers are observed; identification of a rapidly applicable technique would allow identification of those of interest and facilitate distinguishing among them. Non-destructive 20-200x magnification surface microscopy is investigated for trans-phylogenetic recognition of and distinguishing among uroliths (kidney/bladder stones), gallstones, bezoars, pellets, coprolites, gastroliths, egg shells, and geological concretions. Reference collections were accessed for independently validated samples. The surface appearance of uroliths is independent of phylogeny, but lacks specificity with respect to composition, the rare silica stones excepted. They typically have smooth surfaces with level or lobulated configurations. Facets, typically associated with gallstones, were also observed in struvite, calcium oxalate, calcium carbonate, urate, and cysteine stones. Mammiform surface appearance characterized struvite, calcium oxalate, and cysteine stones, but not urate and xanthine varieties. Plate-like surfaces were present in struvite, calcium carbonate, and urate stones. Stones and xanthine stones have a mask-like ceramic appearance. Gallstones are variable in shape with smooth or porous surfaces. The presence of sand grains and bone fragments permits recognition of pellets, bezoars, and coprolites, but does not necessarily distinguish among them. Recognition of biologically modified geologic concretions (i.e., gastroliths) is the most challenging. Curiously pore-like structures, a characteristic of egg shells, are also occasionally found in other biologic concretions and mimicked by geologic concretions. The uneven diameters of “pores” in the latter distinguishes them from egg shells. Surface microscopy of biological concretions provides an additional window into the

recognition of biological concretions, their normal variation, and facilitates distinguishing among them. Uroliths are distinguishable among most biological concretions, with gallstones the major differential consideration.

## Biomechanics & Functional Morphology

### ASSESSING SKULL FUNCTION IN TYRANNOSAUROIDS USING 3D FINITE ELEMENT ANALYSIS

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Tyrannosauroids are an iconic and well-studied group of fossil taxa, with *T. rex* often serving as a model organism for studies of extinct vertebrate musculature, function, and biomechanics. Tyrannosauroids varied greatly in their body size distribution, with certain genera such as *Alioramus* achieving half the body size of *T. rex* at identical growth stages. More derived genera including *Daspletosaurus* and *T. rex* are noted for their broad, deeply set jaws and large skulls. Tyrannosauroids are one of at least three phylogenetically disparate clades of theropod dinosaurs that achieved extremely large size during their evolutionary history. Although the impact of size on locomotory ability has been studied in theropods, the impact of large body size on feeding performance is largely unknown. Here we assessed the feeding performance of six tyrannosaur genera of variable body size, including (from smallest to largest): *Raptorex*, *Alioramus*, *Bistahieversor*, *Albertosaurus*, *Daspletosaurus*, and two *Tyrannosaurus*. We used 3D finite element analysis (FEA) to test whether skull shape becomes more or less resistant to feeding induced forces as body size increases. Sensitivity analyses were performed to account for error in reconstructions of muscles forces and their influence on feeding abilities. Additionally, 3D models of *Bistahieversor* with and without deformation were analyzed to better understand the impact of fossil deformation on FEA results. It was found that individuals with broader skulls and more deeply set jaws were relatively more resistant to feeding stresses when skull models were scaled to equivalent

lengths, particularly in *T. rex*, *Daspletosaurus*, and *Albertosaurus*. These results may indicate that the wide crania which are characteristic of tyrannosaurids convey a functional advantage that more basal tyrannosauroid taxa lacked. This advantage may have better enabled large tyrannosaurid taxa to prey on large herbivorous dinosaurs that were common in Late Cretaceous North America.

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## **Taphonomy, Paleoenvironments, & Stratigraphy**

### **SEDIMENT-ENCASED PRESSURE-TEMPERATURE MATURATION ELUCIDATES THE NATURAL DIAGENESIS OF POLYENE-DERIVED AVIAN PIGMENTS**

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Colors and macroscopic patterns in modern animal integuments are intricately linked to life history and behavioral strategies (aposematism, crypsis, physiology, sexual, and social selection). Reconstruction of coloration permits evidence-supported inferences into the life-history, ecology, and behaviors of long extinct animals. Thus far, studies have focused on melanin pigments due to its high preservation potential and comparatively better understanding of its diagenetic transformations. However, a large portion of the avian color palette comprises polyene-derived pigments (carotenoids and psittacofulvins), producing yellow, orange, pink, and red colors, have largely been ignored. Carotenoids are thought to have independently originated multiple times in passerine birds and is hypothesized to occur in the most recent common ancestor of archosaurs. Psittacofulvins have evolved only once, are restricted to feathers of parrots, and have most likely been present in ancient parrots. In this study, we simulate the diagenesis of carotenoids and psittacofulvins through sediment-encased pressure-temperature maturation to better understand the preservation of these pigments. Maturation was carried out on modern feathers at 40°C, 100°C, 150°C, and

200°C / 250 bars for a duration of 24 hrs. The persistence of organic staining through the different temperatures was investigated and UV-Vis-NIR, FT-IR-ATR, micro-Raman spectroscopy and mass spectrometry (ToF-SIMS) was employed to shed light on the diagenetic fates of these pigments. The results show that these pigments underwent increased saturation (loss of double bonds/addition of H-groups) with increased temperatures. Organic staining from polyene pigments do not survive beyond 150°C. Furthermore, these pigments decompose to amorphous carbon between 150 and 200°C resulting in a lack of characteristic peaks in UV-Vis-NIR, FT-IR and Raman spectroscopy. Mass-spectroscopy suggests that: (1) no crosslinking reactions like that of melanin occur; (2) no evidence of keratin breakdown products preserving beyond 100°C; (3) persistence of saturated remnants of carotenoids till 150°C. Therefore, for the first time, it has been possible to establish the diagenetic pathway of carotenoid-based feather colors and suggest that it is possible to detect carotenoid remnants in fossil feathers from less harsh diagenetic environments.

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## **Non-avian Theropod Systematics, Biology, and Evolution**

### **TWO NEW EUDROMAEOSAURS FROM KHULSAN (CENTRAL MONGOLIA) REVEAL MODERN-LIKE FAUNAL PREDATORY STRUCTURE AMONG NON-AVIAN DINOSAURS**

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In modern ecosystems, closely related taxa of similar body size commonly coexist throughout part or all of their ranges. Although anthropogenic factors have caused the ranges of many species to contract, historical records show that even apex predators are capable of coexistence without competitive exclusion. Such patterns, however, are rare among non-avian dinosaur faunas—typically, localities only attest to the presence of a single predatory species, and when multiple taxa are present, they differ in

body size. The faunal structure of dromaeosaurid dinosaurs from Mongolia has been suggested to show a similar pattern, in which a single small halszkaraptorine and a single mid-sized velociraptorine are present at localities from which both are known. Here, we describe two new eudromaeosaur specimens, one from the Khulsan locality (Barun Goyot Formation) and one from Zos Wash locality (near Ukhaa Tolgod, Djadokhta Formation), that contradict this interpretation. The first, IGM 100/3503, represents a new taxon that is distinguished from all other eudromaeosaurs by possession of dual posterior surangular foramina, a surangular shelf that is totally dorsal in orientation, and anteriorly displaced pleurocoels on the dorsal centra, as well as a unique combination of mandibular, dental, and postcranial characters. The second, IGM 100/981, appears referable to *Velociraptor*, although it differs from other *Velociraptor mongoliensis* specimens in some respects such as the absence of a dorsal ectopterygoid recess. It is distinct from the coeval *Tsaagan mangas*, the only eudromaeosaur hitherto known from Ukhaa Tolgod. IGM 100/981 preserves ulnar papillae for feather attachment, and therefore preserves the only direct evidence of feathering in a eudromaeosaur. Phylogenetic analysis places IGM 100/3503 as a eudromaeosaur that is not sister to *Shri devi*, confirming that two species are present at Khulsan. IGM 100/981 is too incomplete to place confidently, but its clear distinction from *Tsaagan mangas* similarly attests to the presence of two eudromaeosaur species at Ukhaa Tolgod. Given that these specimens are almost identical in body size to the dromaeosaurs with which they coexisted, the fossils demonstrate that multiple closely related and morphologically similar dinosaurian predators existed in some Mesozoic faunas, and calls into question specimen referrals based on size and provenance rather than shared derived characters.

**Funding Sources** Macauley Family Endowment; Newt and Calista Gingrich Endowment

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## Romer Prize

### HOW SEALS CONQUERED THE WORLD: INFERRING THE DISPERSAL CAPABILITIES OF ANCIENT TRUE SEALS (FAMILY PHOCIDAE)

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Today, true seals (Family Phocidae) are distributed around the world, after an origin in the North Atlantic during the Early Miocene. The majority of southern true seal (Subfamily Monachinae) evolution occurred in the southern hemisphere, with monachines crossing the equator at least eight times during their evolutionary history. This is unusual because the equator is hypothesized to be a soft barrier to marine mammal dispersal. Anti-tropical distributions in phocids are influenced by Bergmann's rule; with large marine mammals restricted to colder polar waters, and small marine mammals present in warmer equatorial waters. Why then were true seals unaffected by these ecological limitations?

To investigate the unusual dispersal capabilities of true seals, we investigated two phenotypes, sea surface temperature (SST) and total body length. A total-evidence Bayesian phylogenetic tree of 18 extant and 19 extinct species true seals were used to compare both phenotypes via phylogenetic comparative methods. Body size and SST data were taken from the literature, with the body length of extinct species estimated using linear metrics taken from fossil specimens housed at multiple museums around the world. Ancestral state estimations and evolutionary rate shift analyses for both phenotypes were performed using the package 'RRphylo' in R. Bergmann's rule was also tested for true seals by performing a phylogenetic generalized least squares (PGLS) regression of total body length and median SST. Our analyses found that there was considerable variation in body size and SST in true seals. The last common ancestor of the true seal was estimated to be medium sized (1.7–2.5 meters long) and adapted to temperate (~19°C) waters. This contrasts with most previous inferences of true seals being an ancestrally cold-adapted clade. However, there was little variation in the evolutionary rates of either phenotype, with no significant shifts in evolutionary rate in crown phocids. The PGLS regression showed no relationship between total body length and SST. Therefore, true seals as a clade appear to be tolerant of a broad range of environmental temperatures in the past, and were not limited by Bergmann's rule. This implies that would have had no difficulty either crossing the equator or colonizing polar environments. The environmental tolerances of true seals hint at the capacity of extant true seals to adapt to future changes in climate.

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## Education & Outreach

### CAPTURING CURIOSITY: ADULT VISITOR ENGAGEMENT AT THE STERNBERG MUSEUM FOSSIL PREP LAB

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A working fossil preparation laboratory, or ‘fish bowl’ lab, is a publicly accessible space within a museum where visitors can view and speak with the staff and volunteers actively preparing fossils. These labs provide a unique behind-the-scenes experience where visitors can observe and engage with science in action. The Oceans of Kansas Fossil Prep Lab at Fort Hays State University’s Sternberg Museum of Natural History completed renovations to become a modern, ‘fish bowl’ fossil prep lab in 2019. Currently, the lab relies solely on university student workers and volunteers and is only in use on average ten hours per week during normal museum hours. Previous research indicates that positive visitor experience is largely dependent on interaction with a preparator while visiting a working lab. However, there has been no research on how to maintain a positive visitor experience at a working lab while unstaffed. While the possibility of incorporating interpretive and supplemental media such as videos, illustrations, and signage into the visitor’s experience at the lab exists, there has been little focus on creating these forms of media. The purpose of this study was to determine the best ways to provide an engaging and positive experience to adult visitors while visiting the prep lab when unstaffed. A total of 35 visitors between the ages of 18-65 were surveyed using iPads and the online survey platform Qualtrics in front of the Oceans of Kansas Fossil Prep Lab. To encourage visitor participation, the survey consisted of only 11 questions and was designed to require less than 5 minutes to complete. Survey results indicate the majority of visitors prefer to be engaged through interactive activities, videos, and social media with the topics of field work, paleoecology of Kansas, and geographic origin of fossils. This study represents a first attempt at better understanding visitor experience at a working fossil prep lab while the lab is not in use.

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## Paleohistology & Paleopathology

### EXPLORING THE ONTOGENY AND PALEOBIOLOGY OF THE LATEST CRETACEOUS CHASMOSAURINE DINOSAUR *TRICERATOPS* THROUGH RIB HISTOLOGY

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In 1975 an incomplete *Triceratops* sp. skeleton was recovered by Appalachian State University students in Slope County, North Dakota. After initial excavation and preliminary preparation, the *Triceratops* remained either on display or undisturbed in storage for decades. The skeleton, (BDM 061), is repositied at Badlands Dinosaur Museum in Dickinson, ND. It includes a nearly complete dorsal vertebra, the right jaw, both squamosals, a postorbital horn core, occipital condyle, other skull fragments, a fragmentary proximal femur along with several ribs and dozens of rib fragments. While the *Triceratops* is fragmentary, there are multiple indications that it was an adult, including well developed cornual sinuses, rounded epoccipitals, one forward facing horn core, and neural arches fused to the dorsal centra. Although many dinosaur taxa have been histologically sampled, ceratopsians are poorly represented. Sampling therein is phylogenetically uneven, being almost entirely represented by basal (non-ceratopsid) taxa or much more derived forms. By 2018, there were only two postcranial histological studies of chasmosaurines, leaving a nearly nonexistent understanding of their growth patterns. Studies have shown that Lines of Arrested Growth (LAGs) are almost nonexistent in chasmosaurine limb bones, however other bones could be a suitable alternative to limb bone studies. While two centrosaurine taxa have been sampled for rib histology (*Pachyrhinosaurus* and *Avaceratops*), there are no studies for rib histology of chasmosaurines. We studied the histology of two ribs associated with the skeleton to assess the preservation of bone microstructure and utility of rib histology on chasmosaurine dinosaurs to better understand their growth patterns. For this study, a rib fragment was used to assess the preliminary microstructure preserved. Afterward, a section was taken from the proximal end of a complete dorsal rib for comparison. Both ribs were embedded in epoxy resin and mounted to glass slides using a curing adhesive. Both thin sections showed preserved

microstructure including dense, overlapping secondary osteons and a transition into cancellous bone in the medullary region. This indicates the ribs of this individual are composed almost entirely of dense Haversian tissue, with no preserved primary osteons or LAGs. The level of secondary remodeling of the ribs suggests that ribs may not be a suitable alternative to limb bone studies for chasmosaurines.

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## Macroecology & Macroevolution

### RELAXING SELECTIVE PRESSURES ON COMPLEX STRUCTURES: FEATHER EVOLUTION AFTER FLIGHT LOSS IN RECENT BIRDS

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Feathers are complex structures with high diversity across species and within plumage and have varied functions (e.g. thermoregulation, flight). Flight is lost in many crown lineages, frequently observed in island 'founding' or semiaquatic context. Different extant lineages lost flight across three orders of magnitude of time. Flight loss's effect on sensory capacity, brain size, and skeletomusculature have been studied, but less work exists on relations between flightless loss and feathers. To understand how flight loss affects feather anatomy, we measured feather metrics (e.g. barb length, barb angle) on skins of 30 flightless taxa and their volant sister taxa supplemented with broader sampling of primaries across orders of volant crown birds. We sampled many independent losses of flight; we measured nearly half the extant flightless species count and match its ~3:2 terrestrial:semiaquatic ratio. A digital microscope was used to measure relevant metrics at apical, basal, and middle regions of exposed feathers across the plumage. PCA and regression results indicate that flight loss promotes increases in barb and barbule lengths, with greater shifts in terrestrial species. Semiaquatic flightless taxa exhibit relatively wider rachi and barbs. Vane symmetry increases in flightless lineages. All patterns are strongest in flight feathers and weakest in coverts.

Greatest changes in feathers are in the oldest flightless lineages like penguins, which show robust filaments on small feathers, and ratites, which show high interspecific diversity with elongated filaments and/or filament loss. Kiwi feathers bear alternating well- and poorly developed barbs with partial barbule loss. Some parameters such as barb length in terrestrial taxa and barbule length and rachis width in semiaquatic might correlate with lineage age, but are not independent of body mass increase and relative wing and tail fan reduction.

Upon relaxing selection, feathers do not rapidly lose flight adaptations. Feathers of recently flightless lineages are similar to those of their volant relatives. We see some evidence of selection for robust feathers in semiaquatic flightless taxa.

Feather microstructure evolution is subtle in flightless taxa, except when flight loss is ancient, perhaps because developmental constraints act upon feathers. Changes in skeletomusculature of the flight apparatus are more evident in recently flightless taxa and may be a more reliable way to detect flight loss in fossils.

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## Non-avian Theropod Systematics, Biology, and Evolution

### FIRST DEFINITIVE RECORD OF ABELISAURIDAE FROM THE BAHARIYA FORMATION, BAHARIYA OASIS, WESTERN DESERT OF EGYPT INCREASES DIVERSITY OF LARGE-BODIED THEROPODS IN THE MIDDLE CRETACEOUS OF NORTHEASTERN AFRICA

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Although purported fossils of abelisaurid ceratosaurs have been previously reported from the Upper Cretaceous (lower Cenomanian) Bahariya Formation of the Bahariya Oasis, Western Desert of Egypt, unambiguous material of the clade has yet to be documented from this unit. Here we report Mansoura University Vertebrate Paleontology Center (MUVP) specimen 477, an isolated, well-preserved tenth cervical vertebra of a medium-sized abelisaurid from the Bahariya Formation of the Gebel El Dist region of the northern Bahariya Oasis. The new vertebra shows affinities with derived Upper Cretaceous abelisaurids from Madagascar and South America, such as *Majungasaurus crenatissimus*, *Carnotaurus sastrei*, *Viavenator exxoni*, and the generically indeterminate Patagonian form Museo Padre Molina (MPM) specimen 99. Widely recognized cervical vertebral synapomorphies of Abelisauridae present in the specimen include: (1) long axis of diapophysis forms angle of 65° to midsagittal plane; (2) dorsal surface of neural arch clearly delimited from lateral surface of diapophysis; (3) deep spinoprezygapophyseal and spinopostzygapophyseal fossae; and (4) well-developed epiphyses, comparable to those observed in the tenth cervicals of *Majungasaurus* and MPM 99 (but smaller than those of *Carnotaurus* and *Ekrixinatosaurus novasi*). Phylogenetic analysis following the addition of MUVP 477 to a recently published dataset recovers the Bahariya form within Abelisauridae, either in a polytomy of all included abelisaurids (strict consensus tree) or, interestingly, as an early branching member of the otherwise South American clade Brachyrostra (50% majority rule consensus tree). MUVP 477 therefore represents the first confirmed abelisaurid fossil from the Bahariya Formation, rendering it the oldest definitive record of the clade from Egypt and northeastern Africa more generally. The new vertebra demonstrates the wide geographic distribution of Abelisauridae across North Africa during the middle Cretaceous and augments the already extraordinarily diverse large-bodied theropod record of the Bahariya Formation, a record that also includes representatives of Spinosauridae, Carcharodontosauridae, and Bahariasauridae.

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## Crocodylomorphs & Pterosaurs

### THE FIRST INVESTIGATION OF CROCODYLIAN REMAINS FROM THE UPPER PLEISTOCENE OF SUDAN

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Here we describe crocodylian material from the Upper Pleistocene of the Blue Nile region, southeast of Sudan. It comprises two premaxillae, which are housed now in the Natural History Museum, United Kingdom. The material was collected from unconsolidated calcrete deposit of El Atshan Formation (namely, Singa and Abu Hugar areas). The fossiliferous bed of Singa is dated using U-Th for the calcrete deposit, giving an age of at least 133±2 ka, while those from Abu Hugar yielded an age of ca. 17 ka based on radiocarbon dating on a crocodylian tooth. The material is the first description of Pleistocene *Crocodylus* from Sudan and may represent the youngest occurrence of *Crocodylus* in East Africa and suggest a migration and divergence from the *Crocodylus* reported from Lake Turkana Basin of Kenya where the oldest African *Crocodylus* dated as 7 Ma. The newly described crocodylian material helps in understanding the Pleistocene crocodylian diversity in Sudan and east Africa as well.

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## Crocodylomorphs & Pterosaurs

### THE FIRST PTEROSAUR FROM THE UPPER CRETACEOUS (LOWER CENOMANIAN) BAHARIYA FORMATION, BAHARIYA OASIS, WESTERN DESERT OF EGYPT

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Upper Cretaceous localities in Egypt are well-known for yielding the genoholotypic specimens of a number of distinctive non-avian dinosaurs, such as *Carcharodontosaurus*, *Paralititan*, *Mansourasaurus*, and, most famously, *Spinosaurus*; nevertheless, material of other ornithomimid archosaurs has remained elusive. Here we report an isolated, three-dimensionally preserved left first wing phalanx (left manual phalanx IV-1) of a medium-sized pterosaur from an amalgamated braided-channel-fill deposit of the lower Cenomanian Bahariya Formation of the Bahariya Oasis, Western Desert of Egypt. The specimen represents the first pterosaur record from Egypt, and it compares favorably with the equivalent element in pteranodontian (*sensu stricto*; i.e., pteranodontid and nyctosaurid) pterosaurs, rather than ornithocheiromorphs or azhdarchoids. The fused and ossified extensor tendon process (ETP) indicates that the individual in question was osteologically mature. The proximal ETP of the specimen is comparable in overall morphology to that of Pteranodontia in features such as the subrectangular extensor tubercle, the position of the prominent pneumatic and the small nutrient foramina, the expanded curvature of the dorsal cotyle, the thin bony wall, and the posterior flare of the proximal articulation. Moreover, the specimen differs morphologically from the first wing phalanx of penecontemporaneous azhdarchoids, which typically possess a subtriangular extensor tubercle and weaker curvature of the dorsal cotyle. The presence of a pteranodontian in the lower Cenomanian Bahariya Formation represents one of the earliest known occurrences of the clade and adds to mounting evidence of high taxonomic diversity of the group in the Upper Cretaceous of North Africa.

**Funding Sources** Mansoura University research fund, American University in Cairo Intramural grant and National Geographic Society Committee for Research and Exploration Grant 9144-12

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## Holocene & Pleistocene Mammalian Faunas

### CHANGES IN THE RELATIVE ABUNDANCES OF THE MICROFAUNAL COMMUNITY AT NATURAL TRAP CAVE, WYOMING OVER THE LAST 20,000 YEARS

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Natural Trap Cave is an 80-foot-deep karst sinkhole located at the base of the Bighorn Mountain range in Wyoming, USA. As the cave is on a plateau, it acted as a natural trap for larger animals who could not see the cave entrance. Smaller animals are believed to have been accumulated mostly through packrat middens. Microfaunal remains are found from well-stratified layers in the cave stretching back 30,000 years ago, before the end-Pleistocene megafauna extinction, up until a few hundred years ago. The Holocene experienced a range of climatic conditions including multiple drought periods spanning up to 700 years in length. As all of the species identified from the cave so far are extant today, Natural Trap Cave is a useful and informative site to study how past microfaunal communities shifted in response to climate and what might be expected from these groups in the future. The number of identified specimens (NISP) and the minimum number of individuals (MNI) were compared across 3 layers at the site, from the late Pleistocene, the middle Holocene, and the late Holocene, and relative abundances of each group, as well as changes in richness and evenness in the community, were calculated. We found that the community was dominated by lizards, cf. *Phrynosoma*, at each layer in the cave, making up to 83% of the middle Holocene community, and that *Peromyscus spp.* was the most abundant rodent through time. Richness was lowest in the late Pleistocene and highest in the middle Holocene. Evenness, however, was the highest during the late Pleistocene and lowest in the middle Holocene as a consequence of having two genera not found from the other layers, *Cynomys spp.* and *Perognathus spp.*, at low abundances and cf. *Phrynosoma* being found at its highest abundance. These trends remain the same when examining just the small mammal community from the site with evenness values being higher overall with cf. *Phrynosoma* excluded from those analyses. Building upon what was found in this study through increased sampling and radiocarbon dating, we can better understand how microfaunal communities at Natural Trap Cave responded to changes in climate, like aridity, by examining changes in functional traits, the dynamics between rare and abundant species, which groups have longer or shorter population recovery times after disturbance, and thresholds for when groups are no longer able to withstand changing climate.

## Turtle & Marine Reptile Diversity & Biology

### UNIQUE PALATE MORPHOLOGY IN A PARTIALLY COMPLETE POLYCOTYLID PLESIOSAUR FROM THE TROPIC SHALE (EARLY TURONIAN) OF SOUTHERN UTAH

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The Tropic Shale is a Late Cretaceous (Cenomanian–Turonian) formation exposed in southern Utah that represents a western arm of the Cretaceous Western Interior Seaway during the maximum extent of the Greenhorn Cyclothem. Exposures of the Tropic Shale around Big Water, Utah (both within Glen Canyon National Recreation Area and Bureau of Land Management property—formerly the southern margin of Grand Staircase-Escalante National Monument) have revealed an incredible biodiversity of large marine predators. The vertebrate predators discovered within this area include a variety of sharks, bony fish, plesiosaurs, and fragmentary mosasaurs. To date, five genera of short-neck plesiosaurs from two families (Family Pliosauridae and Family Polycotylidae), including three new species, have been described from the Tropic Shale. MNA V.11350 consists of a partial skeleton of a polycotylid plesiosaur (Family Polycotylidae) that was discovered in exposures of the Tropic Shale in Glen Canyon National Recreation Area in 2012 and excavated in 2013. The stratigraphic position of the specimen is 1.5 m above bentonite C, placing the specimen in the Early Turonian. The specimen includes the complete skull and mandible, associated teeth, pectoral girdle elements from the right side of the body, the right humerus, and isolated vertebrae and ribs. The specimen was partially articulated, with the left side of the body and the posterior portion of the body eroding out of the hillslope prior to discovery. The morphology of the palate of MNA V.11350 is distinct and unusual when compared to other polycotylid plesiosaurs. Posteriorly, the pterygoid comprises a large portion of the palate. It is separated into two plates by the posterior interpterygoid vacuities. A robust parasphenoid with a pronounced ventral keel is located along the midline. Anteriorly, the pterygoids join to form a sheet of bone, but do not separate again to form the anterior interpterygoid vacuity, as seen in most other polycotylids. The lack of an anterior interpterygoid vacuity has only been described in one other polycotylid plesiosaur,

*Pahasapasaurus haasi*. *P. haasi* was described by Schumacher in 2007 and is from the Cenomanian Greenhorn Limestone in South Dakota. The unique palate morphology of MNA V.11350 confirms the presence of a sixth unique plesiosaur taxon from the Tropic Shale, further supporting the rich biodiversity of marine predators known from this formation.

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## Macroecology & Macroevolution

### QUANTIFYING THE COMPLETENESS OF THE PALEOZOIC CHONDRICHTHYAN FOSSIL RECORD

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The chondrichthyans (cartilaginous fishes) are a highly successful group of predominantly predatory fishes that originated and first diversified in the early Paleozoic. Contrary to the majority of jawed vertebrates, chondrichthyans possess an endoskeleton mainly made out of cartilage rather than bone which is rarely preserved in the fossil record. As a consequence, reconstructing their evolutionary history, especially within the Paleozoic, is often a challenge and biased towards isolated and mineralized remains such as teeth, scales, and fin spines. Here, we address these issues and quantify the quality of the Paleozoic chondrichthyan fossil record 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. We compiled a database of 838 chondrichthyan species from museum collection visits and literature. Temporal completeness patterns show major peaks in the Famennian, Serpukhovian, Moscovian, Asselian, and again in the Wordian and lows throughout the Silurian and in the Tournaisian–Visean. Chondrichthyans show a significantly lower completeness distribution than any published tetrapod group. If isolated material, including teeth, scales, and fin spines, is excluded, chondrichthyan completeness increases significantly and is similar in range to pelycosaurs and parareptiles but still lower than plesiosaurs and

ichthyosaurs. Environmental influences favor completeness of chondrichthyans in freshwater deposits in the Lower Devonian, around the Devonian–Carboniferous boundary and again throughout the Permian while marine deposits predominantly yield more complete skeletons throughout the Carboniferous. Changes in chondrichthyan completeness through time show a significant correlation with sea level and time variables. Our results reveal relatively weak spatial biases influencing the Paleozoic chondrichthyan fossil record but relatively strong environmental and temporal biases. The observed variation in completeness highlights the importance of understanding the influences different biases exert on the chondrichthyan fossil record and how they need to be taken into account when observing patterns in early chondrichthyan evolution.

**Funding Sources** This research is funded by the Natural Environment Research Council (NERC) CENTA DTP.

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## Macroecology & Macroevolution

### DINOSAUR BODY SIZE EVOLUTION ACROSS THE TRIASSIC–JURASSIC BOUNDARY: INSIGHTS FROM SOUTH AFRICA’S ELLIOT FORMATION

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The End-Triassic Extinction event (ETE) took place approximately 201 million years ago (Mya) and is regarded as being triggered by the breakup of the supercontinent Pangaea. The Stormberg Group’s Elliot Formation in South Africa’s Main Karoo Basin preserves a rich tetrapod fossil record, and is one of the few formations globally to preserve the ETE on land. Mass extinction events such as the ETE are hypothesized to cause major upheavals in ecosystems, which may be captured by ecological proxies such as body size. For example, some researchers hypothesize that extinctions select for smaller body sizes leading to a “Lilliput effect” and others hypothesize that the relaxation of niche

occupancy paves the way for some lineages to become much larger. Thus, we investigated the body size distribution of dinosaurs across the lower Elliot Formation (IEF) and upper Elliot Formation (uEF) by collating a dataset of 363 specimens (belonging to 20 genera) and including metadata on stratigraphic, osteological and skeletal measurements. To this dataset, we applied established fair methods for correcting for sampling and geographical biases. We found that the overall pattern of body size distribution is similar, with each unit of the formation having more small than large taxa. In the IEF, dinosaur faunas generally have lower body size maxima and mass variance compared to the uEF where we observe the appearance of greater body size minima (notably the ~500kg bipedal *Massospondylus carinatus*) and maxima (the 12-tonne quadruped *Ledumahadi mafube*). We find no support for a “Lilliput Effect” in sauropodomorph dinosaurs after the ETE, suggesting either that sauropodomorphs were unaffected by it or rebounded rapidly. Our results run counter to anecdotal statements in the literature suggesting IEF taxa are larger than the uEF taxa. However, our results support findings by other studies that show sauropodomorph dinosaurs explored greater locomotive strategies after the ETE in the Karoo, with increases in body size maxima possibly reflecting their experimentation with quadrupedality, ultimately leading to the evolution of Sauropoda in the Jurassic.

**Funding Sources** DSI-NRF Centre of Excellence in Palaeosciences (CoE-Pal), Palaeontological Scientific Trust (PAST) & National Research Foundation African Origins Platform

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## Symposium - Vertebrate dental ecomorphology: Tooth traits that reflect ecology

### DENTAL TOPOGRAPHIC ANALYSIS OF LIVING AND FOSSIL LORISOIDS: A NEW SIGNAL FOR EXUDATE FEEDING IN LORISES AND GALAGOS

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Dental topographic analysis (DTA) is a series of methods that quantify functional aspects of molars including curvature, complexity, and relief. These metrics covary with major dietary guilds (e.g., insectivory, frugivory) in living taxa, meaning they can be used to reconstruct diet in fossil taxa. However, less is known about the relationship between dental topography and more finely parsed out dietary behaviours such as exudativory. Lorisioidea is an ideal group in which to examine the effects of exudativory because some taxa consume large quantities of exudates, whereas others consume none. In the following, we use DTA to quantify lower second molar morphology in a sample ( $n = >50$ ) of extant lorisoids representing 17 taxa, and one extinct taxon (*Karanisia clarki*). We also used ancestral state reconstruction to estimate topographic parameters for the last common ancestors (LCA) of Lorisioidea, Lorisidae, and Galagidae. As with previous studies, we found that higher topographic values relate to insectivory, whereas low values relate to frugivory. We reconstruct the LCA of Lorisioidea, Lorisidae, and Galagidae as insectivorous, with Galagidae slightly more insectivorous than Lorisidae. Importantly, we identified a significant interaction influencing dental topography that exists between the primary dietary component and the level of exudate feeding. Taxa that engage in exudativory exhibit lower topographic values than calculated for exclusive insectivores. *Karanisia clarki* has previously been reconstructed as a frugivore; however, within the context of the diversity of Lorisioidea (and not strepsirrhines more generally), we reconstruct the taxon as insectivorous. Moreover, previous assessment of enamel thickness in the front teeth suggested that *K. clarki* may have relied on some exudates. Our results suggest that if the taxon did consume exudates, they did not consume enough to produce the difference in molar topography we note in some living exudativorous taxa. Overall, our results provide a framework for testing ecological hypotheses about lorisoids and may point to a unique pattern of molar topography among living and extinct exudativores.

**Funding Sources** Funding provided by a NSERC Discovery Grant to MTS.

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## Biomechanics & Functional Morphology

## THE EFFECTS OF SKULL FLATTENING ON SUCHIAN JAW MUSCLE EVOLUTION

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Jaw muscles are key features of the vertebrate feeding apparatus and often show adaptations to aspects of diet. However, the jaw musculature is housed in the skull, with morphology that reflects a compromise between multiple functions, and the skull and its contents constrain the geometry of jaw muscles. Thus, jaw muscle anatomy is often suboptimally constructed. Crocodylians are a group of vertebrates that generate the highest bite forces ever measured, with a flat skull suited to their aquatic ambush predatory style. However, fossil ancestors of crocodylians (e.g. *Prestosuchus*) were terrestrial predators with plesiomorphic skull shapes, and thus the origin of modern crocodylians involved a substantial reorganization of the feeding apparatus and its jaw muscles. Here, we reconstruct jaw muscle anatomy in select crocodylians and fossil suchians and investigate the impact of skull flattening on jaw muscle anatomy. We used CT data to create 3D models of extant and fossil suchians that demonstrate the evolution of the crocodylian skull, using osteological correlates to reconstruct muscles. We hypothesize that taxa with flatter skulls have less efficient jaw muscle resultants and that modern crocodylians will have larger size-standardized gross muscle masses or longer lever arms in order to generate high bite forces with inefficient muscle configurations. We found that jaw muscle anatomy in early fossil suchians reflected the ancestral archosaur condition but experienced progressive shifts in the lineage leading to Mesoeucrocodylia (e.g., Neosuchia+Notosuchia). In early fossil suchians, Musculus Adductor Mandibulae Posterior (mAMP) and Musculus Pterygoideus (mPT) were of comparable size, but by Mesoeucrocodylia, the jaw musculature is dominated by mPT. We found that taxa with flatter skulls have less efficient muscle orientations. However, extant crocodylians did not have either larger size-standardized muscle masses or lever arms for jaw muscles, suggesting that crocodylians use alternate means to offset their inefficient muscle orientations. This study highlights the

diversity and evolution of jaw muscles in one of the great transformations in vertebrate evolution.

**Funding Sources** NSF EAR 163753; Society of Vertebrate Paleontology Estes Memorial Grant; University of Missouri Research Board; University of Missouri Research Council

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## Late Cenozoic Mammalian Evolution and Ecology

### WHAT WAS THE MAIN DRIVER OF HYPHODONTY ACQUISITION IN NORTH AMERICAN UNGULATES?

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Tooth morphological change due to the evolution of hypsodont teeth over time has led to a classic tale in paleontology that the acquisition of hypsodonty and the widespread appearance of grasslands were synchronous. More recent studies have considered other evolutionary drivers of hypsodonty in ungulates. We tracked changes in crown height (hypsodonty index), relative abrasion (mesowear), and food and grit scars on dental enamel (microwear) to discern the relative contributions of grass vs. grit as a driving force in ungulate tooth changes during the evolution of North American Equidae, Camelidae, Antilocapridae, Dromomerycidae, and Merycoidodontidae and to examine whether hypsodonty acquisition and widespread appearance of grasslands were synchronous. We found that the overall pattern of the timing of the attainment of hypsodonty is inconsistent with grazing as the main impetus for the 'Great Transition' within equids as well as within the artiodactyl families studied as highly hypsodont ungulates post-date the spread of widespread grasslands. There was synchrony in the timing of the acquisition of hypsodonty and increased dietary abrasion incurred during feeding as measured via mesowear in all fossil families. Microwear showed excessive enamel pitting (particularly large pits) and unusually coarse scratch textures in all five fossil families, a finding consistent with exposure to exogenous grit or soil ingestion as the main driver of hypsodonty acquisition prior to the consumption of significant levels of grass. Antilocapridae were mixed feeders throughout most of their evolutionary history but demonstrated

unusual levels of large pitting and relatively coarser scratch textures consistent with exposure to exogenous grit. Dromomerycidae, camelids, and merycoidodontids were committed browsers throughout most of their evolutionary history, but incurred a large amount of abrasion (i.e., 'dirty' browsing). While grass was a much more common dietary item for equids than for the other families, Equidae exhibited a wider array of dietary behavior than the other families through most of their evolutionary history (with the exception of the Recent). This predilection for more grass combined with exposure to exogenous grit, which was more accelerated from the early Miocene onward, helps explain the more extreme acquisition of hypsodonty in equids compared to the artiodactyl families studied, allowing the Equidae alone to become hypergrazers in the Recent.

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## Biomechanics & Functional Morphology

### HINDLIMB EVOLUTION IN ORNITHOPOD DINOSAURS: A GEOMETRIC MORPHOMETRIC APPROACH

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Ornithomimid dinosaurs were among the most diverse, widely distributed and long-lived lineages of terrestrial vertebrates of the Mesozoic. A major trend characterizing their evolutionary history is the increase in body size, which likely shaped the transformations experienced in various areas of the skeleton such as the hindlimb. Here, we use 2D geometric morphometrics for quantifying interspecific osteological changes in the femur, tibia, and metatarsals in a sample of ornithomimid species spanning their taxonomic diversity and morphological disparity. We aim at providing a more thorough quantitative understanding of the morphological evolution experienced by these major hindlimb elements, in connection with body size changes and possible implications for biomechanics.

Ornithomimid outgroups to Ornithomimidae are primarily distinct in lacking a *fossa trochanteris* and a sigmoidal shaft in the femur as seen in anterior view, as well as a



tibia with a lateral malleolus that is less anteriorly divergent from the shaft. Non-iguanodontian ornithopods display high morphological disparity in all hindlimb elements, and variation is largely influenced by allometry (with the exception of the greater mediolateral expansion of the distal end of the femur that characterizes these animals). Dryosaurids are distinct in possessing a laterally bowed proximal extent of the femur and a shallower lateral malleolus of the tibia. Non-hadrosauriform ankylopollexians are characterized by a mediolaterally robust metatarsal II lacking a laterodorsal flange. Despite extensive morphospace overlap between non-hadrosaurid hadrosauroids and hadrosaurids, the former are distinct in having a more slender metatarsal IV lacking a protruding ventromedial flange.

Our analysis recovers previously reported evolutionary trends in Ornithopoda, such as the distal migration and loss of a pendant morphology in the fourth trochanter, and the acquisition of a straight femoral shaft. These transformations are associated with allometric changes caused by increasing body size. We interpret the mediolateral expansion of the distal femur as relating to the mediolateral eccentricity of the shaft and a more laterally splayed orientation of this element in non-iguanodontian ornithopods. Allometry greatly influenced the development of the ventromedial and anterolateral flanges of metatarsals II and IV, supporting previous studies positing that these flanges aided in a greater appression of the metatarsus.

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## Permo-Triassic Ecosystems

### A JUVENILE RHYNCHOSAUR SPECIMEN FROM THE OTTER SANDSTONE FORMATION OF SOUTHERN ENGLAND (ANISIAN, MIDDLE TRIASSIC)

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Rhynchosaurs are an abundant group of extinct basal archosauromorphs that played a structural role during the Early and Middle Triassic as ecosystems recovered from the Permo-Triassic mass extinction. They had unique tooth and jaw interaction and a tooth replacement cycle

that was evolved to handle tough vegetation. Although many adult specimens have been collected in large quantities all over the globe, only a few juvenile specimens have been collected. Here we describe a new juvenile rhynchosaur specimen from the Otter Sandstone of southern England (Anisian, Middle Triassic). Major differences in the skull and jaw morphology in the juvenile suggests the possibility of an ontogenetic dietary shift. Evidence of such a shift would present a new factor in the success of rhynchosaurs in the Triassic recovery period. The differences in the dentition are especially marked, with the juvenile showing well-defined tooth crowns standing clear of the jaw margins and suggesting a diet in which the teeth tore the food material. In x-rays of the dentary, the juvenile shows no replacement teeth below the emergent teeth, but in the adult, trains of two or three teeth can be seen deep in the jawbone and moving up and forward into place below the teeth currently in occlusion. Jaw shape differences are also significant. The juvenile glenoid process is positioned ventroposterior to the coronoid process, whereas the adult glenoid process lines up with the coronoid process posteriorly. Biomechanical calculations based on the jaw morphology and assumed jaw muscle dimensions and orientation indicate quite different jaw mechanics between juvenile and adult.

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## Taphonomy, Paleoenvironments, & Stratigraphy

### DEPOSITIONAL ENVIRONMENT AND TAPHONOMIC INTERPRETATIONS OF AN EOCENE BRIDGER FORMATION SITE (WYOMING) CONTAINING CROCODYLOID AND *ECHMATEMYS* MATERIAL

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The Eocene of North America represented a time of high diversity and abundance for reptiles, particularly for crocodylians and turtles. New material recovered from a site in the Bridger Formation of south-central Wyoming provides an insight into this diversity and environment. The site lies in the lower portion of the Bridger B Unit within the Blacks Fork Member of the Bridger Formation. Substantial fossil remains from the site can be identified

as associated cranial and post-cranial elements belonging to a basal member of Crocodyloidea and a well-preserved carapace and plastron attributable to the turtle genus *Echmatemys*. The crocodyloid specimen may pertain to the genus *Brachyuranochampsia*; however such a diagnosis would be tentative, due to the fragmentary nature of the specimen and pending thorough research and reevaluation of basal crocodyloid taxa. CT scanning of the turtle shell revealed the presence of skeletal and skull remains inside, a unique instance of directly associated cranial and appendicular elements that is pertinent considering the few cranial remains known for *Echmatemys*.

Certain features of the site, as well as of the material recovered, provide a look into the depositional environment and taphonomic processes at work. The close proximity of the *Echmatemys* and crocodyloid specimens (with the turtle abutting the anterior end of the crocodylian), the association yet disarticulation of these specimens, and the preservation/breakage patterns imply a taphonomic situation for the organisms correlating to a shallow, low-energy fluvial environment—one that perhaps saw the occurrence of flooding events. The deposits of the lower Bridger B unit have, in the past, been attributed to perennial streams that experienced regular flooding, a conclusion that is supported by the findings at this site. Additionally, the site appears to demonstrate decomposition in place, possibly providing an explanation for the preservation of turtle elements within the shell (as well as for the partial disarticulation of the specimens). These environmental conclusions are also supported by the presence of gastropods, gravel-sized particles, gar scales, and isolated turtle scutes near and among the remains of the crocodyloid and *Echmatemys* specimens. Taken as a whole, this Bridger site and the fossils found therein provide a unique look into an Eocene ecosystem and the reptilian taxa which occupied it.

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#### Preparators'

#### ACCESSIONING A LARGE FOSSIL COLLECTION FROM THE FAIRMEAD LANDFILL LOCALITY, CITY OF CHOWCHILLA, MADERA COUNTY, CALIFORNIA

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Maintained and operated by the Madera County Public Works Department (MCPWD), the Fairmead Landfill is a well-known Irvingtonian fossil locality with thousands of specimens collected over the past 28 years from paleontological mitigation. While some specimens are on display at the Fossil Discovery Center (FDC) of Madera County adjacent to the Landfill, they do not have a collections facility on-site. The University of California Museum of Paleontology (UCMP) is the primary repository for specimens from 1993–95 whereas the remainder are stored temporarily at a decommissioned library in downtown Madera in anticipation of a future repository at the FDC. The library is in disrepair and is unsuitable as a permanent repository. As such, MCPWD officials decided to move the remaining fossils to the UCMP for curation.

While in temporary storage, the fossils have been subjected to theft by vandals, pest infestations, and water damage as a result of ceiling leaks. Specimens that sustained the worst water damage were covered in black mold and dried ceiling insulation. The MCPWD retained Applied EarthWorks, Inc. (Æ) to prepare and transfer the fossils of over 4,000 specimens to UCMP. To address the mold, Æ paleontologists used cotton swabs to apply rubbing alcohol to affected surfaces. Æ replaced moldy jackets of oversized specimens, using quilt batting to avoid mold regrowth. Æ replaced damaged specimen trays, and fossils and trays were sealed inside plastic zip-closure bags. Æ also transferred all microvertebrates into new screw-top vials. Lastly, Æ re-inventoried and re-labeled the entire collection and assigned catalog numbers to over 2,000 additional uncatalogued specimens. Æ plans to transport the collection to the UCMP in summer 2021. For stability, Æ will keep specimens in their existing wooden cabinets and then will transfer them to permanent metal cabinets at the UCMP. Oversized fossils in jackets will be secured with foam sheets and plastic wrap onto wooden pallets during transport. These efforts highlight the value of mitigation paleontology for scientific contributions from fossils that would otherwise have been lost during construction. The successful transfer of these fossils and their associated data to an accredited curation facility ensures suitable conditions for long-term preservation and scientific research. The Fairmead Landfill fossils will significantly expand the present understanding of Irvingtonian paleoecology in California's Central Valley.

**Funding Sources** All work for this project was supported by the Madera County Public Works Department.

## Fishes Evolution & Distribution

### COMMENTS ON THE BODY FORM OF THE EXTINCT MEGATOOTH SHARK, *OTODUS MEGALODON*, BASED ON EXTANT LAMNIFORM SHARKS

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The megatooth shark, *Otodus megalodon*, is an iconic Neogene lamniform shark known only from teeth and vertebrae in the fossil record. Its thermophysiology is previously inferred to have been regionally endothermic, like the extant lamnids that are active predatory lamniforms. By considering the entire Lamnidae as the ecological and physiological analogue to *O. megalodon*, a recent study proposed inferred body dimensions of *O. megalodon* based on morphometric analyses on body forms of extant lamnids. However, whether or not the body plan can vary between ectothermic and endothermic lamniforms in the first place has never been tested. Here, we reanalyzed the previous study by also including all other extant lamniforms to test whether or not their observed body forms are indeed influenced by thermophysiology (ectothermic vs. endothermic). Morphometric comparisons of the whole body as well as different body parts (e.g., head, different fins, and precaudal body with and without fins) among the 15 extant species of Lamniformes were conducted using principal component analyses and simple clustering methods. The distributions of endothermic taxa (lamnids and *Alopias vulpinus*) with respect to ectothermic taxa (all other lamniforms, including the planktivorous *Cetorhinus*) in the generated scatter plots and cluster trees were then examined. Whereas no particular patterns are detected for the analyses on the precaudal body without fins, head, first dorsal fin, or pectoral fin, our generated plots and trees based on the whole body, precaudal body with fins, and caudal fin show that the ectothermic *Cetorhinus* (Cetorhinidae), that is phylogenetically sister to Lamnidae, is morphometrically nested within Lamnidae. Likewise, the endothermic *A. vulpinus* consistently occurs closely with the other two ectothermic *Alopias* spp. for those three body shape variables. The lack of any clear separation between endothermic and ectothermic taxa in our study strongly suggests that

thermophysiology has little effect on determining the body forms of lamniforms. Rather, their body form evolution is simply strongly dictated by phylogeny. Because *O. megalodon* belongs to Otodontidae that phylogenetically lies most certainly outside of the clade consisting of Cetorhinidae and Lamnidae, our study thus indicates that the justification for the previously inferred body form of *O. megalodon* on the basis of considering ecological and physiological analogue to extant lamnids is questionable.

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## Biomechanics & Functional Morphology

### THE TOPOGRAPHY OF DIET: USING MOLAR TO PREDICT FEEDING HABITS IN TURTLES

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In order to understand the structure and function of an ecosystem, we must understand the diets of the animals that live in it. Our ability to predict diet in extinct taxa, particularly those with highly derived feeding morphologies and no living descendants, such as the dicynodont therapsids that dominate many Permian and Triassic ecosystems, is often vague. Dental complexity is an important source of data for resolving the diets of extinct animals. Software packages like MorphoTester and molaR utilize 3D models of extinct and extant animal dentition to produce an Orientation Patch Count Rotated (OPCr) value, which measures the surface complexity of a particular 3D model. In general, higher OPCr values correlate with more herbivorous diets among extant amniote taxa. OPCr has only been used to predict the diets of animals with teeth, including primates and crocodylians. Yet, many amniote lineages have independently lost their dentition (birds, turtles, dicynodonts, shuvsaurid pseudosuchians), instead evolving an edentulous rhamphotheca that is still utilized to process a diversity of food items. The ‘beak’ morphology of edentulous taxa, including monotremes and avian dinosaurs, has been examined to better understand the relationship between overall beak structure and diet, but no edentulous group has been analyzed using

OPCr. Complicating matters is the fact that the actual tritulating surface in most edentulous groups is keratinous, and keratin tends not to fossilize. In this study, we used OPCr to determine the complexity of the bone and keratinous rhinothecae across nine extant turtle families and a variety of diets. We then compared these values to determine if the complexity of keratin and the complexity of bone correlate, as well as if correlations exist between bony rhamphotheca surface complexity and animal diet. Results indicate that the correlation between bony and keratinous rhamphotheca surface complexity varies across diet. Additionally, we find that—much like the increased complexity of herbivorous teeth—keratin OPCr increases with more herbivorous diets. This also indicates that herbivorous turtles from different families (Testudinidae, Emydidae) have convergently evolved increased beak complexity. These promising results suggest we can more confidently predict the morphology of keratinous rhinothecae in dicynodonts and other extinct beaked taxa.

**Funding Sources** Field Museum of Natural History; Idaho State University

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### Mammalian Skeletal Morphology

#### **STRAIGHTENING THE HORSE'S MOUTH? NON-DENTAL MANDIBULOMETRY IN DERIVED EQUIDS, AND THE ORIGIN OF *EQUUS CABALLUS***

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The origin of the domestic horse (*Equus caballus*) remains contentious, with the species never receiving a satisfactory definition. A few provisional diagnoses of *E. caballus* alleged a straightness of the inferior border of the gracile mandibular corpus in lateral profile; conversely, other equid species were described as displaying a convex inferior border below p3–m1. However, published morphometric comparisons between equid mandibles failed to recover any phylogenetic or taxonomic signals, besides the same gradual transformation from bunolophodont to selenolophodont mandibles seen in other ungulate clades (i.e., deepening and shortening of the corpus with respect to the ramus). An online open access database compiled by Vera Eisenmann provides an opportunity to revisit equid

mandibulometry, using data gathered from 838 extant *Equus* (incl. 92 *E. caballus*), 150 fossil and subfossil *Equus* (incl. 21 *E. caballus*), and 115 hipparionins. This abstract discusses preliminary comparisons between selected extant and fossil *Equus*, using 11 non-dental measurements (out of 16) and 55 ratios.

Pearson correlation tests for a pooled sample of extant *Equus* show the most 'linearly' correlated measurements to be diastema length and muzzle length; this is true for all species except *E. caballus*, for which the most correlated measurements are greatest basal length and ramus height. However, multiple analyses of variance (MANOVA), together with maximum parsimony cladistic analyses in TNT 1.5, do not uphold proposed diagnoses of *E. caballus*, as corporal measurements do not distinguish *Equus* species. In all taxa, corporal height in front of p2 is less than that at p4–m1, which in turn is less than that behind m3, regardless of the concavity or convexity of the inferior border. Grevy's zebra (*E. grevyi*) is the most distinct extant species, exhibiting increased symphyseal length relative to breadth.

Middle–late Pleistocene 'caballines' from Eurasia (*E. gallicus*, *E. mosbachensis*) and North America (*E. occidentalis*, *E. scotti*) differ from modern *E. caballus* and *E. przewalskii* in ways broadly similar to *E. grevyi*. *E. mosbachensis* in particular recalls 'stenonine' equids (i.e., *E. granatensis*, *E. livenzovensis*) with its elongated diastema and symphysis relative to corpus height at p4–m1, which in turn is high relative to least symphyseal breadth. Therefore, the extinct 'caballines' are too apomorphic to be direct ancestors of the more plesiomorphic *E. caballus*.

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### Macroecology & Macroevolution

#### **DETECTING STRENGTH OF SELECTION AND MOSAIC EVOLUTION DURING THE RISE OF TETRAPODS**

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The fish-to-tetrapod transition is one of the most iconic events in vertebrate evolution, yet fundamental questions regarding the dynamics of this transition remain unresolved. These questions include precisely dating the time of origin of tetrapods, recognizing the closest fish-

like relatives to elpistostegalians, and detecting the pace of phenotypic change that led to the origin of the tetrapod body plan. Here we use both recent and new advances in Bayesian morphological clock modeling to reveal the evolutionary dynamics of early tetrapodomorphs (tetrapods and their closest fish relatives) and to answer these long-standing questions. We combine both osteological and ichnological data and introduce a new method to automatically detect morphological character partitions for inferring evolutionary trees. Further, we adapt a technique from molecular phylogenetics for measuring the strength of selection upon partitions based on rates of morphological evolutionary change. Our data show that combining osteological and ichnological data results in major shifts on the time of origin of all major groups of tetrapodomorphs (up to 25 Myr into the past) and that low rates of net diversification (not fossilization, as previously suggested) explain long ghost lineages in the early tetrapodomorph fossil record. Further, our results show that most early tetrapodomorph lineages are characterized by extremely low rates of morphological change, indicating widespread stabilizing selection upon their “fish-like” morphotype. This pattern was broken only by elpistostegalians, especially among early tetrapods, which underwent sustained high rates of morphological evolution for ~30 Myr. The fastest rates detected were concentrated on the skull, including several adaptations for feeding, suggesting that as primary evolutionary driver towards the acquisition of the tetrapod body plan. Fast phenotypic changes coupled with low taxonomic diversity and inferred low rates of net diversification of early tetrapods during the Late Devonian provides a strong example of the decoupling between periods of taxonomic and phenotypic radiation. This taxonomic-phenotypic rate duality has been recently detected for other vertebrate lineages and may thus be more common than previously assumed by traditional evolutionary theory.

**Funding Sources** Natural Sciences and Engineering Research Council (NSERC) postdoctoral Fellowship to TRS.

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## Paleohistology & Paleopathology

### OSTEOHISTOLOGY SUPPORTS IMMATURE ONTOGENETIC STATUS OF NORTH AMERICAN OVIRAPTOROSAURS *APATORAPTOR PENNATUS* AND *CHIROSTENOTES PERGRACILIS*

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Understanding baseline species diversity leading up to the end-Cretaceous mass extinction (~66 million years ago) is necessary to resolve long-standing debates about non-avian dinosaur extinction. The Late Cretaceous diversity of maniraptoran theropods has received little attention due, in part, to a paucity of specimens. Notoriously, the fossil record of North American oviraptorosaurs consists largely of specimens without comparable elements among individuals and among taxa. This lack of articulated or associated specimens has led researchers to combine elements from different specimens on the basis of relative size, and assumed ontogenetic status, in order to define species. Additionally, these previous studies did not analyze histological indicators of skeletal age that can establish somatic maturity of fossil specimens. This lack of ontogenetic context may hinder understanding of oviraptorosaur diversity through conflating juvenile specimens belonging to a single species with small adults of new species, a persistent problem in paleontology. In order to assess the ontogenetic status of specimens previously hypothesized as skeletally mature, we sampled two Late Cretaceous North American caenagnathid species—RTMP1993.51.1 *Apatoraptor pennatus* (holotype) and RTMP1979.20.1 *Chirostenotes pergracilis* (referred specimen). The *Apatoraptor pennatus* holotype was previously described as skeletally mature on the basis of neurocentral suture fusion and smooth external bone texture. *Chirostenotes pergracilis* referred specimen TMP1979.20.1 was previously described as mature on the basis of muscle scar development. However, histological assessment of the *Apatoraptor* femur and *Chirostenotes* tibia reveals an abundance of primary bone tissue, reticular to plexiform vascularity, lack of remodeling, and only 1-2 growth marks in both individuals. These features indicate that both the *Apatoraptor pennatus* holotype and *Chirostenotes pergracilis* referred specimens were not yet skeletally mature, and were actively growing at time of death.

These preliminary histological results indicate that previous estimates of growth stage based on body size and external bone texture alone may be misleading for caenagnathids. This study has important implications for interpreting the growth, diversity, and taxonomy of caenagnathid oviraptorosaurs, demonstrating the need for further evaluation as the number of taxa represented in the literature may not reflect biological diversity.

**Funding Sources** Jurassic Foundation, NSERC Ontario Trillium Scholarship, University of Washington Burke Museum Vertebrate Paleontology Collections Grant, Dinosaur Research Institute

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### **Paleohistology & Paleopathology**

#### **A HADROSAUROID WITH AGE-RELATED DISEASES BRINGS A NEW PERSPECTIVE ON DINOSAUR SENESCENCE**

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Senile vertebrates are extremely rare in the fossil record, making their recognition difficult. Here we present the largest known representative of the Late Cretaceous hadrosauriform *Gobihadros mongoliensis*, exhibiting advanced age in its anatomy, bone microstructure, and non-traumatic bone pathology. The specimen, aside from its large size, shows an external fundamental system (closely spaced growth marks) in the external cortex of its bones, closure of transcortical channels indicating growth cessation, nearly complete remodeling of bone tissue (evidence of a long time passed since skeletal maturity), and primary calcium pyrophosphate deposition disease (CPPD) on its vertebrae and foot. Primary CPPD is an age-related pathology exceptionally rare in young animals, recognized here for the first time in a non-avian dinosaur. The presented specimen is important in the context of recognizing senile individuals from specimens that achieved terminal size and brings new information about diseases faced by non-avian dinosaurs.

**Funding Sources** National Science Center, Poland (www.ncn.gov.pl), grant no. 2019/32/C/NZ4/00150.

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### **Paleohistology & Paleopathology**

#### **SHELL HISTOLOGY OF THE TRIASSIC TURTLE, *PROTEROCHERSIS POREBENSIS*, PROVIDES NOVEL INSIGHTS ABOUT SHELL ANKYLOSIS**

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Shell suture obliteration (ankylosis) was exceptionally frequent in the earliest turtles, in contrast to post-Triassic taxa. Because modern turtles grow mostly along sutures, early ankylosis in Triassic taxa is intriguing. The Triassic turtle *Proterochersis porebensis* is known from numerous specimens, allowing observation of shell microstructure changes during ontogeny. All the shell-building elements, including the unusual dermal carapacial mosaic of that species, are histologically homogenous. The integument of *Proterochersis porebensis* seems to have been unusually thick, because the interwoven structural fibers of the dermis are commonly found in the visceral cortices of carapacial elements. Shell ankylosis occurred seemingly randomly in individuals of variable size, including small and morphologically juvenile, and completely obscured the initial bony composition. We propose that this phenomenon in the Triassic turtles can be an effect of early evolutionary stages of shell histogenesis and physiological mechanisms still used in shell and suture regeneration in modern species. Microstructural changes imply that *Proterochersis porebensis* could change habitat during ontogeny, small individuals appearing more aquatic and larger more terrestrial.

**Funding Sources** National Science Centre (Narodowe Centrum Nauki), Poland grant no. 2016/23/N/NZ8/01823

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

#### **A MARINE TURTLE (PROTOSTEGIDAE, CHELONIOIDEA) FROM THE ARLINGTON ARCHOSAUR SITE (CENOMANIAN), TEXAS**

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Protostegidae is a clade of large, marine-adapted chelonoid turtles that have been recovered from the Early

to Late Cretaceous, disappearing from the fossil record at the K–Pg boundary. The earliest representative of the family, *Desmatochelys padillai*, is known from the upper Barremian–Lower Aptian (120 Ma) of Colombia. It is followed shortly thereafter by a congeneric,

*Desmatochelys lowii*, from several Late Cretaceous Laramidian and Appalachian sites along the Western Interior Seaway of North America. Here we present a brief description and phylogenetic analysis of a newly identified protostegid from the Cenomanian (96 Ma) Arlington Archosaur Site (AAS) of Texas.

The AAS protostegid is represented by several isolated costals and a partial cranium. The costals are large, and the rib ends are exposed dorsally. Mostly notably, the cranium has a well-developed pineal foramen as in *D. padillai*, a character which unites the *Desmatochelys* clade. It also shares characters with other protostegids, such as jugal–quadrate contact. In a phylogenetic analysis, the AAS protostegid was positioned within the *Desmatochelys* clade as the sister to *Desmatochelys lowii*. The AAS protostegid and *D. lowii* share two characters to the exclusion of to the exclusion of *D. padillai*: a squamosal that contributes to the posterodorsal margin of the cavum tympani and the presence of a foramen palatinum posterius.

The AAS protostegid joins a growing list of newly identified turtle taxa from the Cenomanian of Appalachia, including a bothremydid (*Pleurochayah applachius*), baenid (*Trinitichelys maini*), Testudinata (*Naomichelys speciosa*), and trionychid. Because the AAS was positioned on a western Appalachian peninsula that stretched into the Western Interior Seaway, it was a coastal environment with evidence of terrestrial, freshwater, and marine geology and fossils. The presence of a fully marine-adapted protostegid turtle at AAS (in addition to a pleurodire with known marine adaptation) further demonstrates the extent of marine influence at the site.

**Funding Sources** National Geographic Society, Midwestern University

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### **Taphonomy, Paleoenvironments, & Stratigraphy**

#### **TAPHONOMY AND SITE FORMATION HISTORY OF VERTEBRATE-BEARING BRECCIA IN THE CAVES OF SUMATRA**

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Integrating thermal neutron tomographic imaging and the soil science of micromorphology has revealed the taphonomic histories of vertebrate assemblages in Sumatran cave deposits. Because tropical karst deposits are formed in very complex depositional environments, one might expect that the loss of microstratigraphic relationships and sedimentary constituents means that the taphonomic and environmental histories of incorporated fossil remains cannot be determined. However, these data have formed a detailed reconstruction of the mechanisms of accumulation in vertebrate-bearing cave breccia deposits from Lida Ajer, Ngalau Gupin and Ngalau Sampit caves in the Padang Highlands of western Sumatra for the first time. This study reveals principal evidence of the original animal community, taphonomic history and palaeoenvironment of Pleistocene Sumatra. These results strongly suggest that the conventionally labelled ‘homogeneous’ breccia are in fact a source of relatively untapped taphonomic data in archaeological and palaeontological studies in tropical caves. Further studies re-creating these methods would help establish the provenance of hominin and non-hominin mammal remains pertinent for our understanding of human evolution and migration in Southeast Asia. Should this novel multi-method contextual approach be developed further, it may strengthen our understanding of ancient rainforest dispersals, human occupation and dispersal, human/megafauna interaction, and faunal evolution and extinction events in Southeast Asia and beyond.

**Funding Sources** Postgraduate Research Scholarship, Palaeontology Research Scholarship, ANSTO Grant, Winifred Violet Scott Estate Fund, Australian Research Council (ARC) Future Fellowship

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### **Biomechanics & Functional Morphology**

#### **MUSCULATURE OF THE BIZARRE FORELIMB OF THE ALVAREZSAURID *MONONYKUS OLECRANUS* (DINOSAURIA: THEROPODA) AND ITS IMPLICATIONS FOR DIGGING**

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*Mononykus olecranus*, from the Late Cretaceous of Mongolia, was a small, nonavian theropod dinosaur belonging to the clade Alvarezsauria. Some have hypothesized that derived members of this clade may have had an insectivorous diet, and in particular might be specialized as ant or termite eaters, due to the unusual morphology of the forelimb. The forelimbs of *Mononykus* are distinctly stunted in size with only one digit and claw on each hand, and the perplexity of this morphology has prompted many hypotheses of their function. In order to investigate the hypotheses that these forelimbs were used in digging, we completed the first muscular reconstruction of the forelimb of *Mononykus*. Previous reconstructions of the musculature of the early theropod *Tawa hallae*, representing a primitive condition, and the ceratosaur *Majungasaurus crenatissimus*, which also displays extreme forelimb reduction, were used as a foundation and combined with an analysis of homologous osteological correlates found in *Mononykus* to develop a phylogenetically-informed muscle reconstruction and help us better understand its forelimb function. Comparisons with the myology of more basal taxa allowed us to identify extreme modifications in the forelimb that greatly improve the leverage of a number of muscles acting on the shoulder, elbow, and wrist. *Mononykus* exhibits an enlarged posteroventral process of the scapulocoracoid along with a projecting deltopectoral crest and internal tuberosity on the humerus, which suggests the substantial development of muscles like Coracobrachialis and Supracoracoideus and an increased emphasis on shoulder flexion and adduction. The massive olecranon process of the ulna indicates improved leverage of elbow extensors, and the expansion of the ectepicondyle of the humerus suggests improvement of the extension and flexion at the elbow (Anconeus and Supinator, respectively) along with extension of the wrist and digit. The near-midshaft location of the tubercle for Biceps brachii and Brachialis on the ulna also suggests powerful flexion at the elbow. The modifications identified in the forelimb musculature in this taxon suggest enhanced movement of the arm and claw along with increased stabilization of the joints, which is consistent with the hypothesis that *Mononykus* used its remarkably reduced forelimbs for digging or scratching when foraging for insects, similar to extant insectivorous diggers like the pangolin.

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## Education & Outreach

## ACTIVATING COLLECTIONS FOR STUDENT RESEARCH AND EDUCATION: THREE YEARS OF RESULTS FROM THE NATURAL HISTORY MUSEUM OF LOS ANGELES COUNTY STUDENT COLLECTIONS STUDY AWARD

Smith, Nathan, Celestian, Aaron, gusick, amy, Hendy, Austin, Thacker, Christine

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In 2016, the Natural History Museum of Los Angeles County created a Student Collections Study award, offered biannually to undergraduate and graduate students. Program goals are to activate collections for research, but also contribute to the training and education of the next generation of specimen-based researchers. Six award solicitations have been offered, but the program is temporarily halted due to the COVID-19 pandemic. To date, the award has funded 28 students (out of 58 applicants) with \$32,633 in awards (out of \$70,833 requested). The award has had impacts on the training, education, and research outcomes of a diverse group of students across the U.S. and internationally. Six awardees have completed Ph.D.s, three have completed M.S.s, and two have completed undergraduate degrees. Additionally, at least 14 awardee publications have been produced utilizing collections data. Awardee research has also benefited collections through additional curation (e.g., taxonomic revision) and increase of natural history data (e.g., specimen imaging).

Application numbers varied significantly over submission cycle ( $p = 0.005$ ), but overall have grown. Applications came from 20 U.S. states and 10 countries, with a marginally non-significant ( $p = 0.087$ ) disparity in domestic vs. international applications. Funding rates are higher for domestic (56%) vs. international (36%) applicants, though not significantly so. There is a significant difference ( $p < 0.001$ ) in the educational level of applicants, with the majority (76%) of applicants being Ph.D. students (18% M.S., 9% undergraduate), but funding success rates are comparable across academic status. Awardees have conducted research in 12 collections departments, with 45% of proposals submitted for research in paleontological collections. Our data show a marginally non-significant ( $p = 0.087$ ) gender disparity in applications, with 63% more men (36) than women (22) applying for awards. Despite this gap, funding rates for women (55%) are higher than for men (44%), though not statistically different. Several areas for improvement in proposal solicitation include increasing the female and undergraduate applicant pools, and soliciting more



applications from the “Global South” internationally. We envision a three-pronged approach of enhancing program solicitation, fundraising, and evaluation as the path to future sustainability and educational impact of this collections study award.

**Funding Sources** Natural History Museum of Los Angeles County, Research & Collections

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### **Romer Prize**

#### **THE DEVELOPMENT OF THE TETRAPOD LIMB MUSCULATURE**

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Based on the embryonic origin of limb muscles from opposed ventral and dorsal muscular masses in tetrapod embryos, A.S. Romer theorized almost 100 years ago, that the musculature of the tetrapod limb had evolved from the simple opposed ventral and dorsal muscles of the fin. In following decades, Romer and others described the development of the limb muscles, specifically the muscles of the shoulder and the thigh region, in different species of amniotes showing superficially similar patterns of muscle development. Using modern immunostaining techniques and confocal imaging I followed the development of both the forelimb and hindlimb musculature in representatives of six major clades of amniotes finding that their developmental pattern is not only superficially similar, but rather extremely stereotyped and conserved across all species. These conserved splitting patterns found among limb muscles make it possible to determine most of their homologies across amniotes on the basis of development alone, and challenge some assumed homologies. While retaining the same number of early divisions and their original topologies, therian mammals depart drastically from the inferred ancestral amniote developmental pattern by changes in position, translocations, extensions and reductions of the muscle divisions resulting from the early muscle cleavage, which result in the highly derived musculoskeletal anatomy of the therian shoulder, chest, hand, thigh and tail musculature; changes that can also be associated with the anatomical modification seen in the mammal-line fossil record.

The stereotyped pattern of amniotes, even with the transformed therian pattern, allows to reconstruct the

ancestral amniote pattern and anatomy, however this is not the case for the ancestral tetrapod pattern. Modern amphibians show a number of particularities regarding their life history, and limb and muscle development. Intriguingly, their limb musculature seems to follow a developmental pattern different from that of amniotes, not allowing to compare and establish homologies based on development. Study of actinopterygian fin muscle development, shows that the lissamphibian pattern might be unique to this group, however further investigation on lungfish fin muscles might help resolve the ancestral condition for sarcopterygian and tetrapod fin and limb musculature and provide additional information regarding the fin to limb transition.

**Funding Sources** Yale Earth and Planetary Sciences department  
Yale Peabody Museum

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### **Colbert Poster Prize**

#### **TOOTH BIOMECHANICS USING 2D FINITE ELEMENT ANALYSIS IN *DIMETRODON* (SYNAPSIDA, SPHENACODONTIDAE)**

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Throughout the early to middle Permian, *Dimetrodon* diversified into 14 recognized species, all with generally conservative cranial morphology. Conversely, dentition underwent significant change, from smooth-edged teeth with plicidentine (folded tooth roots) towards deeply rooted, non-folded teeth with serrated crowns. Derived members also increased in size, a trend shared with many early Permian amniotes, including emerging large-bodied herbivores. It is not currently known if these dental and size changes led to differences in feeding style and capabilities throughout the 20-million-year evolution of *Dimetrodon*.

2D and 3D models created from computed tomography of three *Dimetrodon* skulls were subjected to digital biomechanical experiments. Muscle reconstruction and dynamic analysis provided input forces, accelerations and tooth reaction forces. 2D finite element analysis applies bite force values onto the tooth structure, providing a localized examination of the transition from teeth with

plicidentine lacking serrations to non-folded possessing serrations. Variations in von Mises stress indicate that deep tooth roots more effectively dissipate stress to the surrounding jaw structure. Greater resistance allows higher imparted forces and reduces stress concentration in the tooth compared to those with plicidentine. The presence of denticles changes the effectiveness of the feeding apparatus from a grab-and-hold system to one adapted for eviscerating along shearing surfaces, as in theropod dinosaurs. This suggests that smaller *Dimetrodon* species were restricted to preying on slippery, aquatic prey and derived members adapted for ripping apart larger terrestrial amniotes.

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## Stem Tetrapod, Squamate, & Amphibian Diversity & Biology

### COMPARATIVE CRANIAL ALLOMETRY AND ONTOGENY OF A DIMINUTIVE BURROWING STEREOSPONDYL

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Developmental sequences are an increasingly significant subject in early tetrapod evolution. Studying ontogenetic patterns in temnospondyls provides important data for understanding morphological diversification in later lineages due to potential constraints as a result of ontogenetic allometry. The development of a diminutive stereospondyl is analyzed, based on a series of 13 prepared specimens among dozens more from the Late Triassic (Carnian) Jelm Formation of west-central Wyoming. Preliminary phylogenetic analyses suggest the placement of this taxon on the stem caecilian lineage sister to the clade containing caecilians and other diminutive stereospondyls *Rileymillerus* and *Chinlestegophis* – known from only one and two specimens, respectively. This lineage demonstrates diminution compared to their significantly larger

stereospondyl relatives, from the approximately 5 cm adult skull length of the Wyoming stereospondyls, to the 3.5 cm skull length of *Rileymillerus* and 3 cm skull length of *Chinlestegophis*. Miniaturization has previously been suggested to be a significant factor in modern lissamphibian evolution, which is explored again here. In the absence of histological proxies for age, we supplement skull length with qualitative features as indicators of growth stage, such as the depth and extent of ornamentation present on the dermal elements and qualitatively compared our analysis with the results of ontogenetic sequence studies of other temnospondyls. Preliminary qualitative analysis shows the loss of sinusoidal sutures between skull roof elements and the loss of an interfrontal element in adult specimens. We also quantified ontogenetic allometries of the skull using publicly available data of other ontogenetic sequences and geometric morphometrics. These specimens are members of a putative stem caecilian lineage, and the analysis of them will provide important information on the potential heterochronic processes constraining the evolution of caecilians. The comparatively large sample size and range of size classes of this new taxon allow for comparison of ontogenetic trajectories in this species relative to other stereospondyls as well as caecilians.

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## Paleohistology & Paleopathology

### RECONSTRUCTING GROWTH AND BODY SIZE IN *ALLOSAURUS* ACROSS ITS PALEOLATITUDINAL RANGE IN NORTH AMERICA

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Within some extant taxa, body size and life history traits vary considerably with latitude. Detecting latitudinal variation in many fossil taxa is difficult due to low sample sizes and/or poor temporal control. One exception is the theropod dinosaur *Allosaurus*, whose fossils have been recovered from across the Morrison Formation of North America. We created a novel paleohistological dataset of *Allosaurus*, including ten hindlimb elements of eight individuals from five North American localities. These were combined with published data for another nine individuals, creating a dataset spanning a 5° palaeolatitudinal range. All specimens in the dataset are

from the Brushy Basin Member or equivalent horizons in the upper part of the Morrison Formation, suggesting that they come from a narrow temporal interval. We used the circumferences of annual cortical growth lines to estimate body mass each year and mixed-effects modeling to estimate asymptotic size in skeletally mature specimens. We then regressed asymptotic body mass and maximum annual growth rate against paleolatitude. Somatically mature *Allosaurus* individuals vary at least 5-fold in both body mass and maximum annual growth rates. Within this substantial variation, neither asymptotic body mass nor maximum annual growth rate vary systematically with paleolatitude, mirroring the lack of geographic variation in size and growth found in similar studies of sauropodomorphs and ornithischians.

**Funding Sources** Jurassic Foundation Research Grant; Paleontological Society Steven M. Stanley Student Research Award; Adelphi University Horace McDonnell Summer Fellowship

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## Fishes Evolution & Distribution

### A PERMIAN ACTINOPTERYGIAN FROM THE MINNEKAHTA LIMESTONE OF SOUTH DAKOTA, USA

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The interrelationships and phylogenetic position of extinct Paleozoic and early Mesozoic ray-finned fishes (Actinopterygii) are obscured by a low-quality fossil record and understudy of late Paleozoic (Permo–Carboniferous) actinopterygians. To help address this issue, we describe a new genus and species of ray-finned fish from the late early Permian Minnekahta Limestone of South Dakota. This taxon is represented by two specimens, Field Museum of Natural History (PF) 3721 and Yale Peabody Museum (YPM) 18649. PF 3721 is an exceptionally well-preserved partial three-dimensional head and trunk preserving the external anatomy of and some internal elements from the skull, paired fins, and scale cover. YPM 18649 is a partially articulated, laterally compressed individual with a heavily disarticulated skull. This taxon has features of the paraphyletic "paleoniscoid" assemblage of lower actinopterygians, including an immobile maxilla with a narrow suborbital process and a broad postorbital expansion, a heterocercal caudal fin, and

rhombic ganoid scales. This species is approximately 10–15 cm in standard length, has a prominent snout, a lacrimal that is excluded from the oral margin, broad and triangular pectoral fins, triangular dorsal and anal fins, a deeply forked caudal fin, and scales ornamented with straight, concentric ridges at their margins (oriented parallel to corresponding scale margin) and diagonal ridges at their centers. We conducted an equally weighted maximum parsimony analysis in PAUP and a Bayesian analysis with the Mkv model of morphological evolution in MrBayes that placed this taxon in a polytomy with other late Paleozoic and early Mesozoic "paleoniscoids". Resolving the interrelationships of the "paleoniscoids" will require examining existing but understudied museum collections of late Paleozoic and early Mesozoic actinopterygians. We recommend the application of both parsimony and Bayesian inference techniques to address the problems in unraveling early actinopterygian interrelationships and to provide necessary caution and direction to future work.

**Funding Sources** Michigan State Distinguished Fellowship and EES Alumni Fellowship, a Rodney M. Feldmann Award (Paleontological Society), and a GSA Graduate Student Research Grant.

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## Mesozoic & Paleogene Mammals

### REASSESSMENT OF THE DENTAL REDUCTION SEQUENCE IN PLESIADAPIDAE (MAMMALIA, PLESIADAPIFORMES) AND IMPLICATIONS FOR EVOLUTIONARILY CONSERVED PATTERNS OF LOSS OF VESTIGIAL STRUCTURES

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Reduction in the size and number of anterior tooth loci is an evolutionary process that seems common in the mammalian fossil record. It has been documented for most clades of plesiadapiforms, a diverse radiation of primate-like animals from the Paleogene. Dental formulae have been used to assist in demarcating boundaries between species comprising apparent anagenetic lineages, and are often used as characters for phylogenetic analysis. Therefore, the details of which teeth are present or absent

may inform various questions related to species boundaries, or relationships among taxa. In Plesiadapidae, early members of the clade retain lateral incisors, canines and anterior premolars that are variably lost in later representatives. *Pronothodectes*, *Nannodectes*, and *Plesiadapis* have been diagnosed by differences in dental formulae: in particular *Nannodectes* is thought to differ from *Pronothodectes* in lacking a lateral incisor (i2), while *Plesiadapis* differs from both in additionally lacking a canine (c1).

We propose an alternative hypothesis in which *Nannodectes* differs from *Pronothodectes* through loss of the anterior premolar (p2) instead of through loss of i2. This hypothesis is based on several lines of evidence including the crown morphologies of the retained teeth in *Nannodectes*, comparisons to crown morphology of anterior loci in primitive Carpolestidae (the sister clade to Plesiadapidae), and details of the morphology of the roots and alveoli of the anterior dentition (revealed by microCT scans). For example, comparing the c1 and p2 of *Pronothodectes matthewi* (USNM 9332) to teeth in *Nannodectes intermedius* (USNM PAL 309902) reveals that the 'p2' crown of *N. intermedius* is more similar to the c1 crown of *P. matthewi* than to its p2 crown, and that the alveolus/root of the i2 in *P. matthewi* has a similar location and orientation to that of the 'canine' of *N. intermedius*.

Our new interpretation suggests the pattern of anterior tooth loss in the plesiadapids matches what has been documented in its sister clade, the Carpolestidae. This newly revealed similarity in the pattern by which structures become vestigial and lost in sister clades is surprising and intriguing. We explore the implications of these observations for differential diagnoses and phylogenetic relationships. More broadly, we investigate whether there are developmental or adaptive mechanisms that can explain such detailed and extensive parallels in dental reduction across time and phylogeny.

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## Avialan Evolution & Biology

### COMPARATIVE MORPHOLOGY OF THE PASSERINE CARPOMETACARPUS: IMPLICATIONS FOR INTERPRETING THE FOSSIL RECORD OF CROWN PASSERIFORMES

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The major crown bird subclade Passeriformes (passerines) comprises >6,000 extant species, making up over half of extant avian diversity. However, despite constituting one of the most diverse clades of living vertebrates, relatively little is known about the early evolutionary history of crown Passeriformes. Recent work provides a robust phylogenomic framework for extant passerine diversity, yet limited work has targeted passerine comparative anatomy on a broad phylogenetic scale. This has contributed to a long-standing misconception that passerines exhibit morphologically “uniform” skeletons, which may have dissuaded workers from pursuing large-scale comparative osteological studies of passerines. As such, many components of the passerine skeleton are understudied, and existing morphological matrices tend to identify relatively few phylogenetically informative characters for each skeletal component. This has hindered interpretation of the passerine fossil record, as many isolated fossils of passerine bones remain unassigned beyond the ordinal or subordinal level. Isolated carpometacarpi are preserved relatively frequently, with numerous passerine carpometacarpi known from the Cenozoic. Here, we present a detailed analysis of the passerine carpometacarpus, towards the goal of improving comparative morphological knowledge across Passeriformes. We identify morphological synapomorphies for major passerine subclades, sampling >100 taxa distributed across extant passerine diversity. Our approach marshalled both published characters and a substantial amount of previously undescribed anatomical variation, resulting in >50 phylogenetically informative characters that were optimized across a robust phylogenomic scaffold derived from recent studies. Our results show high levels of homoplasy within the passerine carpometacarpus, and that several frequently quoted “diagnostic” characters for particular clades exhibit previously unrecognized homoplasy. Despite this, we identify numerous diagnostic character combinations for key passerine clades. The character matrix from this study will aid in future diagnoses of isolated passerine carpometacarpus fossils, enabling insight into when and where representatives of major passerine clades first appear in the fossil record. This work provides a starting point for large-scale comparative analyses of the

passerine skeleton, and reveals a substantial degree of previously unrecognized morphological variation among Passeriformes.

**Funding Sources** NERC Research Training Support Grant NE/S007164/1; ERC TEMPO Starting Grant 677774; UKRI Future Leaders Fellowship MR/S032177/1.

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## Fishes Evolution & Distribution

### LAST FISH IN THE RHEIC OCEAN: PRELIMINARY REPORT ON EARLY CARBONIFEROUS CHONDRICHTHYANS FROM NORTHEAST TENNESSEE AND SOUTHWEST VIRGINIA

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The early Carboniferous (Tournaisian–Serpukhovian) is represented in northeast Tennessee and southwest Virginia as a narrow (~2–4 km) band of mostly marine sedimentary rocks approximately 135 km long and is made up (from oldest to youngest) of the Grainger Formation, MacCrady–Price Formation, and Newman (Greenbrier) Limestone, and represent a series of transgressive and regressive sea-level episodes. These marine rocks (and the fossils therein) are important because they preserve some of the latest records of the Rheic Ocean during its closure in advance of the Alleghenian Orogeny and subsequent uplift and deformation of Paleozoic strata in the southern Appalachians. At least two vertebrate specimens are known from these exposures (both chondrichthyans), a now lost specimen of “*Cladodus*” collected from Hancock County in northeast Tennessee in the mid-twentieth century and a ctenacanthiform chondrichthyan from southwest Virginia (EH23, a 1.5 cm median cusp of a fragmentary cladodont tooth collected in 1975, first reported here and attributed to cf. *Saivodus* sp.). Eleven samples were collected from Mississippian roadside exposures in northeast Tennessee and southwest Virginia and surveyed for fossils. Carbonates were dissolved in a buffered acetic acid solution, then screened and picked for vertebrate remains. Eight of the eleven samples produced macro- and/or microfossils, though no vertebrate remains have been recovered as of yet. The project continues in an attempt to locate the stratigraphic provenience of EH23

and other vertebrates, and better understand the marine systems of the latter Paleozoic from the southern Appalachians.

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## Turtle & Marine Reptile Diversity & Biology

### A EUROPEAN MOSASAURINE (SQUAMATA: MOSASAURIDAE) WITH AFFINITIES TO A CLADE FROM NEW ZEALAND

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The Royal Belgian Institute of Natural Sciences houses an extensive collection of Maastrichtian-aged mosasaur fossils. Among the numerous specimens of these marine reptiles is a skull and associated vertebral column, IRSNB 3211. This specimen was originally assigned to *Plioplatecarpus houzeaui*, but more recent studies have suggested that it represents an immature individual of *Mosasaurus lemonnieri*. New three-dimensional surface scans of IRSNB 3211 contribute to a detailed description of the specimen. Several characters strongly disagree with the diagnosis for *Plioplatecarpus houzeaui*, including the height of the coronoid process and the presence of zygosphenes and zygrantra. The proportions of the quadrate, the complex frontal/parietal suture, and the morphology of the posterior mandibular elements identify this specimen as belonging to Mosasaurinae. However, the morphology of the skull and vertebrae differs from that of *Mosasaurus lemonnieri*. Skeletal immaturity could account for some of these differences, such as the relatively longer rostrum or shorter quadrate of IRSNB 3211. However, ontogenetic change does not explain the differences in the morphology of the maxilla or braincase elements.

Phylogenetic analyses do not find a sister-group relationship between *Mosasaurus lemonnieri* and IRSNB 3211. The results of these analyses instead indicate a relationship between this specimen and *Moanasaurus mangahouangae* within a clade of mosasaurines from the Pacific Ocean. Characters that unite IRSNB 3211 with *Moanasaurus mangahouangae* include dorsal excavation of the maxilla for the external naris and cervical vertebrae with laterally extended postzygapophyses. However, skull

proportions and differences in dental morphology do not support assigning this specimen to *Moanasaurus mangahouangae*. The qualitative results of morphological comparisons and the quantitative results of phylogenetic analysis support assigning IRSNB 3211 to a new taxon. *Moanasaurus mangahouangae* and its closest relatives have previously been considered to have been endemic to New Zealand. The New Zealand fossils are from Campanian strata, indicating the clade originated in the Southern Pacific and migrated to the Tethys during the Maastrichtian. Other fossils in European collections are likely representatives of this new taxon, but general similarities between this moanasaur-like taxon and *Mosasaurus lemonnieri* masked the diversity of latest Cretaceous mosasaurines from Europe.

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## Mesozoic & Paleogene Mammals

### EVOLUTION OF DENTITION IN MAMMALIAMORPHA

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It seems that we know a lot about the evolution of cynodonts and the origin of mammals. But if we try to understand the evolutionary changes of the dentition in both groups, some gaps appear in the picture. *Brasilitherium* and other Brasilodontidae are closest to *Morganucodon* and *Sinoconodon* according to recent phylogenetic analyses. However, as Martinelli and Bonaparte noticed in 2011, the postcanine tooth replacement in Brasilodontidae is in the posteroanterior direction, whereas it is in an anteroposterior direction in basal mammaliaforms (e.g., *Sinoconodon* and *Morganucodon*). All Brasilodontidae have the multicuspidated lingual cingulum shelf on the lower postcanines (in *Morganucodon* on lower and upper) and all postcanines are single rooted (double rooted in *Morganucodon*). The recently described *Kalallitkigun* (only slightly younger stratigraphically than most Brasilodontidae) from Greenland has double roots, and advanced multicusped crowns in the lower postcanines, which further complicates the situation. The new study on the very small Carnian eucynodont *Polonodon*, that shows a small size difference between the smallest and largest postcanines, suggests that the first step to diphyodont dentition was made through the very small size of the

skull, such as in *Adelobasileus*. Analyzing the size of the small teeth of *Polonodon*, Sulej and coauthors recently suggested that the fast replacement of teeth in very small eucynodonts was possibly the first step in the evolution to diphyodont dentition as an example of heterochrony. However, we still do not know the sequence of the appearance of the apomorphies leading to the dentition of *Morganucodon*, such as double rooted teeth, multicuspidated lingual cingulum shelf, and diphyodont dentition.

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## Mammalian Skeletal Morphology

### AN ISLAND APART: ENDOCAST VARIATION WITHIN THE TENRECOMORPHA

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The afrotherian clade Tenrecomorpha contains a vast array of distinct sensory ecomorphotypes including arboreal, fossorial, semiaquatic, and even echolocating behaviors distributed among ~35 extant, narrowly distributed species. Small mammals with similar sensory adaptations exhibit highly specialized internal sensory structures, but despite their obvious interest in this regard, the sensory apparatus of tenrecs has yet to be investigated with modern techniques. Presented here is a geometric morphometric analysis of virtual endocasts of 23 tenrecomorph species (~67% of extant diversity), obtained from museum specimens and reconstructed via the use of  $\mu$ CT techniques. PGLS and PCA analyses identify allometry and evolutionary history as statistically significant factors underlying inter-clade shape variability. Distinct clusters form in the tenrec endocast morphospace corresponding to the independent evolution of aquatic and fossorial behaviors, with marked shape differences within the olfactory and cortical regions of the brain. Implications for the ancestral state of the Tenrecidae and the sensory system of the enigmatic fossil *Plesiorcyteropus* are also discussed. These results showcase remarkable instances of sensory convergence within the tenrecomorpha and provide a template for inter- and intra-clade analyses of this unique branch of the mammal tree.

**Funding Sources** NSF GRFP (Grant No: 1447167)  
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## Biomechanics & Functional Morphology

### MULTI-SCALE STUDY OF OSSIFIED TENDONS OF LATE CRETACEOUS ORNITHISCHIANS

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Ossified or mineralized tendons of non-avian Dinosauria originated from tendon-like structures, formed by metaplastic mineralization due to transformation from dense connective tissues to mineralized tissue. Elongated structures of micrometer-scale referable to collagen fibrils were identified in vascular canals of caudal tendons of the pachycephalosaurid *Homalocephale calathocercos* from the Campanian of Mongolia and saurolophine *Edmontosaurus* sp. (“*Ugrunaaluk kuukpikensis*”) from the Maastrichtian of Alaska, comparable to those reported previously in the mineralized tendons of birds. The structures were studied using a scanning electron microscope (SEM) and an atomic force microscope (AFM) to evaluate the location and function of the collagen fibrils in the caudal tendons. The AFM revealed a striped pattern, perpendicular to the long axis of each fibril with the size comparable to the collagen D-spacing (~67 nm). Although the D-periodicity is poorly defined and mostly faded due to diagenetic processes, we propose that the structures represent mineralized collagen fibrils and not crystallites of bioapatite, contaminants, or artifacts. Furthermore, we measured Young’s modulus and other mechanical properties of the studied tendons to evaluate their nanomechanical significance and function in the tail biomechanics. The results highlight the preservation potential of nanostructures in Cretaceous specimens and the utility of high precision imaging techniques for fossil material.

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## Permo-Triassic Ecosystems

### A NEW STAHLCKERIID FROM POLAND

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The Triassic central and eastern European record of dicynodonts is scarce. Aside from dubious remains from the Upper Muschelkalk of Germany reported as aff. *Dinodontosaurus*, more diagnostic materials of Stahlckeriids were found in the Stuttgart Formation of Germany and the Grabowa Formation of Poland. The latter consist of the Norian/Rhaetian large dicynodont *Lisowicia bojani* and a smaller form from the Wozniki locality. The Wozniki dicynodont is represented by a fragmentary skeleton of an immature individual including the preorbital and frontal part of the skull, mandible, parts of the cervical and dorsal vertebral column and ribs, pectoral girdle, and fragmentary limbs. The specimen represents a new taxon, as evidenced by its autapomorphic scapula, which is very slender, lacks pronounced spine, and has a hook-like, craniodorsally directed acromion, as well as a unique combination of characters in other parts of the skeleton. Based on the phylogenetic analysis using the newest (2021) iteration of dicynodont character matrix, the new species is recovered in a polytomy with *Eubrachiosaurus browni*, *Zambiasaurus submersus*, *Ufudocyclops mukanelai*, (*Stahleckeria potens* + *Sangusaurus*) and (*Lisowicia bojani* + *Pentasaurus goggai* + *Moghreberia nmachousensis* + *Placerias hesternus*), more derived than *Angonisauros cruickshanki*. The mandible is morphologically consistent with the Stuttgart Formation specimen, supporting the Carnian age of the Wozniki assemblage.

**Funding Sources** This work was supported by the Narodowe Centrum Nauki as the project No. 2017/27/B/NZ8/01543 (grant of Tomasz Sulej).

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## Turtle & Marine Reptile Diversity & Biology

## OBSCURE BY NAME: THE TALE OF THE ENIGMATIC *CHELYTHERIUM OBSCURUM*, THE FIRST DESCRIBED TRIASSIC TURTLE

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The Triassic (Norian) testudinate material from the vicinity of Stuttgart (now housed in The Natural History Museum, London, England) historically referred to *Chelytherium obscurum* von Meyer 1863 is exceptional for a number of reasons. It is the first described Triassic turtle—long before the much more famous *Proganochelys quenstedti* (1887) and *Proterochersis robusta* (1913)—as well as the oldest testudinate among the British paleontological collections and one of the oldest testudines in the world. Despite that, ever since the 19<sup>th</sup> century, it was catastrophically misunderstood and scientifically mishandled—erroneously described, never photographed, over the decades either routinely synonymized with *Proganochelys quenstedti* without any morphological arguments or proclaimed entirely undiagnostic, virtually ignored since 1865, and eventually nearly forgotten. The only available figures, published in 1865 and consisting of idealized pencil drawings, presented only part of the material attributed to that species, and rendered revision without personal study of the specimens virtually impossible. However, the recent reconsideration of proterochersid turtles, with improved understanding of their anatomy, allows reassessment of *Chelytherium obscurum* as a member of the Proterochersidae, subjectively synonymous with *Proterochersis robusta*. The most informative specimen, posterior right part of the carapace (not the first costal or skull fragment, as historically interpreted), captures a rounded caudal notch characteristic to the latter species, and a strong co-ossification of the ilium to the visceral surface of the shell. Despite nomenclatural priority, in accordance with the suggestions of previous authors, the name *Proterochersis robusta* is endorsed to be upheld.

**Funding Sources** National Science Centre (Narodowe Centrum Nauki), Poland grant no. 2016/23/N/NZ8/01823

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### Colbert Poster Prize

## EVOLUTIONARY PROCESS TOWARD ENDOTHERMY IN DINOSAURIA ELUCIDATED BASED ON NASAL STRUCTURES

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Extant amniotes are physiologically categorized into either endotherms or ectotherms in general, and it has long been discussed which metabolic status non-avian dinosaurs represent. Although numerous studies have attempted to answer this question, no consensus has been reached. The respiratory turbinate in the nasal cavity, which is present only in endotherms among extant amniotes, has been regarded as an important clue for elucidating the metabolic status of fossil forms, although comparative studies on this structure have rarely been conducted in both extant and extinct amniotes. In this study, the surface area and volume of the nasal cavities, which are expected to become larger in animals with a highly-developed respiratory turbinate, were measured in a wide range of extant amniotes based on CT-scan data sets and were compared between endotherms and ectotherms. Regression lines of these values against body mass were not significantly different between endotherms and ectotherms. However, significant differences were found when these values were regressed against the skull volume, suggesting that the large size of the nasal cavity associated with the presence of the respiratory turbinate is primarily important as a thermoregulation apparatus for the head, not for the entire body. This leads to a new hypothesis that a large nasal cavity may be a prerequisite for evolution of a relatively larger brain characteristic of endotherms.

The same measurements on the nasal cavity of the dromaeosaurid theropod *Velociraptor mongoliensis* reconstructed based on CT-scan data fell at an almost exact midpoint between the regression lines of endotherms and ectotherms against the skull volume. Based on the above hypothesis, this result suggests that the nasal cavity of this rather derived non-avian dinosaur was not large enough to carry out the role required for cooling a large brain that would have been present in a fully-endothermic animal. Thus, a further expansion of the nasal cavity was required for evolution of the modern avian condition. By integrating these results, a hypothesis that the development of the nasal cavity for selective brain cooling has led to the modification of the skull in



the dinosaur lineage toward birds is proposed. In turn, the reduction and downward displacement of the maxilla, which made the enlargement of the nasal cavity possible in derived avialans, may have coincided with the timing of acquisition of full endothermy.

**Funding Sources** The Sasakawa Scientific Research Grant

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## Dinosaur Systematics, Diversity, & Biology

### A NEW LAMBEOSAURINAE (DINOSAURIA, HADROSAURIDAE) SPECIMEN FROM THE UPPER CAMPANIAN JUDITH RIVER FORMATION WITH ITS BIOGEOGRAPHIC IMPLICATIONS

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The late Campanian Judith River Formation of northern Montana has long been recognized as a dinosaur-bearing rock unit. Despite this long history, and unlike the fossil record from the contemporaneous Dinosaur Park Formation, most vertebrate fossils from the Judith River Formation are isolated or incomplete, making high-level taxonomic identifications difficult. Lambeosaurine hadrosaurids are among the most well-known herbivorous dinosaurs during the late Campanian but remain ambiguous in the Judith River Formation. Here we report the first well-preserved and generically-identifiable lambeosaurine skeleton from the Judith River Formation, which contributes significantly toward a more comprehensive understanding of the dinosaur fauna of this unit.

The lambeosaurine skeleton described in this study was collected from a private ranch approximately 5 miles north of Winifred, Montana, in 1989. This skeleton is composed of partial cranial elements and virtually all major postcranial bones. The Judith River Lambeosaurinae possess characters that are all congruent with those of *Corythosaurus*. In contrast, the skeleton differs from *Hypacrosaurus* in the presence of the premaxilla-nasal fontanelle and the short neural spines of the dorsal vertebrae. It also differs from *Lambeosaurus* in

wide crest-snout angle and the laterally exposed ophthalmic canal of the laterosphenoid.

Although *Corythosaurus* is the most abundant hadrosaurid taxon in the Dinosaur Park Formation of Alberta, it has not been documented from the contemporaneous parts of the dinosaur-bearing formations in Montana (e.g., the Judith River and the Two Medicine formations). This is the first definitive *Corythosaurus* record outside of the Dinosaur Park Formation and is a significant southward biogeographic range extension of this taxon. Given the biostratigraphic and geographic extent of the ornithischian faunal zones previously recognized in Alberta, the affinity of the Judith River lambeosaurine to *Corythosaurus* suggests that the new specimen is from the Coal Ridge member of the Judith River Formation, and, by extension, we predict that many of the well-known herbivorous dinosaur taxa known from the Dinosaur Park Formation may also have less restricted geographic ranges than previously recognized, and extend further south into Montana.

**Funding Sources** Grant-in-Aid for JSPS Research Fellow (Grant Number 20J01696).

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## Avialan Evolution & Biology

### A HESPERORNITHIFORM FROM THE UPPER CRETACEOUS NEMEGT FORMATION IN THE GOBI DESERT OF SOUTHWEST MONGOLIA: IMPLICATIONS FOR PALEOECOLOGY OF INLAND HESPERORNITHIFORMS

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Hesperornithiformes are extinct foot-propelled diving birds that flourished during the Cretaceous. While hesperornithiform remains are recovered predominantly from marine deposits, a few have been collected from terrestrial deposits of Mongolia and North America. Among the hesperornithiforms, those from Mongolia represent the most inland occurrences with no marine influence. Here we report a new hesperornithiform tarsometatarsus from the Nemegt Formation in the Gobi

Desert of southwest Mongolia. An analysis of its bone microstructure, which has been suggested to reflect buoyancy control and the swimming mode of aquatic animals, will elucidate potential ecological adaptations in fully marine vs. inland hesperornithiforms.

The Nemegt specimen is represented by the distal end of the left tarsometatarsus, and shows the following features unique to non-hesperornithid hesperornithiforms: (1) the proximally positioned distal edge of metatarsal trochlea II which does not reach the base of metatarsal trochlea IV; (2) metatarsal trochleae III and IV which distally extend to a similar level; and (3) the equally mediolaterally wide metatarsal trochleae III and IV. Additionally, the broad and flat anterodistal surface of the tarsometatarsus suggests this specimen can be tentatively assigned to *Brodavis* sp.

The Nemegt *Brodavis* specimen is significantly different from the North American taxon in terms of the relative cortical bone thickness (RCBT). While less interiorly-habiting *Brodavis americanus* from the Frenchman Formation (Canada) has thick cortical bone (RCBT = 84.9%), the RCBT of the Nemegt specimen reaches only 66.7%, a pattern similar to that of extant foot-propelled diving birds. Coastally-inhabiting *Phalacrocorax capillatus* (Japanese cormorant) is known to dive deeper than interior-inhabiting *Phalacrocorax carbo* (great cormorants) and has higher RCBT. Along with the RCBT of extant cormorants, the differences in hesperornithiforms suggest that the Nemegt *Brodavis* has different aquatic adaptations compared to *B. americanus* from North America. As hesperornithiforms expanded their distribution to inland habitats, they might have changed their diving habits. Additional data of hesperornithiforms from marine deposits (e.g. those in the Western Interior Seaway of North America) will highlight more detailed adaptations of this clade in marine vs. inland habitats.

In the last 30 years, pterosaur tracks have received increased scientific attention as an important source of information on matters such as pterosaur terrestrial locomotion and ecology. The first named and most widely distributed ichnogenus *Pteraichnus* Stokes 1957 was erected for trackways consisting of tridactyl, laterally oriented manus and tetradactyl pes imprints combined with the feet overstepping the hands. Most Upper Jurassic occurrences have been reported from marginal marine deposits.

The Wiehengebirge in northwestern Germany mostly consists of Middle and Upper Jurassic marine rocks deposited north of the Rhenish Massif. During the Kimmeridgian, a regression resulted in the establishment of a tidal flat suitable for preservation of terrestrial tetrapod tracks. The most frequent finds are sauropod and theropod tracks, which are, among other locations, occasionally found in the Störmer quarry north of the village Bergkirchen. In late 2019, a sandstone slab with pterosaur manus and pes tracks was discovered in the quarry and subsequently reported to the LWL-Museum of Natural History Münster. Additional prospections in 2020 recovered more ichnites. The initial as well as most later finds are referable to *Pteraichnus*. Many finds are isolated manus and pes prints, ranging from 20 to 60 mm and 20 to 90 mm in anteroposterior length, respectively. However, there are at least three associated manus-pes-sets, two of which belong to a potential trackway. Additional observations include dry cracks, potential swim tracks, and possibly beak scrapes. So far, only a single manus hypichnium of the pterosaur ichnogenus *Purbeckopus* cf. *P. pentadactylus* Delair, 1963 had been described from Germany, making this the second occurrence of pterosaur tracks and the first of *Pteraichnus* in Germany. The high number and impressive size range of the tracks found, during only a few dedicated searches of the quarry, highlight its potential as an important new pterosaur tracksite.

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## Crocodylomorphs & Pterosaurs

### PTEROSAUR TRACKS FROM UPPER JURASSIC TIDAL FLAT DEPOSITS OF THE WIEHENGEIRGE IN NORTHWESTERN GERMANY

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## Mammalian Skeletal Morphology

### THE PETROSAL MORPHOLOGY OF *HEPTACODON OCCIDENTALIS* (ANTHRACOTHERIIDAE)

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Anthracotheres are a family of “suiform” artiodactyls that were distributed throughout North America, Eurasia, and Africa from the middle Eocene to the late Pliocene. Anthracotheres are frequently placed as stem hippopotamids, in part because of similarities in the petrosal morphology between the two groups. Petrosals of three taxa from the anthracothere subfamily Bothriodontinae (*Brachyodus onoideus*, *Elomeryx armatus*, *Bothriogenys* sp.) have been described in detail, but there have yet to be any descriptions of petrosals from the subfamily Anthracotheriinae, which split from Bothriodontinae in or before the middle Eocene. We recently acquired computed tomography (CT) data from an immature specimen of *Heptacodon occidentalis*, a member of the Anthracotheriinae. This specimen retains its deciduous dentition but its upper first molars are erupted. Petrosals are some of the first skull bones to chondrify, and they are typically ossified at or soon after birth. Petrosals are not known to change in shape after initial ossification, so the petrosal morphology of this individual should not be affected by its immaturity. *Heptacodon occidentalis* has characteristic similarities to hippopotamids: a ventral basicapsular groove, a sharp crista petrosa, a wide prefacial commissure fossa, a reduced mastoid region, and a hyperinflated tegmen tympani. A reduced mastoid region and a hyperinflated tegmen tympani may indicate a semiaquatic lifestyle. *Heptacodon occidentalis* also has a combination of features variably present in *E. armatus*, *B. onoideus*, and *Bothriogenys*. Like *B. onoideus* and *Bothriogenys*, but unlike *E. armatus*, *H. occidentalis* lacks a subarcuate fossa and has a hyperinflated tegmen tympani. Conversely, the internal acoustic meatus of *H. occidentalis* greatly resembles that of *E. armatus* but not *B. onoideus* and *Bothriogenys*. A petromastoid canal could not be identified in *H. occidentalis*, implying an absence of the structure. A petromastoid canal is absent for *E. armatus* and *Bothriogenys* but present for *B. onoideus*. This combination of features is particularly striking because *H. occidentalis* is from a different subfamily than the previously examined taxa; the petrosal morphology of *H. occidentalis* may aid in determining the plesiomorphic anthracothere condition and in identifying instances of convergence within Anthracotheriidae.

**Funding Sources** Funding was provided by an NSERC Discovery Grant awarded to J. Theodor.

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## Biomechanics & Functional Morphology

## TIMING OF ONTOGENETIC NICHE SHIFT IN *ALBERTOSAURUS SARCOPHAGUS* AND *GORGOSAURUS LIBRATUS* (TYRANNOSAURIDAE: ALBERTOSAURINAE) INDICATED BY MANDIBULAR BIOMECHANICAL PROPERTIES AND ONTOGENETIC CHANGES IN TOOTH MORPHOLOGY AND BITE FORCE

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Tyrannosaurids were the apex predators of Late Cretaceous Asiamerican ecosystems. Attaining gigantic adult sizes (9–12 m long, 2000–6000 kg), these predators underwent major morphological changes over their lifespan. Juveniles had long and slender hindlimbs, narrow skulls, and a ziphodont dentition, whereas adults had robust builds with massive skulls and incrassate teeth. Such dramatic morphological differences between juveniles and adults suggest that the diet, feeding behavior, and ecological niche of tyrannosaurids changed during ontogeny, although the timing of these changes is unknown. The albertosaurines *Albertosaurus sarcophagus* and *Gorgosaurus libratus* are known from nearly complete growth series and are among the best-represented tyrannosaurids in the world. These taxa provide a unique opportunity to study mandibular biomechanical properties and tooth morphology to identify changes in feeding behavior and bite force through ontogeny in tyrannosaurids. Dentary depth and width were measured at the 3<sup>rd</sup> and 9<sup>th</sup> alveolus on 12 specimens of *Albertosaurus sarcophagus* and 23 specimens of *Gorgosaurus libratus* to derive mandibular force profiles using beam theory. Crown base length and width of *in situ* teeth (anteroposterior and mediolateral diameters of the alveoli when absent) were also measured. Mandibular force profiles reveal that the symphyseal region is consistently stronger in bending than the middentary region in albertosaurines, indicating that the anterior extremity of the jaws played an important role in prey capture and handling through ontogeny. This conclusion is supported by results indicating that the symphyseal region of albertosaurines was adapted to withstand major torsional stresses, although not to the extent seen in *Tyrannosaurus rex* and spinosaurids. Because albertosaurines retained the same feeding strategy through ontogeny, prey size/type had to change between juvenile and mature individuals to explain the

constant mandibular biomechanical properties observed at all growth stages. This ontogenetic niche shift likely happened as individuals reached the late juvenile stage (~11 years old), a size at which we show dentition shifts from being ziphodont to incassate and bite force begins to increase exponentially. Mandibular force profiles reveal that large albertosaurines were capable of generating bite forces equivalent to similar-sized tyrannosaurines but far greater than similar-sized or larger non-tyrannosaurid theropods.

**Funding Sources** NSERC Discovery grant (DKZ), a University of Calgary Eyes High scholarship (JTV), and Izaak Walton Killam scholarship (JTV)

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## Crocodylomorphs & Pterosaurs

### THE PHYLOGENY OF AZHDARCHOIDEA (PTEROSAURIA) AND THE RISE OF TOOTHLESS PTEROSAURS

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The phylogeny of Pterosauria remains a highly contentious topic. Finer-scale phylogenetic relationships of Azhdarchoidea, and Azhdarchidae in particular, have been poorly explored as of yet. The fragmentary or poorly-preserved nature of many azhdarchoid specimens has precluded their placement in large-scale cladistic analyses of pterosaurs. The internal relationships of Azhdarchidae have yet to be tested in depth, as the majority of azhdarchid remains consist of isolated or scattered skeletal elements and are poorly covered by character sampling of existing phylogenetic datasets. To investigate this, I constructed a phylogenetic dataset of pterodactyloid pterosaurs with a focus on Azhdarchoidea. The taxon sample includes every diagnostic species of azhdarchoid, numerous unnamed azhdarchoid specimens, and an extensive outgroup sampling. The character sampling focuses on the anterior skull, cervical vertebra, and humerus; these elements are commonly preserved in azhdarchoids, and thorough character sampling can help resolve possible phylogenetic positions of isolated elements.

Parsimony-based phylogenetic analysis recovers a dichotomy in Azhdarchoidea between a Tapejaridae-Thalassodromidae-*Keresdrakon* lineage and a Chaoyangopteridae-Azhdarchidae lineage. The analysis

recovers a novel topology within Azhdarchidae, including a basal Gondwanan clade with prominent modifications of the upper and lower jaws, a predominantly European clade of robust and sometimes short-necked taxa, and a cosmopolitan clade of derived taxa with particularly elongate cervical vertebrae. Several azhdarchoids of uncertain affinities, including *Montanazhdarcho* and *Leptostomia*, are recovered as basal azhdarchids. The earliest potential azhdarchids appear in the Aptian–Albian; isolated elongate cervical vertebrae from the Late Jurassic and earliest Cretaceous are recovered as ctenochasmatids. After a decline in toothed pterosaurs across the Cenomanian–Turonian boundary, azhdarchids become the most diverse component of the toothless Coniacian–Maastrichtian pterosaur record. Azhdarchids with giant wingspans (>9 meters) do not form a clade, suggesting giant size evolved multiple times within Azhdarchidae.

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## Permo-Triassic Ecosystems

### TRACING THE ARCHOSAURIAN BEAK USING THE LATE TRIASSIC ARCHOSAURMORPH, *TRILOPHOSAURUS BUETTNERI*

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Beaks, which include some combination of edentulism (partial or full), lack of wear on edentulous jaw bones, densely-packed neurovascular foramina, and the presence of a keratinous sheath (=rhamphotheca), have evolved repeatedly. Keratinous beaks are present in all extant birds and turtles, and been inferred in some extinct synapsids and in other reptiles. The morphological details for rhamphotheca for nearly all archosaurs and archosauromorphs are lacking, despite their likely presence across multiple archosaurian lineages, because rhamphotheca are rarely preserved. Therefore, the early evolutionary history of rhamphotheca is poorly understood. Trilophosaurids are Late Triassic early-diverging archosauromorphs with partial edentulism and an inferred rhamphotheca. However, no rhamphotheca has been preserved for this group and detailed osteocorrelates of the presence or extent of keratin are missing. Here, we provide a detailed description of the edentulous portion of the skull and mandible of the trilophosaurid *Trilophosaurus buettneri* to evaluate

potential osteocorrelates of rhamphotheca in an early archosauromorph. The premaxilla of *Trilophosaurus* lacks abrasive wear around the ventral margin, and the neurovascular foramina in the ventral surface have no discernable patterns, in contrast to clear clustering and regularity in the neurovascular foramina in turtles and probing birds. Directional grooves around the naris are inferred to be the attachment of the rhamphotheca. The anterior portion of the dentary has small and less densely packed neurovascular foramina compared to turtles, but is comparable to non-probing birds (chickens). Posteriorly, the dentary preserves small anteroposteriorly oriented grooves trending parallel to the anteriormost edge of the dentition; these are interpreted as a possible attachment site for the rhamphotheca based on similarities seen in living turtles.  $\mu$ CT data reveal porosity difference in the cortical bone of the premaxilla and dentary. We interpret *Trilophosaurus* as having had a rhamphotheca that covered the premaxilla, some anterior portion of the nasal, and the anterior portion of the dentary up to where the dentition starts. The inferred keratinous beak sheath of *Trilophosaurus*, while showing some similarity to turtle and bird rhamphotheca, presents a combination edentulous jaw morphology not found in living archosaurs and lays the groundwork for future comparative studies for other beaked extinct archosauromorphs.

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### Mammalian Skeletal Morphology

#### PULLING TEETH: COMPARING BODY SIZE INFERENCES FROM TEETH VERSUS EMPTY SOCKETS

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Body size is a fundamental property of animals connected to myriad ecological and evolutionary factors including life history, diet, climate adaptation, and intra/interspecific interactions. For extinct mammals paleontologists often use tooth row length as a body size proxy. However, fossilized jaws often lack some or all

teeth, so lengths of dental alveoli are often substituted. The assumption that tooth dimensions should match socket dimensions is intuitive, but teeth may flare, taper, and/or overhang their sockets. Here, we quantify the relationship between tooth row length and alveolar length to determine whether the two lengths are interchangeable, if there are taxon-specific offsets, or if a new body-size-to-alveolar-length regression is warranted. We measured tooth row length and alveolar length before and after pulling teeth for hundreds of rodent jaws for several genera (*Onychomys*, *Chaetodipus*, *Reithrodontomys*, *Microtus*, *Neotoma*, *Sigmodon*, and *Peromyscus*). For these specimens, we measured tooth row and alveolar lengths using high-resolution photographs and ImageJ, a method that exceeds the accuracy and precision of caliper-based measurements. We also used Geomagic to collect finer tooth row and alveolar lengths from microCT scans for >150 rodent species across a wide body size range. For both physical specimens with teeth pulled and virtual microCT-derived measurements, we found that tooth row length and absolute alveolar length significantly differed for each genus ( $P < 0.01$ ) and thus cannot be used interchangeably. Preliminary regressions of microCT-derived tooth row and alveolar lengths across species ( $n = 50$ ) showed a tight relationship ( $R^2 = 0.99$ ). However, initial alveolar to tooth row length regressions derived from photographs were unexpectedly weak both within ( $R^2 \approx 0.2$ ) and among taxa ( $R^2 = 0.41$ ). We identified damage to the alveolar margin incurred during tooth loss, broken tooth roots obfuscating the alveolar margin, and differences in camera focal plane for toothed vs. toothless specimens as the cause of anomalous alveolar measurements that weakened these regressions. This case study underlines the importance of accounting for these sources of error in application of photograph-based alveolar measurements, particularly for tiny specimens. Overall, our results corroborate that alveolar lengths of toothless rodent jaws can be accurately transformed to tooth row lengths for use in body size estimation.

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### Education & Outreach

#### ILLUMINATING SCIENCE: WOMEN PALEONTOLOGISTS AND ILLUSTRATORS

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illuminating science: Women paleontologists and illustrators is an exhibition that was developed by the Paleontology Chair at University of La Rioja during 2019 and opened in February 2020 at La Casa de las Ciencias in Logroño, La Rioja. The main topics of the exhibition were: the participation of women in the findings and advances of geology and paleontology, the invisibility of their work, the differences between the sexes in educational matters, and the important role of illustration in this field of science. The objectives we wanted to achieve were for visitors to meet the pioneering women of geology and paleontology, discover new inspiring examples that are not necessarily male, learn about paleontology and geology, discover the wide world of illustration and paleoart, and the current women who are leading paleontological research at national and international level.

Debates regarding gender studies have become incredibly important in recent times. Likewise, the rescue and enhancement of the work of women, who for a long time were anonymous, is having a great reception both in academia and cultural institutions. It is important that the new narratives that are generated at the university level reach society, especially when they address issues that help to open the mind, make knowledge accessible to all, and advocate for a fairer world.

The exhibition focused on different blocks ranging from the Industrial Revolution to the present through the figures of Mary Anning, Elizabeth Philpot, Charlotte Murchinson, Gertrude and Alice Woodward, and pioneering Spanish paleontologists like Asunción Linares, Nieves López Martínez or Dolores Soria, who have led top research groups and held positions of great importance in universities and scientific institutions. Their work is an inspiration for the paleontologists of today and tomorrow, who carry out their work, not in the dark, but in the light and in a bright way.

In addition to the exhibition, complementary activities such as virtual guided tours and conferences through social networks were carried out due to the pandemic. Almost 10,000 people in a city of 150,000 habitants have been reached both in person and online with a great impact on the media. Through different feedback surveys, emails, and comments on social media we obtained feedback that 85% of the visitors were more interested and understood better the role of women in paleontology and in science.

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## Romer Prize

### **BIRD NEUROCRANIAL AND BODY MASS EVOLUTION ACROSS THE END-CRETACEOUS MASS EXTINCTION: A UNIQUELY AVIAN RESHAPING OF THE BRAIN LEFT ALL OTHER DINOSAURS BEHIND**

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Birds today are the most diverse clade of terrestrial vertebrates on Earth, and understanding why extant birds (Aves) alone among dinosaurs survived the Cretaceous-Paleogene (K-Pg) mass extinction is crucial to reconstructing the history of life. Hypotheses proposed to explain this pattern demand identification of traits unique to Aves. However, such identification is complicated by a lack of data from non-avian birds. To help fill this gap, I report a new, nearly complete skull of Late Cretaceous stem bird *Ichthyornis* preserving unprecedented data on the palatal and brain anatomy. I use these data as well as the most compressively sampled analysis of stem bird body masses yet published to revise our understanding of when major shifts in bird neurocranial anatomy and body size occurred and their possible contributions to K-Pg survivorship dynamics. *Ichthyornis* lacks the expanded cerebrum and ventrally deflected optic lobes that characterize extant bird brains but does exhibit a wulst, a dorsal projection of the brain corresponding to a region responsible for coordinating visual and somatosensory information. A wulst had previously only been observed among extant birds and has been hypothesized to have contributed to avian survivorship. *Ichthyornis* also had a segmented and possibly mobile palate, suggesting that this condition arose prior to the divergence of, and was ancestral for, extant birds. Previously, this condition was thought to be derived within Neognathae, one of the basal-most lineages within extant birds and for which a mobile palate serves as namesake. Many traits proposed by others to have influenced survivorship are known to scale allometrically (e.g. brain size), and so a robust understanding of body size evolution across the avian divergence is crucial. My estimates of ancestral body size were highly sensitive to outgroup (i.e., non-avian bird) sampling. I found no statistical difference in body sizes between stem birds alive just prior to the K-Pg extinction and early members of Aves either in the Late Cretaceous

or the Early Paleogene, inconsistent with patterns predicted by previous hypotheses that uniquely small body sizes contributed to crown bird survivorship. Together, my results indicate cognitive or sensory shifts associated with a reshaping of the brain may have contributed to the unique survivorship of Aves into the Paleogene, but not the presence of a wulst, mobile palate or uniquely small body sizes.

**Funding Sources** University of Texas at Austin Graduate School Continuing Fellowship

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

#### **NEW FOSSIL SEA TURTLES FROM THE LATE MIOCENE (TORTONIAN) OF CALIFORNIA INFORM THE EVOLUTION OF FEEDING ECOMORPHOLOGIES**

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Modern hard-shelled sea turtles (crown group Cheloniidae) are represented by six species with feeding ecologies that range from herbivorous to durophagous. The evolution of the ecomorphologies associated with these different diets has been recorded in the fossil record, with parallel iterations occurring in the Late Cretaceous and Paleogene. The timing of the origin of the extant radiation is thought to be in the Neogene, but is not well established. Traditionally, the middle Miocene taxa *Procolpochelys* and *Syllomus* were hypothesized to be within the crown, but this has been challenged by recent studies so that now the oldest certain crown cheloniids are from the Pliocene of eastern North America. Cheloniids have a sparse record after the late Miocene so that the timing and geography of the Miocene transition from stem to crown cheloniids is poorly understood. Here we present two previously unreported sea turtle fossils from the late Miocene (Tortonian) of California, USA, a skull from the Santa Margarita Formation of Santa Cruz County and a skull and partial skeleton from the Monterey Formation of Orange County. The Santa Margarita turtle (12–9 Ma) exhibits the narrow maxillary ridges typical of shearing ecomorphology, and some analysis place it as a member of the crown group, which could make it the oldest member of this clade so far known. The Monterey turtle (8.8–8.6 Ma) is slightly younger and is referable to the genus *Pacifichelys*, an

archaic durophagous form that is already known from the middle Miocene of California and the late Miocene of Peru. The report of the Monterey *Pacifichelys* (combined with fragmentary material from other formations in the region) further establishes that this archaic taxon was widespread and relatively abundant off the coast of western North and South America during the middle and late Miocene. In contrast, recent studies have shown that littoral pleurodires dominated the durophagous niche in the Miocene of the Atlantic basin. Taken together the new data allow us to tentatively refine the origin of feeding ecomorphologies in the crown group. For example, the relatively late appearance of the durophagous crown cheloniids compared with crown or (crown-adjacent) sharp-jawed cheloniids, such as the Santa Margarita specimen and *Syllomus*, not only coincides with the extinction of *Pacifichelys* and durophagous littoral pleurodires, but also mirrors ontogenetic dietary shifts within the modern species.

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

#### **DID MOSASAURS DRINK FRESHWATER? OXYGEN ISOTOPES REVEAL MIGRATION AND CHANGING WATER HABITATS IN THE WESTERN INTERIOR SEAWAY, NORTH AMERICA**

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It has long been debated whether the Cretaceous marine mosasaurs migrated and relied on coastal environments to feed and reproduce. Here we introduce a new perspective on mosasaur paleoecology and paleobiology through stable oxygen isotope ( $\delta^{18}\text{O}$ ) analysis of phosphate in pristine tooth enamel. We present a sclerochronological method in which teeth are sequentially sampled along growth lines to create a time series of water habitats that

the mosasaur inhabited. Each growth line is estimated to record one day; therefore, we are able to splice records of consecutive teeth to produce one to seven month-long life histories of a *Clidastes propython* from the Mississippi Embayment (Mooreville Chalk, Alabama) and of a juvenile and an adult *Platecarpus tympaniticus* from the central Western Interior Seaway (Niobrara Chalk, Kansas).

Importantly, the isotope results allow us to test anatomical models for mosasaur tooth replacement patterns. The tooth records correlate well when the sequential mode of tooth replacement with a back-to front replacement wave is applied. In the spliced 8-tooth record of the *C. propython*,  $\delta^{18}\text{O}$  is relatively constant  $\sim 20.0\%$  and gradually increases to  $\sim 22.0\%$  before a final sharp decrease to  $\sim 20.0\%$ . Superimposed on this long-term trend are prominent, semi-regular negative excursions in  $\delta^{18}\text{O}$  that occur every 12–20 days, are up to  $\sim 4.0\%$  in amplitude, and are well correlated in all spliced teeth. Similarly, the adult *P. tympaniticus* is characterized by a long-term  $\delta^{18}\text{O}$  increase from 16 to 18‰, with seven superimposed negative excursions, up to 2‰, that are repeated every 4–7 days. We find comparable trends in the juvenile *P. tympaniticus* records, with negative excursions of  $\sim 1\%$  which occur every 6–7 days. Notably, the records of all study specimens are characterized by semi-regular negative excursions in  $\delta^{18}\text{O}$ , indicating travel from marine environments to depleted freshwater coastal environments. Weekly to bi-weekly consumption of freshwater by two genera from disparate localities, and including two life stages, implies that mosasaur osmoregulatory function may have driven freshwater consumption, like their extant marine squamate cousins, the sea snakes, which must drink freshwater periodically. We further interpret the 3.7‰ mean difference between the Alabama and Kansas mosasaurs to reflect habitats of the more evaporative Mississippi Embayment versus the open marine central Western Interior Seaway.

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## Late Cenozoic Mammalian Evolution and Ecology

### PERAMELEMORPHIAN (BANDICOOT AND BILBIES) DIVERSITY OF THE ETADUNNA AND WIPAJIRI FORMATIONS, LATE OLIGOCENE TO EARLY–MIDDLE MIOCENE, SOUTH AUSTRALIA

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The oldest fossils referable to the marsupial order Peramelemorphia (which includes modern bandicoots and bilbies) dates to the late Oligocene of Australia. The earliest of these are from the Etadunna Formation in central Australia. Here we describe additional peramelemorphian material from the Etadunna Formation, as well as specimens from the Namba and Wipajiri Formations. The new material fills gaps in the evolutionary history of the order, showing that peramelemorphians were present in every faunal zone of the Etadunna Formation, and demonstrating for the first time the presence of Peramelemorphian in the Namba Formation. We describe three new species of *Bulungu*, including the oldest peramelemorphian known to date (from Faunal Zone A of Etadunna Formation) and a new genus and species of the family Thylacomyidae (which includes modern bilbies), which is  $\sim 10$  million years older than the previous earliest thylacomyid known. We also present a phylogenetic analysis that helps clarify the evolutionary relationships of the new taxa described here.

**Funding Sources** This study was funded by the Winston Churchill Memorial Trust and the Australian Biological Resources Study (ABRS).

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## Colbert Poster Prize

### CHANGES IN EMPLACEMENT PATTERN AND ORGANIZATION OF THE PALATAL DENTITION ACCOMPANIED THE EVOLUTION OF HERBIVORY IN EDAPHOSAURIDAE (SYNAPSIDA, EUPELYCOSAURIA)

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Although palatal dentition is a ubiquitous trait among early tetrapods, all major amniote lineages display a tendency towards its reduction. However, among the



earliest synapsids (i.e., ‘pelycosaurs’), edaphosaurids uniquely elaborated this structure, presumably in response to the evolution of high-fiber herbivory. Although previous studies have detailed the gross morphology of the palatal dentition among pelycosaurs, there has been little consideration of the extent to which feeding strategy influenced the developmental processes that governed the organization of the palatal dentition. We assessed  $\mu$ CT scans of the palatal dentition of *Edaphosaurus novomexicanus* and the ophiacodontid *Varanosaurus acutirostris* using indicators of emplacement patterns first outlined for *Captorhinus aguti*, a contemporaneous eureptilian taxon with a similarly arranged and implanted marginal dentition. These indicators include the cross-cutting relationships of teeth (i.e., when a newly-formed tooth causes partial resorption of an existing tooth), relative tooth size, and the location of emplacement pits on tooth-bearing element. Together, these indicators facilitate the recognition of vectors of tooth addition that inform broader organization of the palatal dentition. There is little pattern to emplacement in *V. acutirostris* and instances of cross-cutting relationships are rare, suggesting its denticle fields lacked strict organization. We consider this state to be representative of the ancestral pelycosaur condition. Conversely, the presence of a clear pattern of palatal tooth addition and numerous instances of cross-cutting relationships in *E. novomexicanus* indicate a greater level of organization of its denticle fields and potentially higher rate of tooth emplacement. This higher level of organization was likely an important component of the elaboration of the denticle fields in *Edaphosaurus* for use in oral processing of food as part of its herbivorous diet. It is known that there is a trend for increased numbers of denticles in derived *Edaphosaurus* species, and future research should investigate whether these increases were accompanied by further refinements to emplacement patterns. The increased organization of the palatal dentition in *E. novomexicanus* demonstrates that the evolution of high-fiber herbivory not only required changes to the morphology of the palatal dentition, but also to the developmental processes governing its formation.

**Funding Sources** University of Chicago Department of Ecology and Evolution Undergraduate Fellowship

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## Biomechanics & Functional Morphology

### THE DEVELOPMENT OF APPENDICULAR JOINT CARTILAGES IN *ALLIGATOR MISSISSIPPIENSIS*:

## EVOLUTIONARY AND BIOMECHANICAL IMPLICATIONS FOR ARCHOSAURIA

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Crocodylians and birds are the two surviving lineages within Archosauria, a clade of morphologically and ecologically diverse vertebrates that evolved highly disparate locomotor postures and appendicular joint morphologies. Recent studies have indicated that the American alligator, an extant crocodylian, use a wide spectrum of cartilaginous and other connective tissues to construct the hip joint. However, little is known about the distribution and use of cartilage throughout other appendicular joints, as well the ontogenetic transition of the crocodylian chondro-osseous interface and metaphyseal junction during early development. In particular, the hyaline cartilage on the proximal femur of late embryonic alligators possesses a convex, cone-like extension that inserts deep into the metaphysis. This morphology is not seen in juvenile and adults, but superficially resembles to the cartilage cone-metaphyseal trough articulation inferred in some early archosauromorphs. The method by which archosauromorphs reduced the cartilage cone during ontogeny and evolution, as well as the functional significance of metaphyseal fibrocartilage during such drastic changes in hyaline cartilage shape, are poorly understood. This study used dissection, histology, and imaging techniques to examine the ontogenetic transitions of proximal appendicular joints in the American alligator. Osteological correlates for joint cartilage were identified on skeletonized limb elements and compared with bony morphology seen in fossils. Shortly after hatching, alligators regress the cartilage cone via multiple invasion fronts of trabecular bones, such that the subchondral growth plate of hatchlings presents a convex surface perforated by numerous cartilage canals. Moreover, the metaphyseal sleeve appears initially similar to cartilage in structural composition, but progressively loses its matrix and become more akin to dense, regular connective tissue during the first year of growth and beyond. These results suggest that the ontogenetic loss of cartilage cone in the alligator is different from the evolutionary loss of cartilage cone hypothesized for early archosaurs, and that cartilage thinning, metaphyseal sleeve development, and metaphyseal bone morphology may be highly associated with ontogenetic and evolutionary changes in joint loading regimes.

**Funding Sources** Missouri State University Faculty Research Grant and Brown University Bushnell Postdoctoral Research Grant

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## Late Cenozoic Mammalian Evolution and Ecology

### REAPPRAISAL OF A SUPPOSED CHALICOTHERIID (MAMMALIA, PERISSODACTYLA) FEMUR FROM THE PLIOCENE OF CENTRAL MYANMAR

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Since the early 19th century, there have been a lot of Neogene vertebrate fossils reported and described in Myanmar. Among the early studies, Noetling, in 1897, described a large mammalian left femur from the Pliocene at Yenangyoung of central Myanmar and identified it as *Hippopotamus irravadicus* (Artiodactyla, Hippopotamidae). Later in 1951, Hooijer restudied this specimen and concluded that it appeared to be a chalicotheriid perissodactyl femur. He mentioned that the specimen would be the first record of the family in Myanmar. However, this has not been confirmed since then.

Here, we reappraise this fossil femur and demonstrate its familial and subfamilial affinities on the basis of the figures by Noetling, because its repository (perhaps in Geological Survey of India, Kolkata?) and specimen number are currently unknown. This femur is distinguished from that of the Hippopotamidae in having a third trochanter. It also differs from that of the Rhinocerotidae in having a proximodistally high greater trochanter, a slightly developed third trochanter on the proximal portion of the lateral side of the shaft, and moderately small and almost parallel keels of the femoral trochlea in dorsal view. In conclusion, we assign this femur to the subfamily Schizotheriinae of the Chalicotheriidae (Perissodactyla) based on the following characteristics: the greater trochanter is developed and proximodistally high; the apex of the greater trochanter projects proximally; the lesser trochanter is weakly developed; the third trochanter is thin and is projected on the proximal side of the shaft; and the keels of the femoral trochlea are almost parallel with a shallow groove. It

would be the first record of the Schizotheriinae in Myanmar, although additional fossils are necessary to completely confirm the presence of this subfamily in the Neogene of Myanmar.

**Funding Sources** JSPS KAKENHI Grant Numbers 15K05330 and 18H01327 to Naoko Egi

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## Romer Prize

### INSIDE THE “BLACK BOX” OF THE CRUROTARSAL ANKLE AND INSIGHTS INTO THE PEDAL ORIGINS OF LOCOMOTOR DIVERSITY IN ARCHOSAURS

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For 250 million years, the crurotarsal ankle has characterized one major branch of Archosauria. This ankle is a classic example of a distinct suite of morphological elements: a highly congruent peg-and-socket joint between unified crural elements and the calcaneum, wedge-shaped distal tarsals, and overlapping proximal metatarsals. The peg-and-socket joint in particular has sparked much debate on homology and phylogeny, yet how this joint and its many surrounding elements function together to achieve ankle mobility is not understood. As extant crocodylians retain this ankle structure, I address these fundamental questions: (1) What is overall crurotarsal ankle mobility? (2) What is the contribution of the peg-and-socket joint? (3) From what other joints does ankle mobility arise? (4) What morphological features can aid in the interpretation of ankle function in extinct taxa?

I measured *in vivo* 3-D crural, tarsal, and metatarsal kinematics of three juvenile American alligators across their locomotor and maneuvering repertoire using a combination of markerless and marker-based X-ray Reconstruction of Moving Morphology. 3-D joint kinematics of individual bone pairs were measured during stance phase to decompose total ankle movement and explore functional relationships to skeletal morphology. Of the over 125° of ankle flexion found, the peg-and-socket joint only accounted for ½ - ¾ of this degree of freedom at a given hind limb pose, with tarsometatarsal joints contributing most of the remainder. As numbers of joints on the medial and lateral sides of the ankle are

asymmetrical, differential distribution of dorsiflexion-plantar flexion across these joints ‘skewed’ the metatarsals, generating over 60° of ankle inversion-eversion. Less than 30° of ankle abduction-adduction was found, some of which was generated within the crus. Like many of their extinct relatives, *Alligator* is capable of postural extremes—from a belly sprawl to a high walk—suggesting this highly mobile ankle is key for maintaining plantar contact across these diverse hindlimb poses. Inversion-eversion is primarily responsible for accommodating the wide range of adducted and abducted hindlimb postures, underscoring the significance of mobile metatarsals. High-resolution form-function relationships from *Alligator* provide a new lens for interpreting variations in the crurotarsal morphological suite in the fossil record and reveal insights into the pedal origins of locomotor diversity in archosaurs.

**Funding Sources** This work was supported by a Brown University Ecology and Evolutionary Biology Doctoral Dissertation Enhancement Grant and the Bushnell Research and Education Fund.

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### Colbert Poster Prize

#### MORPHOLOGICAL VARIATION IN GREENHOUSE FROGS (*ELEUTHERODACTYLUS*, ELEUTHERODACTYLIDAE) AND DIVERSITY IN THE FOSSIL RECORD OF FLORIDA.

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Greenhouse frogs in the genus *Eleutherodactylus* are a diverse clade in the family Eleutherodactylidae that includes over 200 extant species mostly found in the Caribbean, and few taxa from northern Central America. Phylogenomic evidence suggests that *Eleutherodactylus* colonized and diversified in the Caribbean during the early Oligocene, but the fossil record is skewed towards Pleistocene cave deposits on the Antilles and northern Central America. Pre-Quaternary records are restricted to two localities in the Antilles (the Oligocene of Puerto Rico and the Miocene of the Dominican Republic), and the genus was recently identified in late Oligocene deposits of Florida. Fossils assigned to *Eleutherodactylus* are the most abundant anuran taxa in the localities of Brooksville and Live Oak-SB-1A, represented by more than 180 specimens. But it remains uncertain if the fossils

represent a single highly variable population of a single species or multiple closely-related species. To determine if the observed variation in the fossils represents one population or multiple species, we study the inter- and intraspecific variation in extant *Eleutherodactylus*. We do so by analyzing the size and shape variation using the most abundant bones (humerus, ilium, radioulna, sacrum, and urostyle) from these fossil localities, including 3D morphometrics of the humerus, which is among the most complete of elements. To contextualize this variation, we conducted a morphometric analysis on bones digitally isolated from CT scans of 27 species of *Eleutherodactylus* as well as ontogenetic series of two species of *Eleutherodactylus* (*E. planirostris*, n = 11; *E. glandulifer*, n = 18). We estimate body length (snout–urostyle length, SUL) using 10 different measurements on the same elements. The results of linear regression analyses show that our selected measurements have significant and positive relationships with SUL, with coefficients of determination ( $r^2$ ) above 0.85. Using these measurements, we estimate that SUL for *Eleutherodactylus* from the late Oligocene of Florida ranged from 17 to 25 mm, which is similar to SUL for extant species such as *E. planirostris*. The occurrence of *Eleutherodactylus* in late Oligocene deposits in Florida raises questions about the biogeography and dispersal of this genus, including when and how it dispersed to peninsular Florida, whether dispersal happened multiple times, and whether the extinct *Eleutherodactylus* in Florida represented more than one species.

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### Biomechanics & Functional Morphology

#### EXPLORING WALKING AND RUNNING GAITS OF *TYRANNOSAURUS REX* USING MULTIBODY DYNAMIC SIMULATIONS

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Large non-avian dinosaurs were subject to unique mechanical loading regimes that are not seen in extant animals. Although locomotor capacity plays a pivotal role in an animal's survival, dinosaur-specific morphology hinders direct extrapolation from extant taxa. An alternative is to use musculoskeletal modelling, where the skeletal elements are subjected to Newtonian mechanics. Here, we have developed a new musculoskeletal model of an adult *Tyrannosaurus rex* in OpenSim, based on high-resolution 3D scans of specimen RGM.792000. Using convex hulls, we have reconstructed the mass of each body segment, totaling 8,531 kg. Relevant musculature was restored using an extant phylogenetic bracket and published data, combined with our own dissections. The major challenge lies in finding muscle coordination patterns that result in locomotion. Such optimal control problems have previously been solved using genetic algorithms, which are extremely computationally costly (3000 hours per optimization). Previous studies on *T. rex* thus only focused on maximal speed. Instead, we have implemented direct collocation, a state-of-the-art approach for optimizing the behavior of musculoskeletal models. Results have been promising: computational time was reduced by four orders of magnitude ( $\pm 20$  minutes per optimization). This has allowed us to generate a gamut of gaits and speeds (0.5–6 m/s). Our results agree with previous estimates of maximal speed. To our knowledge, the sub-maximal walking gaits are the first such simulations of *T. rex*, and support the notion that *T. rex* employed relatively columnar limb poses to minimize muscle activations during locomotion. The drastic reduction in computational time has allowed us to explore how morphology and reconstruction techniques interact. The tail of bipedal dinosaurs powered their locomotion through muscular contraction, but was suspended passively by compliant ligaments. This combination results in a mechanical function of the tail unique to non-avian dinosaurs, which we have previously modeled in isolation. Our approach is to sequentially reintroduce uniquely dinosaurian features, and compare results to a dataset acquired from a more simplistic 8-tonne biped. Our ongoing investigations focus on the role a compliant tail plays in reducing the metabolic cost of transport and limb stresses at higher speeds. In this manner, we are exploring the mechanical grounds for the highly successful body plan of bipedal non-avian dinosaurs.

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### Preparators'

## PREPARATION OF THE NIEUWDONK COLLECTION (BERLARE, BELGIUM): A WINDOW INTO THE LAST GLACIAL AND INTERGLACIAL FAUNAS OF THE FLEMISH VALLEY

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The Nieuwdonk collection comprises a unique and diverse assemblage of Pleistocene mammals from the Flemish Valley. It covers an important part of Belgium's Quaternary fossil record and offers a window into the regional biodiversity of the last Ice Age and Interglacials (10 ka–126 ka). Within the collection, various remains of roughly 10 different taxa are represented, including herbivores and carnivores. Although sampling bias occurred during collecting in the 1970s, it still counts as the most complete Pleistocene collection originating from this classic location within the Scheldt basin.

After being privately owned for the last 45 years, the Nieuwdonk collection was recently acquired by the municipality of Berlare (province of East Flanders). This acquisition also encloses the transition from private to public property for which an open-access database and inventory was set up. Prior to the inventorization, a thorough restoration was mandatory for approximately 90 to 95% of all specimens.

As a result of years of poor storage conditions, almost all of the specimens suffered from desiccation and fragile cancellous bone tissue. Another important hazard was the visual propagation of pyrite disease, affecting around 40–45% of all pieces. Some items underwent previous restoration attempts with irreversible products such as epoxy glues, plaster, Arabic gum, and other unknown coatings.

The restoration project was set up during the corona pandemic with restrictions imposed by the Belgian government on daily activities. Because the collection needed treatment on site, a temporary restoration laboratory was constructed in the concert hall of the Cultural Center of Berlare. The restoration was carried out in a way that allowed the restoration team to perform their activities whilst the public could witness live preparation. This unique corona proof setting allowed for large social outreach and interest by local and national press. The Nieuwdonk collection will be accessible for scientific research and permanent museal display in the near future. This project is a small but important step

towards the valorization of important paleontological heritage on a regional scale.

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### **Quantitative Paleontological Methods**

#### **UTILIZING EXISTING MUSEUM COLLECTIONS AND GIS FOR PALEONTOLOGICAL SITE ASSESSMENT AND MANAGEMENT**

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Museum collections are held within the public trust for education and research purposes, and are curated to the highest scientific standards. Museums work with federal institutions to preserve paleontological specimens found on public lands in accordance with the Paleontological Resources Preservation Act. Maintaining and preserving these collections using scientific best practices has led to the digitization of paleontological collections. Online collaborative databases such as Integrated Digitized Biocollections and the Global Biodiversity Facility offer museums the chance to engage with other institutions to develop databases that share curated biological and paleontological collections. These types of museum collections can benefit spatial research as biodiversity data standards become more developed. However, this evolution has been slow, and to date the integration of paleontological collections with GIS is limited. The objective of this project was to create a dual geodatabase system incorporating both museum and field collections to assist with site management, assessment, and inventorying in Petroleum County, Montana. Utilizing customized Tasks panels, paleontologists can perform data entry and analysis without needing experience with GIS. A customized model toolbox allows users to run analyses related to their hypotheses. When activated through the Tasks panel, each model can be run separate or in sequence. Topology rules were added to assist with enforcing data integrity rules that comply with museum collection standards as new specimens are added to the geodatabases. This type of versatility and integration with museum collections can benefit management and site assessment practices both in the office and in the field. Records were compiled and entered through direct upload and the Tasks interface was used for testing. Intentional errors were introduced into the datasets to test the

topology rules defined in Tasks to ensure each rule was working correctly and forced the user to reenter data before saving. Models were easily manipulated through the use of Tasks and were updated immediately as data was entered into the database.

The dual geodatabase system created for this study provides an example of the potential of geodatabases to assist museums in streamlining management practices. While museums are already conducting assessment and inventorying, the addition of GIS can bring new possibilities for how their collections are applied.

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### **Preparators'**

#### **APPLICATION OF FULL COLOR 3D PRINTERS TO FOSSIL PREPARATION, RESEARCH, AND COLLECTIONS MANAGEMENT AT THE UNIVERSITY OF WYOMING**

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Full-color 3D printers (3D printers that can print photo-realistic 3D models) have opened up an exciting set of opportunities to improve and assist in paleontological endeavors including applications to collections management, fossil preparation, and to scientific research. Compared to traditional molding and casting techniques, 3D printing of fossil models in full color eliminates time intensive molding and casting work, eliminates storing molds, eliminates cast painting, allows for easy scaling of specimens to be larger/smaller, and allows for printing in transparent colors for visualizing internal detail. Models suitable for 3D printing can be generated from a variety of scanning technologies including, photogrammetry, structured light scanning, laser scanning, and computed tomography (CT). However, the degree of photo-like similarity compared to the original and the resolution of the model is, in part, dependent on the scanning and imaging resolution as well as scanning type. The University of Wyoming (UW) Geological Museum has begun utilizing a full color Stratasys J750 polyjet 3D printer housed at the UW Innovation Wyrkshop, part of the Engineering College. The J750 is capable of printing models with over 360,000 colors combinations (CMYK), at up to 14-micron resolution, with water-soluble

supports, and at a cost of ~\$15 per print hour. Here we present examples demonstrating the use of the J750 in paleontological applications with the goal of inspiring other institutions to consider using color 3D printers. We highlight the use of 3D color prints as aids in fossil preparation, particularly where bones are in close association or hidden. The ability to generate a photo-realistic print of the specimen at several stages during preparation documents important bone associations that are likely lost during preparation. Furthermore, segmented CT scans of specimens with the matrix printed as clear and bones printed as semi-transparent offers unique insight on preparation and research projects. We provide an example where we generated 3D color prints of bones prior to destructive analysis to capture original bone morphology. Lastly, we highlight the utility of 3D color prints in specimen display, loans, and sharing of fossil specimens between researchers, museum, and institutions.

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## Permo-Triassic Ecosystems

### A NETWORK-BASED BIOSTRATIGRAPHIC FRAMEWORK FOR THE BEAUFORT GROUP (KAROO SUPERGROUP), SOUTH AFRICA

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The biostratigraphic assemblage zone (AZ) framework of South Africa's Karoo Basin has become a standard for local and global correlations of Permo-Triassic synapsid, parareptile, temnospondyl amphibian, and archosaur-dominated assemblages. However, few studies have moved beyond a qualitative assessment of these tetrapod communities. We analyzed a dataset representative of the vertebrate fossil record (1402 occurrences of 115 species) from the *Cistecephalus* (CiAZ), *Daptocephalus* (DAZ), *Lystrosaurus declivis* (LAZ), and *Cynognathus* (CAZ) AZs using network analysis to compare alternative assemblage zone frameworks and develop a data-derived biostratigraphic model that facilitates geological and paleontological research. Our results show that older frameworks and those based on lithostratigraphic units obscure the communities. The CiAZ is not well supported in any framework, most likely because it relies more

heavily on lower-resolution historical occurrences and older biostratigraphic schemes. The LAZ is well supported across all network-derived frameworks, and is likely a reflection of significant shifts in community structure during the end-Permian mass extinction event. Our data also identify possible new communities within the uppermost LAZ and lowermost CAZ. A 'mega-community' shift at the base of the CAZ could represent a time-hiatus at this stratigraphic interval, and supports possible Landian-Carnian biostratigraphic links with South American and eastern African assemblages. In addition, new meter-level occurrence data from the DAZ show that sampling stratigraphic intervals of 20 to 50 m thickness are sufficient to capture the network-derived Karoo AZs. Consequently, the first and last appearance datums used to delineate AZ boundaries could be defined at 20–50 m accuracy. Our network-based biostratigraphic framework has the potential to clarify correlations and can be used to design future field campaigns in the Karoo Basin and across southern and eastern Africa.

**Funding Sources** Women's Board, Grainger Bioinformatics Center, Field Museum of Natural History, Chicago, IL.

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### Symposium - Vertebrate dental ecomorphology: Tooth traits that reflect ecology

#### TRANSIENT CHANGES IN RELATIVE CROWN AREA AND ENAMEL THICKNESS IN THE INSECTIVOROUS MAMMAL *MACROCRANION* DURING THE PALEOCENE–EOCENE THERMAL MAXIMUM

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Variation in relative molar crown area (RCA) and crown component (enamel and dentine) thickness are promising phenotypes in which to measure mammalian response to climate change because of their proposed links to both inherited adaptation to diet and non-inherited, plastic

response to nutritional deficit during ontogeny in modern species. One system in which to explore these potential connections is in insectivorous mammals during the Paleocene–Eocene Thermal Maximum (PETM) ~56 Ma. During this interval there was a rapid climatic shift towards warmer mean annual temperatures by ~5–8 °C for ~175 ky, followed by a recovery to pre-PETM mean annual temperature. This warming is associated with evidence of changes in insect abundance and diversity, providing a plausible driver of change in a diet-related phenotype among mammalian insectivores.

We asked whether RCA and associated enamel thickness changed through the PETM in the abundant insectivorous species *Macrocranium junnei* and explored whether any potential change met expectations for dietary adaptation or nutritional deficit. Floral and insect turnover begins in the late PETM, and therefore we predicted that diet- or nutrition-driven change should occur at that time. In addition, nutritional deficit should affect overall crown size and dentine thickness of all three molar positions, but not necessarily enamel thickness based on a prior experimental study of malnutrition using rats as a model organism. We measured RCA from isolated m1–3 (N = 232) and absolute enamel and dentine thicknesses from a subset of m2s and m3s using digital  $\mu$ CT cross-sections and previously published measurement protocols. RCA was constant through much of the PETM, but changed in the late-PETM, resulting in transiently smaller m2–3 compared with m1, contemporaneous with changes to the invertebrate fauna. However, there is little evidence for a shift in m1 crown area, contrary to a model of nutritional deficit. Furthermore, late-PETM specimens have moderately thinner enamel but do not have thinner dentine. Although more work is required to unequivocally argue for RCA change as an adaptive response, based on these results we can reject the hypothesis that transient change was due to non-heritable effects of nutritional deficit.

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## Biomechanics & Functional Morphology

### RECONSTRUCTING ELBOW ARTICULAR CARTILAGE OF THE SAUROPOD DINOSAUR *DREADNOUGHTUS* USING MULTIBODY

## DYNAMICS AND THE EXTANT PHYLOGENETIC BRACKET

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Reconstructing articular cartilage shape and thickness remain a challenge for biomechanical studies of extinct organisms, largely due to poor preservation of cartilage in the fossil record. Several previous studies on extant archosaurs and mammals have shed light on these important aspects, but such insights have yet to see regular implementation in biomechanical modeling. Here, we performed a case study examining the elbow joint of the titanosaurian sauropod *Dreadnoughtus schrani* using articular cartilage reconstructions that are morphologically and kinematically constrained by extant phylogenetic bracketing (EPB). EPB investigations of alligator and chicken articular cartilage revealed a spherical anterior projection of cartilage on the distal humerus providing articulation with the radius during flexion. This shape occurs only in 3D scans of the articular cartilage; its presence is not directly mirrored by the morphology of the underlying bone in each taxon. Using a multibody dynamic simulation created in MSC Adams of the left elbow of *Dreadnoughtus*, we modeled the effect of three different cartilage reconstructions based on these EPB findings. Our three reconstructions differed in mediolateral placement of a cartilage sphere and its anteroposterior thickness so as to encompass a range of possibilities for the condition in *Dreadnoughtus*. We tracked bone kinematics during flexion of the elbow to 90° and produced proximity (contact) maps for time steps throughout each simulation in Geomagic Qualify. These maps allowed us to examine the area of contact between the humeral and radial cartilage throughout each simulation. Each model demonstrated varied levels of stability, and each also varied in the extent of cartilage contact area. Our third reconstruction exhibited the highest degree of kinematic stability and greatest area of contact between the radial and humeral articular cartilages. Therefore, we predict: (1) *Dreadnoughtus*, and likely other extinct archosaurs, had an anterior spherical projection of cartilage on their distal humerus for articulation with the radius and; (2) this spherical cartilage was likely more similar in position and form to that of our third reconstruction: of moderate anteroposterior

protrusion and centered over the radial condyle of the humerus. Our results demonstrate that by using EPB and computer models, it is possible to significantly advance understanding of articular cartilage shape and thickness in extinct organisms.

**Funding Sources** NSF DGE Award 1002809, Drexel University, Rowan University

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## Quantitative Paleontological Methods

### 3D SURFACE SCANNING AND DIGITAL 3D RETRO DEFORMATION OF TIKTAALIK ROSEAE FOR MUSEUM EXHIBITION

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The elpistostegalian tetrapodomorph *Tiktaalik roseae* is an icon of vertebrate paleontology and macroevolutionary transition. Many of the general anatomical features that make *Tiktaalik* a critical taxon in understanding the water-to-land transition for tetrapods (a neck, ‘elbowed’ pectoral fins with no digits, dorsally oriented orbits, etc.) are familiar to the public due to the substantial scientific outreach and popularization surrounding this taxon. Accordingly, we at the Idaho Virtualization Lab in the Idaho Museum of Natural History applied recent advancements in digital 3D surface scanning and digital modeling software, to create the world’s first 3D printed display of the holotype skull (NUFV 108) of *Tiktaalik roseae*. Direct surface scans of NUFV 108 and a referred specimen (NUFV 109) were created using a Faro Edge Arm articulated laser scanner. The subsequent scans have been made available to the public via Morphosource, including a raw surface scan file of the holotype skull. Surface scans were then used in conjunction with a ZBrush digital sculpture life reconstruction. As our reconstruction was created for exhibition purposes, anatomical comparison with other tetrapodomorphs (particularly *Acanthostega* and *Parmastega*) were made to inform details of the dentition, palate, and skull roof which are not clear in the actual specimens. For example, the shape, size, and number of fangs on the vomers, palatines, and dentary are difficult to make out on the surface scan as the mandibles are mostly in occlusion. In published  $\mu$ CT reconstructions the fangs are broken and bent, but the spacing of fangs and empty alveoli are clear.

Therefore we used the morphology of *Acanthostega* fangs to increase our confidence in the finished shape and distribution of these impressive features. *Acanthostega* was also critical to reconstructing the morphology of marginal tooth rows obscured in the surface scan. NUFV 108 is compressed dorsoventrally, requiring a reassembly of the bones of the skull roof along their break points. Unsurprisingly, this resulted in a more dorsal positioning of the orbits with the highest points along the medial margins. After this painstaking effort we are confident that a more extreme orbit morphology, like that of *Parmastega*, is not the condition in *Tiktaalik*. When reconstructed, the division between dermal cheeks and midline skull roof, which allowed some cranial kinesis, is clear. Our 3D printed reconstruction is currently displayed at the IMNH.

**Funding Sources** Idaho Museum of Natural History, Idaho Virtualization Laboratory

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## Non-avian Theropod Systematics, Biology, and Evolution

### ORIGIN AND DISPERSAL OF DERIVED TYRANNOSAURINES (THEROPODA: TYRANNOSAURIDAE) IN ASIAMERICA: INSIGHT FROM A MIDDLE CAMPANIAN TYRANNOSAURINE FROM ALBERTA, CANADA

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Thanks to new fossil discoveries, the known taxonomic diversity of tyrannosaurine tyrannosaurids has more than doubled in the last twenty years, greatly improving our understanding of the evolutionary history of this group. One of the more recently discovered species, *Thanatotheristes degrootorum* from the mid-Campanian (~79.5 Ma) Taber Coal Zone of the Foremost Formation of southern Alberta, represents the earliest known occurrence of a derived tyrannosaurine (i.e., the clade containing the most recent common ancestor of *Daspletosaurus*+*Tyrannosaurus* and all of its descendants). Interestingly, *Thanatotheristes* possesses a combination of features found in two distinct tyrannosaurine lineages: the North American *Daspletosaurus* clade and the Asiatic tyrannosaurine clade containing *Zhuchengtyrannus*, *Tarbosaurus*, and



*Tyrannosaurus*. Although it lacks several characteristics of the genus *Daspletosaurus*, *Thanatotheristes* still shares with this taxon deep grooves in the subcutaneous surface anterior to the antorbital fenestra, a maxillary tooth count of at least 15, and a probable dorsoventrally constricted jugal ramus of the maxilla. These features are absent in Asiatic derived tyrannosaurines. At the same time, *Thanatotheristes* shares with Asiatic tyrannosaurines prominent subcutaneous ridges ventral and anteroventral to the antorbital fossa, a shallow suborbital region of the jugal with a thickened and rounded orbital margin, an anteromedial-orientation of the lacrimal-frontal contact, and anteroposterior ridges along the anterior margin of the intermandibular symphysis. The combination of such characteristics within a single taxon indicates that *Thanatotheristes* occupies a phylogenetic position close to the common ancestor of North American *Daspletosaurus* and the Asiatic tyrannosaurine clade *Zhuchengtyrannus*+*Tyrannosaurus*. These data suggest that derived tyrannosaurines originated in North America and dispersed into Asia sometime in the early–mid Campanian, paralleling dispersal patterns observed in edmontosaurin hadrosaurids and centrosaurine ceratopsids. In light of this dispersal scenario, we hypothesize that future discoveries of tyrannosaurids from pre-upper Campanian deposits in Asia (>~77 Ma) will show morphological similarities to *Thanatotheristes*.

**Funding Sources** University of Calgary, Izaak Walton Killam Memorial Scholarship, Royal Tyrrell Museum Cooperating Society to JTV; NSERC Discovery Grant to DKZ

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## Preparators'

### CONSERVATION OF A MOLD AND FIRE-DAMAGED MOSASAUR SPECIMEN

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The partial skull and associated postcranial skeleton of a mosasaur was originally collected from the Late Cretaceous Mooreville Chalk in Dallas County, Alabama by a private collector and housed in a home collection. The collector prepared the specimen using standard

mechanical techniques and used an unknown thick synthetic resin (possibly a five-minute epoxy) as an adhesive. Unfortunately, the collector's residence was destroyed in a fire, but staff from the McWane Science Center were invited to salvage the fossil material from the home's basement and the specimen was donated to the museum.

The fossils were subsequently loaned to the Texas Vertebrate Paleontology Collections for research, where they were housed in polyester batting lined acid-free boxes and stored in gasketed, epoxy-coated collections cabinets. During a condition assessment prior to preparation and casting, mold growth was discovered on many of the bones. Excessive sooting of the fossils and yellowing and peeling of the adhesive was observed, especially on the upward-facing surfaces of the bones that were exposed to fire. In addition to discoloration from heat and smoke damage, bones exhibited crazing and cracking. This type of damage is discussed in conservation literature, but is rarely documented in real-world conditions. Fortunately, fires in museum conditions are now rare, and field and laboratory methods that employ fire avoid prolonged temperature and direct exposure to flame.

Conservation was undertaken to stabilize the bones for mold-making. The bones were also cleaned for photography and study. Mold was mechanically removed under exhaust ventilation using cotton swabs and neutralized with ethanol. Soot was likewise removed using swabs, non-latex makeup sponges, and ethanol. Degraded adhesive was softened using a cheesecloth poultice saturated with a 50/50 mixture of ethanol and acetone applied to the surface of the adhesive. Excess adhesive was mechanically removed where possible. In areas where peeling adhesive separated the external layers of the fossil, the bone was re-adhered. Cracked areas were consolidated with Paraloid B-72 in acetone, and broken fragments were successfully reconstructed. These conservation treatments allowed for the successful molding and casting of the bones with no further damage, and facilitated the study of the now-clean and reassembled fossils. After two further years in storage, the fossils exhibit no further mold growth or physical deterioration.

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## Dinosaur Systematics, Diversity, & Biology

### COMPARATIVE STUDY ON THE ROSTRAL ENDOSKELETAL MORPHOLOGY OF THE

## TRIGEMINAL NERVOUS SYSTEM IN EXTANT ARCHOSAURS

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In archosaurs, diversity of rostral morphology (e.g., degree of elongation, curvature, and flattening) has been suggested reflecting their eating habits and sensory-accelerated foraging behaviors. Major stimuli received on the surface as well as within the oral cavity are transmitted via the trigeminal nervous system. Nerve pathways of this system leave some osteological correlates on the surface and inside of the cranial bones (i.e., rugose sculptures, foramina, and bony canals). These traits have been used as classical evidence for the presence of rostral integuments in fossil species. However, their endoskeletal nerve pathways in extant species have not been investigated in detail.

In this study, we used a non-destructive soft tissue observation method (DiceCT) to observe and compare such pathways among 11 extant archosaur species and identified phylogenetically justifiable osteological correlates of major trigeminal branches in Archosauria. As a result, we were able to discern more anterior, finer distribution patterns of these nerve branches than those described in previous studies, particularly in the upper jaw.

Between the two species of crocodylians examined (*Crocodylus siamensis* and *Paleosuchus palpebrosus*), the branching pattern was well-conserved. Whereas the maxillary nerve branches went predominantly through bony canals of the jugal and maxilla, no branches crossed the boundary between the two bones. In the premaxilla, the maxillary and ophthalmic nerve branches extending through the bony canals partly formed an anastomosis. In Aves, the ophthalmic pathway within the premaxilla was similar among many lineages although species foraging underwater (*Phalacrocorax carbo*) showed a different branching pattern reflecting the dwarfing of the external naris. In Palaeognathae and Galloanserae species, some maxillary nerve branches entered the bony cavity formed by the maxilla and palatine from the anteroventral aspect of the antorbital sinus.

Based on these observations, the association between the trigeminal nerve branches and bony canals extending through the premaxilla, maxilla and jugal was confirmed representing ancestral traits of Archosauria. This conservativeness assures that some nerve branches

passing outside these bones can be reconstructed in fossil species, contributing to a better understanding of their sensory behaviors, evolutionary trends of the tooth-loss phenomena and development of the rhamphotheca in edentulous taxa of dinosaurs.

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## Romer Prize

### BONE HISTOLOGY OF MULTITUBERCULATE MAMMALS POINTS TO A LIFE HISTORY STRATEGY SIMILAR TO THAT OF PLACENTALS, NOT MARSUPIALS

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The remarkable evolutionary success of placental mammals has been partly attributed to their reproductive strategy of prolonged gestation and birthing of precocial neonates. Although this strategy has conventionally been considered derived relative to that of marsupials with short gestation times and altricial neonates, mounting evidence has challenged this view, suggesting that the placental strategy may be plesiomorphic for therians (metatherian-marsupial and eutherian-placental lineages). Until now, the fossil record has been relatively silent on this debate, but here I establish a new framework for studying the life histories of small-bodied fossil mammals. I examined cross-sections from the femora of a phylogenetically and ecologically diverse sample of 35 extant marsupials and placentals, including adults and subadults. I found that marsupial cortices are predominantly well-organized lamellar bone, whereas placental cortices consist of a disorganized bone layer bordered internally and externally by lamellar bone. These distinct patterns likely reflect their different life histories. Indeed, using phylogenetic comparative methods I found that the amount of outer-cortex lamellar bone is positively correlated with weaning age and negatively correlated with gestation length. I then applied this histological correlate of reproductive strategies to Late Cretaceous and Paleocene members of Multituberculata, an extinct mammalian clade that is phylogenetically stemward of Theria. Multituberculate bone histology closely resembles that of placentals, suggesting that they had similar life history strategies. Using a predictive regression model derived from my extant dataset, I roughly estimate that multituberculates in

my sample were weaned at ~30 days, similar to small placentals (e.g., rodents). That a clade of stem therians exhibits evidence of placental-like life histories lends support to the hypothesis that intense maternal-fetal contact characteristic of placentals is ancestral for Theria. Alternatively, multituberculates and placentals may have independently evolved similar life history strategies; convergent evolution of complex traits has been well documented in early mammalian evolution. In either case, my results refute the hypothesis that the Cenozoic rise of placentals was driven by unique life history innovations and shed new light on the diversification and ecological roles of mammals during the Mesozoic and early Cenozoic.

**Funding Sources** NSF Graduate Research Fellowship, Society of Vertebrate Paleontology, Paleontological Society, American Society of Mammalogists

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

### **NEW JURASSIC TURTLE FROM THE MORRISON FORMATION OF OKLAHOMA EXTENDS KNOWN MORPHOLOGY OF PLEUROSTERNIDAE**

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The near-complete skull of a fossil turtle (OMNH 79260) excavated from mudstones of the Morrison Formation in Cimarron County, Oklahoma, U.S.A., preserves a significant amount of cranial anatomy. Turtles are the most common vertebrates at the site (V-1694), which was deposited in a high-energy environment and produces sculptured shell fragments from individuals of all sizes, as well as limb elements. One fragment preserves raised scale morphology. Study of OMNH 79260 using  $\mu$ -CT preparation reveals characters considered paracryptodiran: the nasals have a midline contact and the prefrontals do not, the frontals and jugals contribute to the orbit, the parietals contact the squamosals, incisurae columella auris is open, foramen posterioris canalis carotid interni lies anterior on the basisphenoid-ptyergoid suture, and the

basisphenoid is elongated. A relatively narrow triturating surface would seem to place it within Pleurosternidae. OMNH 79260 has been dorsoventrally compressed, and we refrain from interpreting its original length-to-width ratio or orbital orientation. It differs from *Pleurosternon* in the shapes of the anterior vomer and external process of the pterygoids. Geography also suggests that it belongs to the genus *Glyptops*. Two partial skulls of *Glyptops ornatus* have been described previously, likely not reflecting the full range of individual variation. Notably, OMNH 79260 has a short contact of the pterygoids so that the basisphenoid does not reach the vomer, contra earlier interpretations of *Glyptops* crania. Missing in other specimens of *Glyptops*, the fragile anterior palatal region is largely preserved in this specimen. Of particular note, the anterior vomer is unique among published Pleurosternidae, enlarging to a spoon-shaped, inferiorly-concave structure that would have contacted the premaxillae. The palatine contacted the jugal, and probably the prefrontal in addition to maxilla, pterygoid and vomer.

The phylogeny of Paracryptodira is uncertain, as new discoveries of stem turtles and expanded application of CT techniques call into question which characters formerly considered synapomorphies may now be considered plesiomorphic. This specimen may help to elucidate those relationships.

**Funding Sources** Whitten-Newman Foundation; Oklahoma State University Center for Health Sciences

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## **Macroecology & Macroevolution**

### **EVOLUTIONARY DRIVERS, MORPHOLOGICAL EVOLUTION AND DIVERSITY DYNAMICS OF A SURVIVING MAMMAL CLADE: CAINOTHERIOIDS AT THE EOCENE-OLIGOCENE TRANSITION**

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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 (EOT; 34–33.5 Ma) coincides with one of the major extinction events of

the Cenozoic. It is indeed associated with important climatic, geographical and ocean circulation changes worldwide. At the same time, a major faunal turnover occurred in Europe, known as the 'Grande Coupure'. This event is associated with the extinction of about 50% of the endemic European mammals, which had evolved in the 'island-Europe' context from the middle Eocene to the late Eocene. Here, using the exceptional fossil preservation from the Quercy multi-site Konzentrat-Lagerstätte (South-West France), we document and analyse the diversity dynamics of the Cainotherioidea (Mammalia, Artiodactyla), that survived the EOT and radiated rapidly immediately after. We infer their diversification history at the species level using Bayesian birth-death models and we show that cainotherioid diversity fluctuated through time, with extinction events at the EOT and in the late Oligocene, and a major speciation burst in the early Oligocene. The latter is in line with our finding that cainotherioids had a high morphological adaptability following environmental changes throughout the EOT, which likely played a key role in the survival and evolutionary success of this clade in the aftermath. We further highlight that speciation is positively associated with temperature fluctuations and continental fragmentation in a time-continuous way, while extinction seems to synchronize with environmental change in a punctuated way. Finally, we suggest that within-clade interactions negatively affected cainotherioid diversification, while inter-clade competition might explain their final decline during the late Oligocene. Our results thus provide a detailed dynamic picture of the evolutionary history of a mammal clade in a context of global environmental change.

**Funding Sources** ANR program DEADENDER (ANR-18-CE02-0003-01) – P.I. M. J. Orliac.

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### Romer Prize

#### A BAYESIAN TIP-DATED PHYLOGENY OF STEM VERTEBRATES, TOTAL-GROUP CYCLOSTOMES, AND STEM GNATHOSTOMES

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Vertebrates, especially jawed vertebrates (gnathostomes) are among the most disparate and diverse animal groups. As such, their origins and early evolution are a central

paleobiological question, before considering the connection to our own evolutionary heritage. Despite this, no integrated framework exists to understand the key evolutionary transitions on the gnathostome stem. Instead, early vertebrates are primarily understood through three overlapping but disconnected phylogenetic lenses: gnathostomes (jawed vertebrates), cyclostomes (extant jawless vertebrates), and the ostracoderm-grade. Gnathostome phylogenies have focused on the crown group (chondrichthyans, acanthodians, and osteichthyans) with placoderms primarily serving as an extended outgroup. This has prompted debate on placoderm monophyly/paraphyly, but phylogenies explicitly designed to test the placoderm question have not polarized them with an extended “ostracoderm” outgroup – instead, representation is skewed towards crown gnathostomes. Cyclostome phylogenetics has focused on questions of monophyly/paraphyly; the broader context among vertebrates is discussed, but for the most part only anaspid “ostracoderms” have been encoded as individual genera in these studies. Conodonts are barely considered despite potentially being the most successful cyclostome group. “Ostracoderm” phylogenies compare class-level taxa with assumed monophyly and ancestral conditions; an oversimplification that extends to their consideration of gnathostomes, despite the considerable uncertainty on the early gnathostome condition. I present the first phylogeny of early vertebrate evolution to consider individual genera spanning the vertebrate, cyclostome, and gnathostome stem groups in a common phylogenetic framework. This is the first study to explicitly test the monophyly of each “ostracoderm” class. Likewise, it is the first study to reconstruct interrelationships across the entire gnathostome stem, allowing the full range of “ostracoderms” to inform placoderm interrelationships and vice versa. The Bayesian tip-dated analysis incorporates over 1200 morphological characters and nearly 200 genera, including a new exceptionally preserved early vertebrate from the Early Ordovician Fezouata Lagerstätte. The phylogenetic results are discussed in the broader context of Paleozoic marine metazoan evolution in the water column.

**Funding Sources** National Science Foundation,  
Directorate for Biological Sciences  
Yale Institute of Biospheric Studies  
American Philosophical Society

## Symposium - Vertebrate dental ecomorphology: Tooth traits that reflect ecology

### DIETARY RECONSTRUCTIONS OF PALEOGENE FOSSIL LIZARDS FROM THE WESTERN INTERIOR OF NORTH AMERICA USING THREE-DIMENSIONAL DENTAL TOPOGRAPHY ANALYSIS AND A MODERN COMPARATIVE DATASET OF EXTANT PLEURODONT SQUAMATES

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Dental topography analysis offers a powerful toolkit for vertebrate dental ecomorphology that is particularly salient for application to the fossil record, given the great abundance of fossilized teeth. Squamates (lizards and snakes) are a prime clade for dental topography applications, given their substantial morphological disparity, ecological diversity, and extensive fossil record. However, applications of dental topography analysis to squamates are still very new, and these methods have not yet been applied to any fossil squamates. Thus, for our study, we used dental topography analysis to reconstruct the diets of some fossil lizards (n=8) from the Paleogene of North Dakota and Wyoming, USA. All of these fossils are referable to Anguimorpha, which includes extant taxa that are mostly carnivores or invertivores, with a sole omnivore (*Varanus olivaceus*) and no herbivores. To constrain the possible diets of our fossils, we used a modern comparative CT dataset of extant pleurodont squamates (n=69) and four 3D dental topography metrics: Orientation Patch Count Rotated (OPCR), Dirichlet Normal Energy (DNE), Boyer's Relief Index (RFI), and Portion de Ciel Visible (PCV). Phylogenetic signal is moderate to strong (Pagel's  $\lambda > 0.60$ ) for most metrics, including when averaged across entire tooth rows based on the total number of teeth present. However, phylogenetic ANOVAs suggest that these metrics are still able to differentiate among four dietary categories (carnivore, invertivore, omnivore, herbivore) even after phylogeny is accounted for. Principal component analysis shows substantial overlap among dietary categories, although carnivores, invertivores, and herbivores are still relatively distinct, with some outliers. Most of our fossils

fall within the carnivore and/or invertivore convex hulls in our ordination, as expected for anguimorph lizards, but a few fossils (with less complete dentitions) occupy unique areas of PC space, including outside all extant dietary convex hulls. This could indicate novel diets and/or highly specialized dental morphologies, but none of these fossils have highly specialized teeth compared to other extant or fossil anguimorphs, and the extant taxa they plot closest to in PC space are non-anguimorph fossorial specialists with fewer teeth. Thus, it appears that incomplete dentitions are responsible for these results, suggesting that fossils with fewer preserved teeth may not be directly comparable to extant specimens.

**Funding Sources** SVP Estes Memorial Grant, UMN Thesis Travel Grant, Bell Museum Davenport Grant (all to E. Whiting); NSF BCS-1440558 (to J. Bloch)

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## Paleohistology & Paleopathology

### THE COMPARATIVE OSTEOHISTOLOGY OF *GREERERPETON* AND *PROTEROGRYRINUS* (TETRAPODA) FROM THE CARBONIFEROUS OF NORTH AMERICA

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The origin and evolution of land-going tetrapods is one of the most consequential events in vertebrate evolution. Extensive research has focused on the origin of tetrapods in the Devonian and the establishment of terrestrial communities during the Permian. In contrast, little is known about tetrapods from the intervening Carboniferous Period, despite their importance in documenting the evolution and diversification of terrestrial tetrapods. A major impediment to their study has been the rare preservation of tetrapod fossils from Carboniferous rocks.

In North America, the Hinton Bonebed and Greer Quarry of West Virginia are known for their abundant preservation of two Lower Carboniferous tetrapods, *Greererpeton* and *Proterogyrinus*. These two taxa commonly co-occur but are anatomically and phylogenetically distinct. *Greererpeton* is reconstructed as an early diverging, primarily aquatic colosteid and *Proterogyrinus* as a more terrestrial, stem-amniote embolomere. Here we present osteohistological data on

the femora of these early tetrapods to provide new insight on the diversity of early tetrapod life histories and possible evolutionary mechanisms for increased tetrapod terrestriality.

Using standard histological procedures and micro-CT imagery, we examined an ontogenetic series of both taxa to conduct comparative histology and to describe features unique to each tetrapod. *Greererpeton* femora are characterized by indicators of an overall moderately-slow growth rate, with significant endosteal deposition through ontogeny resulting in a thick adult cortex. In addition, the ontogenetic series reveals a dramatic juvenile life history event that temporarily reduced bone deposition. In contrast, *Proterogyrinus* femora show evidence of a more elevated growth rate and slender adult cortex, as well as an unusual “mid-cortical gap” that was filled with calcified cartilage or large vascularity.

The divergent histological characteristics of these taxa may represent differences in habitat, phylogenetic history, or a combination of both. For instance, the elevated growth rates in *Proterogyrinus* compared to those of *Greererpeton* could represent adaptations to a more terrestrial habitat and/or amniote life history. Continued histological sampling of additional Carboniferous taxa will provide clarity on the influences that are related to habitat versus phylogeny and contribute life history data for these critical, yet poorly understood, tetrapod fossils.

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## **Taphonomy, Paleoenvironments, & Stratigraphy**

### **MOLECULAR COMPOSITION DETERMINES BIASES IN THE FOSSIL RECORD OF VERTEBRATE SOFT TISSUES**

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Soft tissue anatomy provides phylogenetic and physiological information in modern vertebrates. In fossils, soft tissue structures are commonly preserved as carbonaceous remains that are often encrusted or partially replaced by secondary minerals. Authigenic mineralization has been noted to occur preferentially along organic tissue surfaces, and includes phosphatization (precipitation of apatite:  $\text{Ca}_5(\text{PO}_4)_3\text{OH,F}$ ), and pyritization (precipitation of pyrite  $\text{FeS}_2$ ). Soft tissue preservation through replication in these minerals appears to be biased towards certain types of soft tissue. However,

the nature and tissue-specificity of organo-mineral interactions during early diagenesis is poorly understood and it is not clear whether preservational biases are the result of differences in tissue composition or a product of extrinsic factors, such as burial environment.

Raman microspectroscopy allowed differences in tissue composition and organo-mineral interactions to be characterized in a taxonomically representative sample of modern and fossil vertebrate soft tissues (Paleozoic to Recent) and their associated sediments (total  $n=180$ ). Carbonaceous remains within phosphatized and pyritized fossil soft tissues are shown to be endogenous. A canonical correspondence analysis groups averaged spectra of modern tissues ( $n=6$  types ranging from hard tissue matrices to integument and organs) into thiol-rich (-C-SH) versus amine-rich (-C-NH<sub>2</sub>) templates. An analysis of spectra of phosphatized and pyritized fossil soft tissues shows a significant positive correlation between apatite and thiol ligands, and between pyrite and amine ligands, indicating that early mineralization is influenced by tissue-specific coordination chemistry. A Discriminant Analysis of averaged modern soft tissues, and phosphatized and pyritized fossils soft tissues allows to relatively quantify the affinity of authigenic minerals for different soft tissues. Molecular composition determines the potential of soft tissues for fossilization through phosphatization or pyritization. This provides a basis for predicting which types of vertebrate soft tissues are likely to be discovered replicated by apatite and pyrite in appropriate burial conditions.

**Funding Sources** This project has been funded by Yale University.

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## **Crocodylomorphs & Pterosaurs**

### **A NEW BASAL THALATTOSUCHIAN CROCODYLOMORPH FROM THE EARLY JURASSIC (PLIENSCHACHIAN) OF DORSET, UK, AND IMPLICATIONS FOR THE ORIGIN AND EVOLUTION OF THE GROUP**

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Among archosaurs, thalattosuchian crocodylomorphs experienced the most extensive adaptations to the marine realm. Despite significant attention, the phylogenetic position of the group remains uncertain. Thalattosuchians are either the sister-group to Crocodyliformes, basal mesoeucrocodylians, or form a group with longirostrine neosuchians. The earliest definite thalattosuchians are known from the Toarcian (c.180 Ma), and already possess many synapomorphies of the group. All phylogenetic hypotheses imply a ghost lineage extending at least to the Sinemurian (c. 199 Ma), and a lack of older or more plesiomorphic forms may contribute to the uncertain phylogenetic placement of the group. Fragmentary postcranial material from the Sinemurian and Pliensbachian of South America, Europe, and India has been attributed to Thalattosuchia, but lacks thalattosuchian apomorphies. Here we describe new material from the early Pliensbachian (c. 190 Ma) Belemnite Marl Member of the Charmouth Mudstone Formation (Dorset, UK). The specimen includes partially articulated cranial, mandibular, axial, and appendicular elements. It can be attributed to Thalattosuchia based on the presence of a distinct fossa on the posterolateral corner of the squamosal, a broad ventrolateral process of the otoccipital broadly covering the dorsal surface of the quadrate body, large supratemporal fenestrae that lack a flattened skull table, a broadly exposed prootic, and an orbital process of the quadrate lacking bony attachment with the braincase. This specimen therefore represents the earliest thalattosuchian currently known from diagnostic material. To determine the phylogenetic position of the new taxon, we performed two separate analyses based on different published datasets. Both analyses recover the new taxon as the earliest diverging thalattosuchian, sister to Teleosauroidea+Metriorhynchoidea. We also performed Bayesian time-scaling analyses using a fossilized birth-death model to investigate the impact of the inclusion of the new specimen on estimates of divergence times of Thalattosuchia within Crocodylomorpha. The results show a likely Late Triassic origin for Thalattosuchia (median age=211 Ma), which is constrained between 224.33 and 196.70 Ma (95% highest posterior density). The new specimen extends the fossil record of Thalattosuchia, but the time-scaling analyses demonstrate that a significant ghost lineage remains.

**Funding Sources** NSF DEB 1754596

## Avialan Evolution & Biology

### REPORT OF A DIVING BIRD FROM THE HELL CREEK FORMATION, GARFIELD COUNTY, MONTANA

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Late Cretaceous diving birds are almost entirely known from marine deposits, with very few known from fluvial and lacustrine depositional environments interpreted to be freshwater. Here we report on a new specimen comprising two femora from the upper Hell Creek Formation of Garfield County, Montana. One femur is mostly complete, with some damage to the distal end and mid-shaft. The second femur is a proximal end with the head and trochanter. We infer from the morphology of the two femora that they are of the same species. Hesperornithiformes, the most common Cretaceous diving bird, has two femur morphotypes: 1) the squat and robust femur of *Parahesperornis* and *Hesperornis*, 2) the slender type seen in *Baptornis* and other basal hesperornithiforms. The femora are more similar to the slender than robust types. Key “slender type” characters preserved on these specimens include a rounded femoral trochanter and minimal cranial curvature to the shaft. Proximal characters from both specimens compare to the basal hesperornithiform *Enaliornis*. The shaft and distal end also compare to basal hesperornithiforms. Reports of hesperornithiforms outside of marine deposits, while still short, is growing longer. Hesperornithiforms, like many modern bird orders, may have had member taxa in estuaries and rivers as well as marine habitat.

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## Mesozoic & Paleogene Mammals

### PUSHING THE LOWER LIMITS OF BODY SIZE: BODY MASS ESTIMATES FOR THE STEM-THERIAN EUTRICONODONTA

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Body mass correlates with a range of biological traits and is considered a critical quantity in paleobiological studies. Several methods can estimate body mass in extinct animals, but the most widely applicable to the vertebrate fossil record, where skeletons are often incomplete, is the regression of body mass on linear dimensions. Because much of mammalian history is characterized by diminutive size, we sought to establish highly precise predictors of body mass based on the smallest extant therian taxa. We then used these regression equations to test existing hypotheses within the stem therian clade Eutriconodonta as a means to better understand the dynamics of body size during this important early period of mammalian evolution. Eutriconodonta is a widespread clade of Mesozoic stem therians whose distinctive tricuspid molars likely supported a carnivorous diet. Like other Mesozoic mammal groups, eutriconodonts are mostly small. They also include some of the largest Mesozoic mammals, with the largest approximately the size of a fox. Such disparity makes Eutriconodonta important for understanding the early dynamics of body size in Pan-Theria. Our regression equations are appropriate for taxa under 200 g, which captures much of the size variation in Mesozoic mammal clades. Our data expand the lower range of body mass in Eutriconodonta, with some taxa approaching the theoretical lower mass limit of an endothermic mammal. Further, the disparity in body mass estimations between molar length and width suggests the molars of eutriconodonts were expanded mesiodistally in relation to body mass, a relationship of linear dimension that may have itself evolved along the therian phylogenetic backbone. We also found that some postcranial dimensions produced body mass estimates that are much higher than for other linear dimensions. However, postcranial dimensions were the most accurate estimators in the original construction of the regression equations. This suggests that some aspects of the postcranial skeleton of Eutriconodonta may have been more robust relative to body mass than in extant Theria. Recent discoveries of relatively large fossils have challenged the much-repeated generalization that Mesozoic mammals were uniformly small. Our data add to the overall disparity of this period, but from the lower end of the size spectrum.

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### Paleohistology & Paleopathology

## OSTEOHISTOLOGY OF *PROTOSTEGA GIGAS* (TESTUDINES: PROTOSTEGIDAE) REVEALS UNIQUE LIFE HISTORY STRATEGIES

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Modern sea turtle osteohistology has been surprisingly well-studied, because it is used to understand sea turtle growth and timing of life history events, thus informing conservation decisions. Previous histology studies reveal two distinct bone growth patterns in extant sea turtle taxa, with *Dermochelys* (leatherbacks) growing faster than the cheloniids (all other living sea turtles). *Dermochelys* has a unique life history compared to other sea turtles (large size, elevated metabolism, broad biogeographic distribution, etc.) that is likely linked to bone growth strategies. Despite this abundance of histologic data on modern taxa, extinct sea turtle osteohistology is poorly understood. Here, *Protostega gigas* osteohistology is examined to better understand its growth throughout ontogeny. *Protostega gigas* was the second largest known sea turtle taxon, reaching lengths of 3.4 m and had a reduced carapace. Specimens are found in Santonian to Campanian-aged marine rocks of the Western Interior Seaway and Atlantic coast. Long bones of three Western Interior Seaway *P. gigas* specimens were histologically sampled, revealing bone microstructure patterns similar to *Dermochelys*. Like *Dermochelys*, all *Protostega* bones are well-vascularized and spongiose through the entire section, with no differentiation between a medullary cavity and cortical bone. Annual growth marks show variable but sustained rapid growth through early ontogeny that possibly continued until the onset of sexual maturity. Because of the similarities between *Protostega* and *Dermochelys* osteohistology, it is possible that *Protostega* had elevated metabolic rates like the extant leatherback. Comparison to *Desmatochelys*, a more basal Late Cretaceous protostegid sea turtle, indicates these bone growth patterns (with likely elevated metabolic rates) are not present through the entire Protostegidae, but evolved in more derived, and larger, taxa. Given the uncertainties in the phylogenetic placement of the Protostegidae, these results either reveal convergent evolution towards rapid growth and elevated metabolism in both derived protostegids and dermochelyids, or support a close evolutionary relationship between the two taxa.

**Funding Sources** Fort Hays State University



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## Dinosaur Systematics, Diversity, & Biology

### A NEW LATE CRETACEOUS NODOSAURID (THYREOPHORA: ANKYLOSAURIA) FROM THE CAMPANIAN JUDITH RIVER FORMATION OF NORTHERN MONTANA

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Nodosaurids (Thyreophora: Ankylosauria) are a group of armored dinosaurs that are closely related to polacanthids and are a sister taxon to ankylosaurids. This group of dinosaurs is characterized by numerous scutes along their necks and backs, but lacks the co-ossified tendons, osteoderms, and vertebrae at the end of the tail found in ankylosaurids. Here, we describe a new nodosaurid taxon that was found at Kennedy Coulee of the Judith River Formation in northern Montana. This new specimen, TMDC2011.3, is approximately 70% complete and is represented by a rooted tooth, ulnae, femora, humeri, ilia, sacrum, twelve vertebrae, fifteen ribs, and over 100 osteoderms. Using a New Technology Search in TNT (v.1.5) and a modified character matrix, we assessed the phylogenetic placement of the new taxon. Our analysis produced two most parsimonious trees with tree scores of 530 based on 177 characters identified from 48 species of Ankylosauria. Both parsimonious trees placed the new taxon as sister to other derived Late Cretaceous nodosaurs, such as *Edmontonia* and *Denversaurus*. One tree, Tree 1, recovers the new taxon within *Edmontonia* and as a sister taxon to *Denversaurus*. Tree 1 also places the Masstrichtian nodosaur *Denversaurus* as basal to the monophyletic group of the Campanian taxa, the new taxon, and *Edmontonia*. The other parsimonious tree, Tree 2, places the new taxon as most closely related to *E. longiceps*. This tree also recovered *E. longiceps* as basal to *E. rugosidens* (even though *E. longiceps* first appears approximately 5 million years after *E. rugosidens*) and places the new taxon as a sister to *Edmontonia* and *Animantarx*—thus distinguishing the new taxon as a separate genus basal to the monophyletic grouping of *Edmontonia* and *Denversaurus*. These results indicate that nodosaurine ankylosaurs were more diverse in the Late Cretaceous and that the interrelationships between derived nodosaur species were more complicated than previously thought.

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## Taphonomy, Paleoenvironments, & Stratigraphy

### THE TAPHONOMY AND PATHOLOGY OF DEATH POSE IN ARCHOSAURS

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Since the 1800s there has been an ongoing debate about the relative contribution of taphonomic and pathologic factors to producing a range of characteristic death postures in dinosaurs and other archosaurs. The concept of disease contributing to the opisthotonic neck position is perhaps the most famous example of this, with early neurologic diagnosis by Moodie contrasting with later actualistic taphonomic evidence. There is, however, significant variation in death posture among archosaurs, and the importance of the positioning of many joints beyond those of the neck and tail has been the subject of relatively little study.

Here we develop a process of stepwise specimen evaluation that attempts to separate peri-mortem and taphonomic contributions to body fossil positioning. Only by considering not just the taphonomic patterns of individual elements, but also positioning of cranial, axial and appendicular segments can the peri-mortem status of a specimen be inferred with confidence and links with disease be postulated. We evaluated a dataset of articulated and partially articulated specimens of fossil birds, non-avian dinosaurs, and pterosaurs that have been figured in the literature. We then catalogued both the preserved postures and inferred reverse-modelled postures removing the influence of taphonomic processes into patterns. >90% of the positions of specimens studied showed positions likely not modified by the cause of death, although many were subject to post-mortem taphonomic modification.

Of the specimens preserved in poses considered out of the ordinary, the positioning of the femur with relationship to the pelvis, and the digits of the pes were the most common diagnostic features. Differential diagnoses for the reverse-modelled postures of these specimens suggest a mixture of previously unidentified anatomical and pathological causes for these poses. Minimal superficial bone pathology was noted that might have helped contribute to diagnoses.

## Fishes Evolution & Distribution

### FOSSIL MARINE VERTEBRATES FROM THE JUANA LOPEZ MEMBER OF THE UPPER CRETACEOUS CARLILE SHALE IN SOUTHEASTERN COLORADO, USA

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The Juana Lopez Member of the Carlile Shale is a calcarenite deposit formed in the Western Interior Seaway of North America during the Late Cretaceous approximately 90 million years ago (early late Turonian). Rock samples were collected from a Juana Lopez locality in southeastern Colorado, USA, to examine the taxonomic composition of vertebrate fossils by dissolving the calcarenite with a weak acid. Although almost all of the specimens are represented by isolated bones and teeth that are microscopic, the paleofauna is found to be taxonomically diverse. It includes at least 14 chondrichthyans (*Ptychodus whipplei*, *Chiloscyllium greeni*, *Pararhincodon* sp., *Scapanorhynchus raphiodon*, *Protolamna* sp., *Cretodus crassidens*, *Archaeolamna*(?) sp., *Cretalamna* cf. *C. hattini*, *Squalicorax* cf. *S. falcatus*, *Squalicorax* sp., Lamniformes indet., *Rhinobatos incertus*, *Ischyrrhiza texana*, and *Ptychotrygon* sp.), 19 osterichthyans (*Hadrodus* sp., *Micropycnodon kansasensis*, *Paleobalistem* sp., Caturidae indet., Lepisosteiformes indet., Aspidorhynchidae indet., non-teleostean Actinopterygii indet., *Ichthyodectes* sp., Plethodidae indet., Albulidae indet., *Saurodon*(?) sp., *Pachyrhizodus minimus*, *Cimolichthys nepaholica*, *Enchodus gladiolus*, *E. petrosus*, *E. shumardi*, and at least three other forms of Teleosti indet.), and four tetrapods (Pliosauridae indet., Plesiosauria indet., Mosasaurinae indet. and *Ichthyornis* sp.). While teeth of *Enchodus* spp. are the most abundant vertebrate remains, the taxonomic composition of the paleofauna broadly agrees with other middle late Turonian faunas in North America. The fact that the fossil assemblage includes multiple avian (*Ichthyornis*) teeth, along with teeth of *Ptychodus whipplei* and *Scapanorhynchus raphiodon* commonly found in middle late Turonian nearshore deposits, suggests that at least one of the two shorelines of the

Western Interior Seaway must have been close to the location.

## Macroecology & Macroevolution

### THE COMPLETENESS OF THE FOSSIL RECORD OF LIZARDS AND SNAKES: QUANTIFYING THE EFFECTS OF BIAS ON GLOBAL SQUAMATE DIVERSITY THROUGH TIME

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Studies of the systematics, diversification, and phenotypic evolution of the Squamata (including 10,954 extant species of lizards, snakes, and amphisbaenians) can be augmented considerably by incorporating skeletal morphological data from the group's >242 million-year fossil record. However, spatiotemporal changes in fossil specimen completeness can bias our understanding of the evolutionary history of a given group. The inherent biological, geological, and anthropogenic processes that limit our understanding of the fossil record require a holistic examination of the effects of bias on the fossil squamate skeletal record. We used taxonomic, geological, and geographic data downloaded from the Paleobiology Database (PBDB), and an established metric of fossil skeletal completeness, the Character Completeness Metric (CCM2), to calculate the percentage of phylogenetic characters that can be scored for the roughly 600 fossil lizard and snake species that range in age from the Middle Triassic (Anisian) to the Late Pleistocene. Our results show that the Mesozoic squamate record exhibits higher mean CCM2 values (range: 47.9%–84.3%) in poorly-sampled stratigraphic stages (Anisian, Oxfordian, Tithonian), in which the few squamate species that are known largely originate from hypoxic lacustrine and/or brackish depositional settings with higher skeletal and soft tissue preservation potential. As sampling intensity, taxonomic abundance, and the diversity of terrestrial depositional settings containing squamate fossils increase in the Cretaceous, mean CCM2 values per stage are comparatively lower overall (range: 15.6%–48.4%). The decoupled relationship between fossil squamate skeletal completeness and species-level diversity throughout the Mesozoic showcases the pronounced influence that both

Lagerstätten-type deposits and sampling intensity have on our understanding of squamate evolution in deep time. Our results align with previously-established CCM2 patterns associated with Mesozoic birds, which suggests that the completeness of the fossil record of smaller tetrapods may be subject to the same biases in the preservation of skeletal material.

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### **Quantitative Paleontological Methods**

#### **AUTOMORPH: A SOFTWARE PACKAGE WITH POTENTIAL FOR AUTOMATED IDENTIFICATION OF FOSSIL MAMMAL TEETH**

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Fossil mammal teeth are commonly used for taxonomic identification. However, without a high degree of familiarity, teeth are often difficult to identify due to small differences in tooth morphology among similar-sized or closely related mammal species. AutoMorph, a high-throughput 2D and 3D data extraction software package developed in 2018 by Hsiang and colleagues, may provide a semi-automated method to determine the taxonomic identity of fossil mammal teeth. To date, no published works have utilized AutoMorph for taxonomic identification of fossil mammal teeth. Preliminary explorations of AutoMorph's 2D data extraction module run2dmorph indicate that AutoMorph is able to extract high-fidelity 2D data from color-corrected images of fossil mammal teeth. Here, we explored the utility of AutoMorph's run2dmorph module for taxonomic studies. This study implemented Wasatchian-age (ca. 55.8 Ma–ca. 50.3 Ma) isolated fossil mammal molars (N = 534) from the University of Wyoming Collection of Fossil Vertebrates. The specimens in this study sample represented three orders (Condylarthra, Primates, and Rodentia) and seven families (Hyopsodontidae, Phenacodontidae, Adapidae, Microsypidae, Omomyidae, Paromomyidae, and Ischyromyidae). Run2dmorph's extracted 2D measurements were analyzed with a combination of univariate (ANOVAs) and multivariate (discriminant) analyses to test run2dmorph's utility for

morphological and taxonomic identification. Results indicate that run2dmorph's 2D measurements can be utilized to determine: lower versus upper molar specimens (80–100% classification success rate); some molar numbers, particularly M3/3s (80–100% classification success rates); and (58–73% classification success rates using the complete data set; 73–100% classification success rates for analyses separated by order). Further, tests implementing specimens with unknown taxonomic/morphologic identifications indicate that run2dmorph can be used to develop a statistical model for classifying specimens and flagging potentially misclassified specimens. The results of this study provide the first step towards applying AutoMorph to studies of fossil mammal teeth, and this software package may provide a means of automated specimen identification without the need for substantial knowledge in tooth morphology. Further, AutoMorph will likely be useful for future identification and comparative studies at the collections scale.

**Funding Sources** Institute of Museum and Library Services: Museums for America Grant

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### **Mesozoic & Paleogene Mammals**

#### **FIRST, BIGGEST, AND OLDEST: A COMPLEX, UPPER PALEOCENE MAMMAL TRACKSITE REVEALS IMPORTANT EVOLUTIONARY INSIGHTS**

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A recently discovered tracksite in upper Paleocene (58 Ma), brackish-water deposits of southern Wyoming's Hanna Formation is the earliest direct evidence of mammals utilizing marine environments. It is also the first Paleocene mammal tracksite discovered in the USA and only the fourth in the world. Thousands of tracks arranged into dozens of trackways within at least four stratigraphic intervals demonstrate regular, recurrent utilization of brackish-water environments adjacent to a river mouth. Tracks are preserved as surface impressions on steeply-dipping silt and sandstone ledges and as deeply impressed, cross-sectionally exposed load casts, which exhibit the biomechanical dynamics of angled slide-in and downward rotation during the step cycle. Characteristics of the prints, such as amorphous shape, evidence of

inward collapse, and preservation in beds that also contain traces made by sea anemones, polychaete worms, and marine bivalves, are consistent with having been made in saturated or subaqueous, inter- to subtidal environments. Large (15–24.5 cm-long x 15–25 cm-wide) five-toed tracks are the most common morphotype and were likely made by pantodonts like *Coryphodon*. Smaller (11 cm-wide x 11.5 cm-long) tracks with four clear digit impressions do not match the autopodial skeletal anatomy of any known Paleocene mammal. However, the tracks bear resemblance to tapiroid manus and artiodactyl manus and pes prints, bolstering molecular phylogenetic hypotheses that push the origin of these taxa prior to the Eocene. Likewise, skeletal remains of *Coryphodon* are undescribed prior to the Clarkforkian NALMA (~57 Ma). Discovery of tracks from this taxon in 58 Ma strata would indicate an earlier migration into North America than is generally accepted.

Regular use of or residence in estuarine and marine environments by extant large-bodied, terrestrial to semiaquatic mammals is driven by opportunities for foraging, refuge from biting insects or potential predators, and/or thermoregulation. Notably, tropical and subtropical forest ecosystems experience excessive mineral-leaching from forest soil, resulting in decreased availability of sodium in vegetation and attendant mineral deficiencies in large mammals. Modern mammalian megafauna exploit coastal mineral resources, a behavioral adaptation possibly reflected in these trackways. Ichnological data therefore provide unique insight into behavior and evolutionary adaptations unavailable from body fossils alone.

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## Non-avian Theropod Systematics, Biology, and Evolution

### KEY FINDINGS FROM THE TRANSITION PERIOD: THE EARLIEST FEATHERS OF JEHOL BIOTA

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The Jurassic Yanliao Biota and Cretaceous Jehol Biota of northeastern China that yielded numerous feathered non-avian dinosaurs and early birds are significant for

studying the avialan origin and evolution. Because of volcanic activity and depositional environment changes caused by the craton destruction of North China, there is a 30 Ma gap, with few discoveries of terrestrial vertebrate fossils from the Late Jurassic to Early Cretaceous, which hampers our further understanding of the evolution between the feathered non-avian theropods of the Yanliao Biota and the diverse early birds of Jehol biota, as well as the relationship of these two prosperous Mesozoic ecosystems. Here we report two isolated feather specimens from the oldest sedimentary strata of Jehol Biota dating back to 134 Ma, the Dabegou Formation of Luanping Basin in north Hebei Province, China. SEM examination reveals both feather specimens preserved as carbon traces. Morphology analysis demonstrates that one feather is the typical pennaceous contour feather with comprehensive function of protection, thermo-regulation, and aerodynamic; while the other resembles the simply branched primary feather of non-avian theropods. The discovery of these two feathers is close to the horizon of *Peipiaosteus*, the earliest vertebrate record of the Jehol biota, and represents the oldest feathered theropods (including birds) among the Jehol Group to date, suggesting that the local terrestrial vertebrates were quickly adapted to the climate changes caused by geological tectonic movements at the very beginning of the Early Cretaceous, and then established a complex ecosystem with multiple trophic levels, which lit the way for the flourishing Jehol biota.

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## Macroecology & Macroevolution

### TESTING THE PRESENCE OF ABIOTIC BIOGEOGRAPHIC DRIVERS USING ONLY PHYLOGENY: SUBTROPICAL ARIDITY AS A BARRIER FOR EARLY DINOSAUR DISPERSAL

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Fossils record ancient biogeography, but reconstructing biogeographic patterns is complicated by unique

continental arrangements, climatic shifts, and lack of broad sampling. These challenges are exemplified in the Triassic Period, with the gradual breakup of Pangea coupled with shifts between arid and humid subtropical zones. We use early dinosaurs as a model to test how abiotic factors shape biogeographic patterns, because their global distribution throughout the Late Triassic is thought to be constrained by climate. Subtropical aridity is thought to constrain early Late Triassic (Carnian) dinosaurs to high-latitude southern Pangea, explaining the lack of Carnian dinosaurs from the Northern Hemisphere. However, Norian and Rhaetian dinosaurs from equatorial and northern paleolatitudes show that dinosaurs dispersed northward during the Late Triassic. These contradicting patterns raise questions: do climatic zones limit biogeography, and can climatic events relax these barriers? A short-term global humidity event has been suggested to have relaxed these arid climatic zones and allowed for dispersal, but this has yet to be tested using phylogenetic relationships. Here, we test for temporal constraints on dinosaur dispersal during the Late Triassic. We built a time-calibrated phylogeny in BEAST using a dataset of Triassic and Jurassic ornithomirans. Given this phylogeny, we explore the distribution of dinosaurs throughout the Triassic and the duration of the proposed dispersal event under a maximum likelihood framework using BioGeoBEARS. Three distinct dispersal likelihood matrices (pre-arid band, arid band, and post-Triassic) differ in the likelihood of dispersal of dinosaurs from southern to northern Pangea. Estimating the overall likelihood for the tree given differing ages of arid banding allows us to compare log-likelihood curves over time. We find that maximum likelihood falls to a minimum from 230–220 Ma, suggesting more dispersal occurs in this time than any other point in the Late Triassic. This pattern is robust to sensitivity analyses of potential increased sampling elsewhere in Pangea. This suggests that subtropical aridity limited early dinosaur dispersal but was briefly alleviated by the Carnian Pluvial Event, supporting the notion that aridity was lessened by global humidity. This model suggests that in the absence of geologic signals, phylogenetic relationships retain biogeographic information reflective of global perturbations.

## Crocodylomorphs & Pterosaurs

### MORPHOLOGY AND ANATOMY OF THE HYOID APPARATUS IN CROCODYLIFORMS: THE ORIGIN OF THE GULAR VALVE IN NEOSUCHIA

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Modern crocodylians are successful semi-aquatic predators. The combination of the secondary palate and the closed ventral valve at the base of a tongue allows crocodylians to breathe underwater while keeping their external nostrils above the water surface or holding prey in the mouth by closing the nostril. The secondary palate appeared in the successive stem groups of Eusuchia such as paralligatorids and derived goniopholidids, but the evolutionary history of the gular valve is unknown. The ventral fold of the gular valve embeds a cartilaginous basihyal with a pair of ceratobranchials, which comprise the hyoid apparatus. The evolution of the gular valve in the crocodyliform fossil record is poorly known because the basihyal does not ossify. Here we investigated the gross anatomy of modern crocodylians and scrutinized the internal choana and ceratobranchials in extinct crocodyliforms to better understanding the origin of the gular valve.

We examined palatal (the relative position of the posterior margins of internal choana) and hyoid (the ceratobranchial curvature) morphologies. Statistical analysis and trait-evolution simulation were performed in R with the packages Paleotree and Phytools. Hyoid musculature anatomy and osteological correlates were assessed by dissection of two modern crocodylians (*Crocodylus siamensis* and *Alligator sinensis*). The posterior margin of the internal choana is placed anteriorly in non-neosuchians and posteriorly in neosuchians, supported by the Wilcoxon rank sum test ( $p < 0.0001$ ). Also, based on the ceratobranchial curvature, both extinct and extant neosuchians show the dorsal deflection, while non-neosuchian crocodyliforms exhibit nearly straight ceratobranchials, supported by the Wilcoxon rank sum test ( $p < 0.0001$ ). Furthermore, this study newly finds that the dorsal deflection of the ceratobranchial increases the moment arm of m. branchiohyoideus in modern crocodylians to pull up the anterior portion of basihyal and raise the ventral fold of the gular valve. Our analyses of the posterior extension of the nasopharyngeal passage (secondary palate), the dorsal deflection of the ceratobranchial, and the plausible reconstruction of the muscular anatomy demonstrate that neosuchians had acquired a modern crocodylian-type

respiration separating the nasal and oral regions through the action of a gular valve during the Early to Middle Jurassic.

**Funding Sources** Japan Society for the Promotion of Science; Sasakawa Scientific Research Grant of the Japan Science Society

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## Mesozoic & Paleogene Mammals

### NEW MATERIAL OF *LOPHIPARAMYS* (MAMMALIA, RODENTIA), INCLUDING TARSALS, FROM THE WILLWOOD FORMATION (EARLY EOCENE)

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*Lophiparamys* is a rare small-bodied rodent known from the Wasatchian (early Eocene) of western North America. The genus has been known almost exclusively from dental remains, which are distinctive in possessing a profusion of accessory ridges. *Lophiparamys* has been allied with other small-bodied rodents from the Eocene of North America and Europe in the subfamily Microparamyinae. On the basis of dental morphology, microparamyines have been hypothesized to be ancestral to extant dormice (Gliridae). However, the near-absence of non-dental material has been an impediment to fully testing this hypothesis.

We report new material of *Lophiparamys* from the early late Wasatchian (Wa6) of the Willwood Formation in the Bighorn Basin, north-central Wyoming. The new material constitutes the first record of *Lophiparamys debequensis* from the Willwood Formation and includes well-preserved tarsal (astragalus, calcaneus, cuboid) as well as dental material. A maxillary fragment with P4 is the first known cranial material of *Lophiparamys* and indicates that the infraorbital foramen was relatively large. The morphology of the tarsals of *Lophiparamys* is very similar to larger early Eocene North American rodents such as *Paramys* and *Notoparamys*, but a few small but significant differences are present. On the astragalus, the tibial facet is more asymmetric, with the lateral ridge substantially longer than the medial ridge. Additionally, the neck is longer and the astragalar head is more circular.

On the calcaneus, the ectal facet is more proximally extensive and the calcaneal tuber is shorter. The cuboid has a narrower metatarsal facet. The features of the proximal tarsus are consistent with a modestly more arboreal habit in *Lophiparamys* than in larger Wasatchian rodents. They are also in agreement with a relationship between Microparamyinae and the highly arboreal Gliridae. The astragalar features of *Lophiparamys*, in particular, are present in a more extreme version in fossil and extant glirids.

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## Marine Mammals

### FIRST RECORD OF AN UPPER EOCENE ARCHAEOCETE FROM THE RASHRASHIYAH FORMATION, AL-JAWF REGION, NORTHWESTERN SAUDI ARABIA

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Ongoing paleontological exploration for Palaeogene vertebrate fossils associated with the Neotethyan marine carbonate platform of the Arabian Peninsula has yielded a series of well-preserved caudal vertebrae of an Eocene archaeocete (Mammalia, Cetacea). The new specimen was discovered and excavated in-situ from the pelagic marly and chalky limestone beds of the upper one-third of the upper Eocene Rashrashiyah Formation exposed in and around the city of Al Qurayyat in the northwestern part of Saudi Arabia. Two articulated vertebral segments totaling 13 caudal vertebrae represent the middle and posterior portions of a basilosaurid tail. The first segment includes seven articulated vertebrae found embedded in the calcareous sediments: these are longer than their width and height, and have short neural arches and reduced transverse processes. The second segment is an association of six vertebrae that were found in a weathered cluster less than a meter from the first: these are well preserved and moderately mineralized. After

aligning both segments in sequence, based on size (centrum length), landmark appearance (position of neural spines and chevron articulations), and overall centrum morphology, it is clear that we have much of an archaeocete tail missing the posterior-most vertebrae. Comparison with complete and contemporaneous archaeocetes elsewhere in the Middle East shows that the new Saudi vertebrae are similar in shape and morphology to those of *Dorudon atrox*, but slightly smaller (similar in size to *Stromerius nidensis*). The Rashrashiyah Formation is a Priabonian-age carbonate-rich marine sedimentary unit that varies in exposed thickness between 15 and 50 meters. Age is based on excellently preserved calcareous nannofossils marking the CP14b/CP15 zonal boundary. It is equivalent to the Wadi Esh-Shallalah Formation in Qa' Faydat ad Dahikiya across the international border in Jordan, which yielded a diverse Priabonian marine vertebrate fauna, including archaeocetes, from a glauconite bed. The Saudi Arabian specimen is notably better in having vertebrae preserved in articulation.

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#### **Colbert Poster Prize**

#### **TYLOSAURUS THROUGH TIME: CLADISTIC ANALYSIS OF ONTOGENY RECOVERED EVIDENCE OF PERAMORPHY-DRIVEN ANAGENESIS IN NORTH AMERICAN TYLOSAURINES**

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Mosasaurs were large, globally distributed aquatic lizards that lived during the Late Cretaceous. *Tylosaurus* is a genus of particularly large mosasaurs with long, edentulous anterior extensions of the premaxilla and dentary that lived in Europe and North America during the Late Cretaceous (89 to 66 million years ago). Three species—*Tylosaurus proriger*, *T. kansasensis*, and *T. nepaeolicus*—have robust fossil records with specimens spanning a wide range of sizes, and previous work has proposed that *T. kansasensis* are juvenile *T. nepaeolicus*, rather than a separate taxon. Therefore, these species are ideal models for studying mosasaur intraspecific variation (e.g., ontogeny, sexual dimorphism, individual variation) and testing hypotheses of synonymy, anagenesis (i.e., evolution within a single lineage), and heterochrony.

One hundred seven specimens (62 *T. proriger*, 21 *T. kansasensis*, 24 *T. nepaeolicus*) were scored for 75 characters, including 47 phylogenetic (i.e., diagnostic) and 28 ontogenetic (nine size-dependent, 19 size-independent) characters. Quantitative cladistic analysis was then used to: (1) recover a growth series for each taxon individually; (2) test an existing hypothesis of synonymy of *T. kansasensis* and *T. nepaeolicus* by analyzing them together; and (3) test a hypothesis of anagenesis in Western Interior Seaway *Tylosaurus* by analyzing specimens of all three species together. A Spearman rank-order test resulted in a significant ( $p < 0.05$ ) correlation between size (skull length and quadrate height) and maturity for each species. Evidence for skeletal sexual dimorphism was not found, which is consistent with what is seen in most extant squamates; however, size-based dimorphism cannot yet be ruled out. The separate analyses of each taxon recovered eleven growth characters, including the development of a knob-like rostrum and increase in quadrate height relative to skull length, that were shared by all three taxa. The second analysis, including specimens of *T. kansasensis* and *T. nepaeolicus*, supported their synonymy and that *T. kansasensis* are immature individuals. Finally, the third analysis recovered evidence of intermediate morphologies and peramorphosis of skull size and development in *T. proriger*, supporting the hypothesis of anagenesis in Western Interior Seaway *Tylosaurus* species.

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