

ICVM11



PROGRAM

The 11th International Congress of Vertebrate Morphology

29 June – 3 July 2016

Bethesda North Marriott Hotel & Conference Center
Washington, DC





The Anatomical Record

Advances in Integrative Anatomy and Evolutionary Biology

EDITOR-IN-CHIEF:

KURT H. ALBERTINE

UNIVERSITY OF UTAH
SCHOOL OF MEDICINE,
SALT LAKE CITY, UTAH

SPECIAL ISSUES

The Anatomical Record regularly publishes special 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 *The Anatomy of the Mummy*.



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Journal of Experimental Biology

Journal of Experimental Biology (JEB) is at the forefront of comparative physiology and integrative biology. We publish papers on the form and function of living organisms at all levels of biological organisation and cover a diverse array of fields, including:

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Inland bearded dragon (*Pogona vitticeps*). Photo: Akira Kato.

WELCOME

On behalf of the International Society of Vertebrate Morphologists (ISVM), we warmly welcome you at the 11th International Congress of Vertebrate Morphology (ICVM11-2016), Washington DC, USA.

ICVM is the premier international conference to present work in the broad field of vertebrate morphology. Originally, ICVMs tended to focus more on the musculoskeletal system, but ICVM11-2016 has substantially widened its scope to encompass other systems, more functions, whilst also exploring interfaces with other disciplines such as physiology, global change ecology, and sensory- and neurobiology. New analytical techniques and emerging technologies, such as imaging and 3D modeling, have been firmly integrated into modern 21st-century morphology. Clearly, morphology is alive and kicking, and has made itself indispensable in integrative approaches aiming to answer questions about evolution, function, and the diversity of vertebrate life.

Close to 600 participants from over 30 countries and six continents present their research in no fewer than 19 symposia, a workshop, over 200 contributed talks, and over 150 posters. Five outstanding plenary speakers launch each day's program, and unopposed poster sessions provide a forum for interaction and discussion. We are convinced that ICVM11-2016 will offer the appropriate setting for researchers ranging from talented students to senior scholars to share ideas in an informal and stimulating environment. Achieving this aim is central to ISVM's goal of promoting international collaboration and cooperation in vertebrate morphology and between vertebrate morphology and other biological sciences.

Our sincere thanks go to Larry Witmer, organiser of ICVM11-2016, in his role of Past president and Chair of the Scientific Program Committee. We also acknowledge our sponsors, several of whom have generously supported symposia, thus helping the organisers to establish a great program.

Welcome to Washington DC, and enjoy ICVM11-2016!

Ann Huysseune
President

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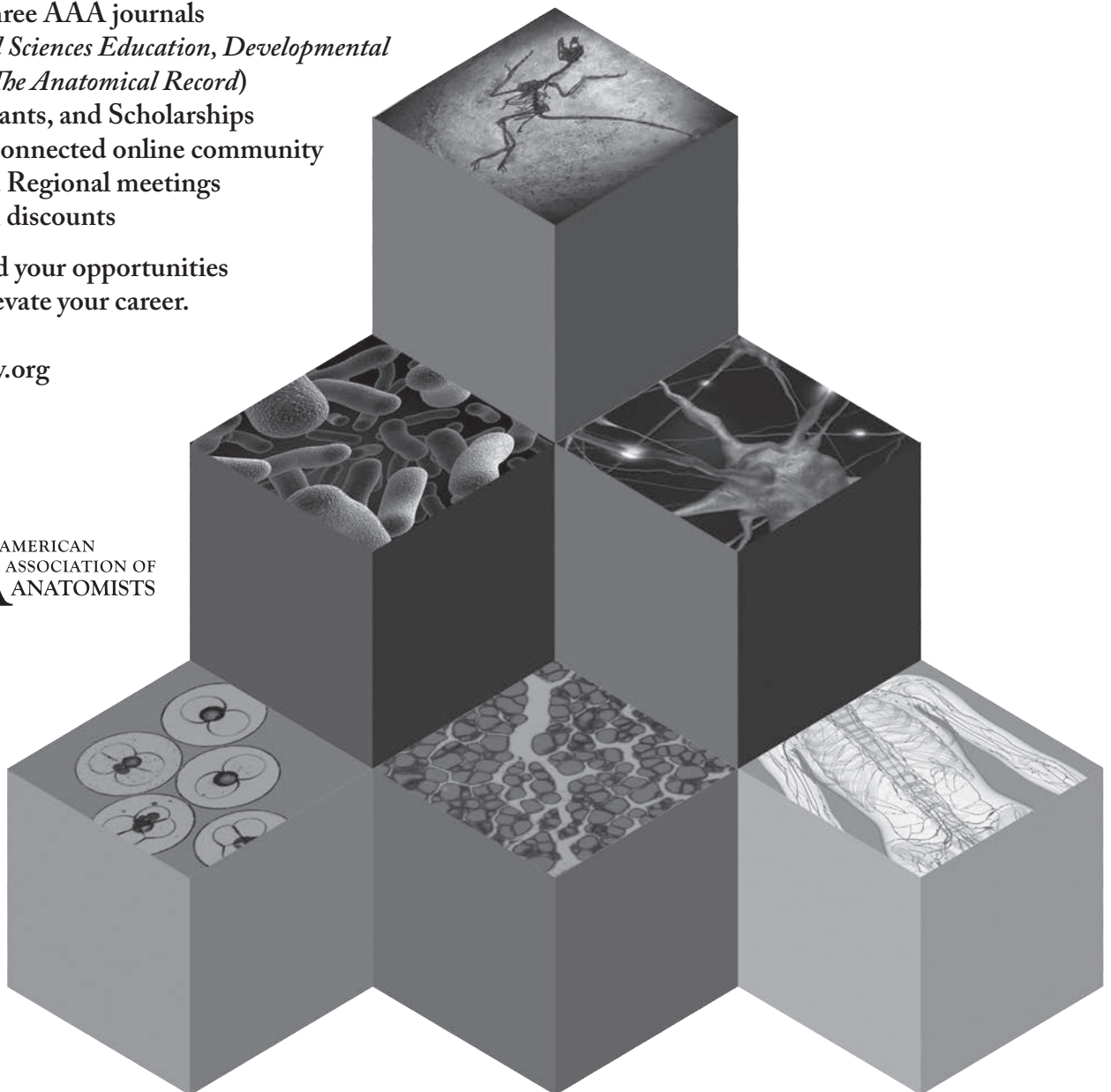
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NOTE FROM *THE ANATOMICAL RECORD*

The Anatomical Record (**AR**) – a flagship journal of the American Association of Anatomists - is proud to host the program and abstracts for the 11th International Congress of Vertebrate Morphology (ICVM 2016) in Bethesda, Maryland this month. Hosting is done on the Wiley Online Library for **AR** web page. To explore the science that will be presented and discussed at the ICVM 2016 meeting, please visit **AR**'s website (search or use the QR code below) and select "ICVM11-2016 Program & Abstracts" in the Special Features section at the lower left of the web page.

Our pride in hosting the program and abstracts is based on the Journal's rich history in publishing landmark studies in all areas of vertebrate morphology. Among these top-tier studies are many incomparable **AR** Special Issues that have become classics in the field, including: "Assessing Function Via Shape: What is the Place of Geometric Morphometrics in Functional Morphology?" (2015), "The Anatomy of the Mummy" (2015), "The Vertebrate Nose: Evolution, Structure, and Function" (2014; from a ICVM 2013 Symposium), "The Anatomy and Biology of Hearing and Balance: Cochlear and Vestibular Implants" (2012), "Evolutionary and Functional Morphology of New World Monkeys" (2011), "From Head to Tail: New Models and Approaches in Primate Functional Anatomy and Biomechanics" (2010), "Unearthing the Anatomy of Dinosaurs" (2009), "The Paranasal Sinuses: The Last Frontier in Craniofacial Biology" (2008) and "Anatomical Adaptation of Aquatic Mammals" (2007), among many others.

We anticipate discovering more fantastic state-of-the-art science at the ICVM 2016 meeting in Bethesda! And we look forward to receiving your manuscripts for consideration for publication in **AR**, and to continuing the tradition of advancing the best science in vertebrate morphology in our journal.

Kurt H. Albertine, Ph.D., FAAA
Editor-in-Chief, *The Anatomical Record*

Jeffrey T. Laitman, Ph.D., FAAA
Senior Associate Editor, *The Anatomical Record*
Past-President, American Association of Anatomists



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Image: A bath for food. Credit: Vincenzo Penteriani.

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** Note: this is an ad hoc committee appointed by the President*

PREVIOUS LOCATIONS

OF THE INTERNATIONAL CONGRESS OF VERTEBRATE MORPHOLOGY

ICVM-1	1983	Gießen, Germany (~300 participants)
ICVM-2	1986	Vienna, Austria (~350 participants)
ICVM-3	1989	Antwerp, Belgium (~430 participants)
ICVM-4	1994	Chicago, Illinois, USA (~450 participants)
ICVM-5	1997	Bristol, UK (~450 participants)
ICVM-6	2001	Jena, Germany (~700 participants)
ICVM-7	2004	Boca Raton, Florida, USA (~470 participants)
ICVM-8	2007	Paris, France (~600 participants)
ICVM-9	2010	Punta del Este, Uruguay (~315 participants)
ICVM-10	2013	Barcelona, Spain (~450 participants)
ICVM-11	2016	Washington, DC, USA (~600 participants)

GENERAL INFORMATION

DATES AND VENUE

Wednesday, 29 June – Sunday, 3 July 2016
Washington, DC

Bethesda North Marriott Hotel & Conference Center
5701 Marinelli Road
North Bethesda, Maryland 20852 USA
1-301-822-9200
add 00 as a prefix when calling from outside the US

CONFERENCE MANAGEMENT

Burk & Associates, Inc.
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McLean, Virginia 22101
1-703-790-1745
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Onsite contact:

Jennifer Rosenberg, jrosenberg@burkinc.com

ON-SITE REGISTRATION

Registration Desk Hours:

Wednesday, June 29	10:30am – 7:30pm
Thursday, June 30	7:30am – 4:30pm
Friday, July 1	7:30am – 4:30pm
Saturday, July 2	8:00am – 4:30pm
Sunday, July 3	8:00am – Noon

- Regular: \$600.00
- Early Career (*received PhD in 2013 or more recently*): \$420.00
- Student (*student ID required*): \$240.00
- Companion: \$100.00

The Regular, Early Career, and Student registration fees include:

- Access to the Welcome Reception and Closing Reception
- Access to all scientific sessions and exhibits
- Name badge, conference bag, program book, sponsors flyers, and a USB drive with a PDF of the program
- Coffee breaks

The Companion registration fee includes:

- Access to the Welcome Reception, the Closing Reception, Exhibits, Posters, and one scientific session (presumably the session in which their companion is presenting).

NOTES FOR ORAL PRESENTERS (SPEAKERS)

1. The standard oral presentation slot at ICVM11-2016 is 15 minutes long (~12 minutes of talk and ~3 minutes for questions). All Contributed talks must adhere to this time limit, with the exception of Lightning talks, which are only five minutes long (~4 minutes of talk and ~1 minute for a question). The length of symposium talks are determined by the symposium organizers but will be multiples of 15 minutes to keep the schedule synchronized; symposium speakers should build time for questions and answers into their allotted time. Session moderators will introduce the presenter and keep track of time.
2. Microsoft PowerPoint will be the standard presentation software supported at ICVM11-2016.
3. Presentation files will be loaded centrally in the Speaker Ready Room (Timberlawn, on the Lower Level) and then served to the breakout session rooms. Note: ICVM will not be archiving or otherwise retaining any presentation files.
4. The Speaker Ready Room and breakout session rooms will be using PCs. Speakers with presentations on Macs are encouraged to use the PCs, and the fidelity of the conversion can be assessed in the Speaker Ready Room. However, if absolutely necessary, a speaker can use their own Mac in the breakout session room, although the hope is to keep computer-swapping to a minimum.
5. Presentation files should be brought to the Speaker Ready Room a minimum of two hours prior to the session, preferably much earlier. They may be brought on a USB flash drive (e.g., thumb or jump drive), downloaded from the cloud (e.g., from the speaker's personal Dropbox, GoogleDrive, etc.), or uploaded via FTP in the period June 20–27 (FTP details will be emailed to presenting authors).
6. Speaker Ready Room – Timberlawn, on the Lower Level

Hours of operation:

Wednesday, June 29	Noon – 5:00pm
Thursday, June 30	8:00am – 5:00pm
Friday, July 1	8:00am – 5:00pm
Saturday, July 2	8:00am – 5:00pm
Sunday, July 3	8:00am – 5:00pm

GENERAL INFORMATION

NOTES FOR POSTER PRESENTERS

1. All posters will be up for nearly the entire meeting in the Grand Foyer immediately outside the breakout session rooms. Poster set-up can start as early as 4:30pm on Wednesday, June 29th. All posters must be removed by 4:30PM on Sunday, July 3rd.
2. The maximum size of posters is 120 cm x 120 cm (4 ft x 4 ft). Poster presenters will share a 4 ft x 8 ft poster board with another presenter, although that other presenter will be in the other poster session to reduce crowding. Push pins will be provided.
3. There will be two unopposed poster sessions (POS1: 7:30–9:30pm on Thursday, June 30th; POS2: 4:30–6:30pm on Friday, July 1st). Presenters in each poster session (check the program for assignments) are expected to be at their posters to solicit feedback and answer questions.

SOCIAL EVENTS

1. **Welcome Reception (REC1):** 7:30–9:30pm, Wednesday, June 29th, Salons A–C
2. **Closing Reception (REC2):** 7:30–9:30pm, Saturday, July 2nd, Grand Ballroom (Salons D–E), sponsored in part by the *Journal of Morphology*. The Reinhard-Rieger Award presentation will take place.
3. The Welcome and Closing Receptions are free for all registered participants and will include a cash bar and light hors d'oeuvres.
4. The poster sessions (POS1 and POS2) are scientific sessions but also will have a cash bar and light hors d'oeuvres.

ICVM MOBILE DEVICE APP FOR IOS AND ANDROID

- Printing Images, Inc. developed a PI ShowApp for ICVM11-2016 that works on all iOS and Android mobile devices, allowing attendees to view the full ICVM program, develop a personalized schedule, receive push notifications, and a range of other interactive functions.
- The PI ShowApp is freely downloadable from the Apple App Store or Google Play. Scan the QR code on the right or go to <https://pishowapp.quickmobile.mobi>.



FREE WI-FI INTERNET CONNECTIVITY

- ICVM has contracted for free Wi-Fi in the Marriott's guest rooms and meeting spaces for ICVM attendees
- **Network name:** MARRIOTT_CONFERENCE
Password: ICVM2016

OFFICIAL HASHTAG: #ICVM2016

NOTIFICATION OF LATE-BREAKING CHANGES AND OTHER ICVM NEWS

1. Most changes that occur after the printing of the program will be incorporated into the online program (www.icvm2016.com/wp/program/sessionlist.php).
2. Other late-breaking changes and news will be posted to Twitter (#ICVM2016) as well as the ICVM Facebook page (www.facebook.com/ICVM10) by ISVM Program Chair Larry Witmer (@WitmerLab) and ISVM Secretary Adam Summers (@Fishguy_FHL).
3. Notifications also will be made to the ICVM Mobile Device app

ICVM11-2016 PROGRAM & ABSTRACTS DOWNLOAD

- Download the ICVM11-2016 Program & Abstracts as a single PDF, graciously hosted by the *Anatomical Record*: <http://bit.ly/1RYjtsb> (under “Special Features” in the column at left)

BADGES AND SECURITY

It is essential that you wear your personal badge at all times while in the Congress venue and during the social events, as it is the official entrance pass to scientific sessions and other Congress activities.

OFFICIAL LANGUAGE

The official language of ICVM11-2016 is English. Simultaneous translation will not be provided.

ICVM CODE OF CONDUCT

The International Congress of Vertebrate Morphology expects meeting attendees to behave in a courteous, collegial, and respectful fashion towards each other, ICVM meeting staff, conventions staff, and the public. Attendees should respect common sense rules for professional and personal interactions, public behavior (including behavior in electronic communication related to the meeting), common courtesy, respect for private property, and respect for the intellectual property of the presenters. Demeaning, abusive, harassing or threatening behavior towards other attendees, staff, or the public is not permitted in either personal or electronic interactions.

NOTE ON PHOTOGRAPHY, OTHER RECORDING, AND SOCIAL MEDIA

1. ICVM Abstracts have been reviewed by the Scientific Program Committee, but authors are responsible for the technical content.
2. Opinions differ widely on the issue of photography and other manner of recording conference presentations. We urge the use of good judgement and courtesy, guided by the ICVM Code of Conduct (above) that emphasizes respect for intellectual property. Asking permission prior to any kind of recording (including photography) or before posting photos online is recommended. Likewise, we encourage discussion of ICVM presentations on social media (#ICVM2016), but again we urge caution and consideration in posting photos or other content that might disclose more than the presenter would desire.
3. Those presenters who do NOT want any of their content recorded, posted, or discussed online have that right, but should inform the audience at the outset of their oral presentation or in a prominent place on their poster.

ISVM MEETINGS

1. **ISVM Business Meeting**
Friday, July 1st, 6:30–7:30pm
Grand Ballroom (Salons D-E)
All attendees are welcome and encouraged to participate
2. **Executive Committee Meeting #1**
(with current members)
Thursday, June 30th, 1:00pm, Great Falls
3. **Executive Committee Meeting #2**
(with newly elected members, current members are also invited)
Saturday, July 2nd, 6:00pm, Great Falls

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SYMPOSIUM & WORKSHOP



Sponsors of the Workshop:

- Anatomical network analysis (AnNA): A new tool to quantify morphological complexity, integration, and modularity in vertebrate evolution and development (Organizers Borja Esteve-Altava, Diego Rasskin-Gutman & Rui Diogo)



Biology Open

Journal of
Cell Science

**Disease Models
& Mechanisms**

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Journal of
Experimental Biology

Donation to the following Symposia:

- Interdisciplinary and Evolutionary Approaches to Vertebrate Biological Materials (Organizers Mason Dean, Alfred Crosby, Duncan Irschick & Ling Li)
- Past, Present and Future of Ecological Morphology (Organizers Lance McBrayer, Eric McElroy & Robbie Wilson)
- Diffusible Iodine-based Contrast-enhanced Computed Tomography (diceCT) and Related Imaging Techniques for Research in Evolutionary Morphology (Organizers Paul Gignac, A. Nele Herdina, Nathan Kley, Ashley Morhardt, Matthew Colbert & Julia Clarke)



Sponsors of the Symposia:

- New insights into the functional relationship between anatomy and physiology of extinct and extant vertebrates (Organizers Ruger Porter & Glenn Tattersall)
- Functional (secondary) adaptation to an aquatic life in vertebrates (Organizers Alexandra Houssaye & Frank Fish)

PROGRAM AT-A-GLANCE

Key to Session Abbreviations and Color-Coding

ANA: Anatomical Network Analysis			FOS: Fossoriality			NPL: Non-pentadactyl limbs		
AQU: Secondary adapt. to aquatic life			GEN: General Morphology			PAL: Paleontology		
BON: Bone microstructure			GMM: Geometric Morphometrics			PHA: Vertebrate pharynx		
BSI: Brain-skull integration			HAL: BK Hall– Many faces of the skel.			PHY: Anatomy & thermal physiology		
CHA: Major challenges for morphology			HRD: Hard-Tissue Biology			PLN: Plenary session		
DCT: Contrast-enhanced CT – diceCT			LOC: Locomotion			PLT: Palate evolution		
DEN: Dentition patterning			LTG: Lightning session (5-min talks)			POS: Poster session		
EAR: Inner and middle ear			MAT: Vertebrate biological materials			REC: Reception		
ECO: Ecological morphology			MFM: Muscle functional morphology			SBN: Sensory Biology & Neuroscience		
EVD: Evo-Devo			MFS: Mammalian Feeding Systems			SEG: Segmentation & serial homology		
FED: Feeding			MIM: Morph. Integration & Modularity			XEN: Xenarthra		
Plenary	Symposium	Contributed		Workshop	Poster		Reception	Business Mtg

Wednesday, June 29th

	Salon E	Salon F	Salon G	Salon H
Morning	Registration			
1:00-2:30	Intro-PLN1	Plenary speaker: Joy Reidenberg (Huysseune, Witmer Intro)		
2:30-4:00	CHA1	MFM1	PAL1	MIM1
4:00-4:30	Coffee			
4:30-6:00	CHA2	MFM2	PAL2	MIM2
7:30-9:30	Welcome Reception (REC1) in Salon A-C			

Thursday, June 30th

	Salon D-E	Salon A	Salon B	Salon C	Salon F	Salon G	Salon H	Forest Glen
8:15-9:30	PLN2	Plenary speaker: Alexander Vargas (Moustakas-Verho intro)						
9:30-11:00		BON1	MFS1	GEN1	SBN1	LOC1	PHA1	
11:00-11:30	Coffee							
11:30-1:00		BON2	MFS2	GEN2	SBN2	LOC2	PHA2	
1:00-2:30	Lunch							
2:30-4:00		BON3	MFS3	GEN3	BSI1	LOC3	PHA3	
4:00-4:30	Coffee							
4:30-6:00		BON4	MFS4	GEN4	BSI2	LOC4	PHA4	
6:00-7:30	Dinner							
7:30-9:30	Poster & reception (POS1) in Grand Foyer							

Friday, July 1st

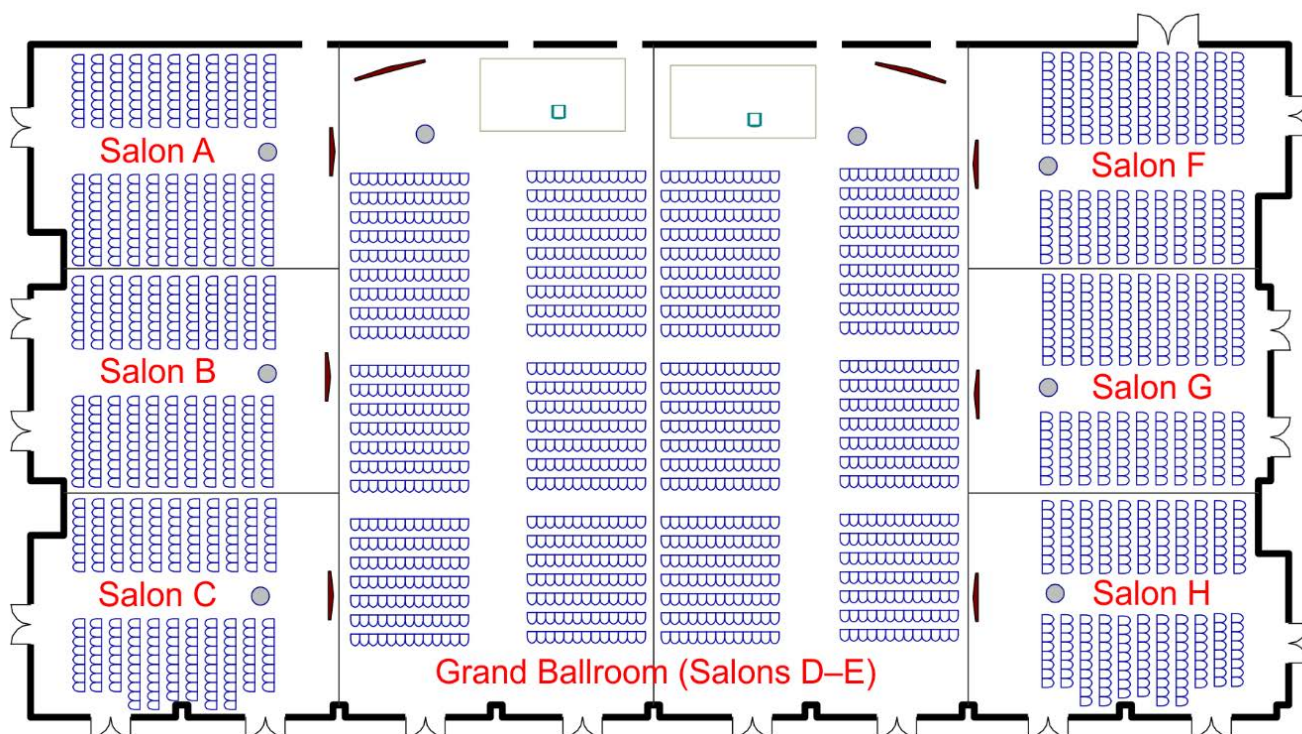
	Salon D-E	Salon A	Salon B	Salon C	Salon F	Salon G	Salon H	Forest Glen
8:15-9:30	PLN3	Plenary speaker: Zerina Johanson (Summers intro)						
9:30-11:00		HAL1	ECO1	GMM1	PAL3	PLT1	NPL1	
11:00-11:30	Coffee							
11:30-1:00		HAL2	ECO2	GMM2	PAL4	PLT2	NPL2	
1:00-2:30	Lunch							
2:30-4:00		FED1	GEN5	GMM3	PAL5	EVD1	LTG	
4:00-4:30	Coffee							
4:30-6:30	Poster & reception (POS2) in Grand Foyer							
6:30-7:30	BUS	ISVM Business Meeting in Grand Ballroom (Salons D–E)						

Saturday, July 2nd

	Salon D-E	Salon A	Salon B	Salon C	Salon F	Salon G	Salon H	Forest Glen
8:15-9:30	PLN4	Plenary speaker: Luis Chiappe (Chinsamy-Turan intro)						
9:30-11:00		DCT1	DEN1	EVD2	FOS1	HRD1	SEG1	
11:00-11:30	Coffee							
11:30-1:00		DCT2	DEN2	EVD3	FOS2	HRD2	SEG2	
1:00-2:30	Lunch							
2:30-4:00		DCT3	DEN3	EVD4	PHY1	HRD3		ANA1
4:00-4:30	Coffee							
4:30-6:00		DCT4	DEN4	EVD5	PHY2			ANA2
6:00-7:30	Dinner							
7:30-9:30	Closing reception (REC2) in Grand Ballroom (Salons D-E)							

Sunday, July 3rd

	Salon D-E	Salon A	Salon B	Salon C	Salon F	Salon G	Salon H	Forest Glen
8:15-9:30	PLN5	Plenary speaker: Stephanie Pierce (Wyneken intro)						
9:30-11:00		AQU1	MAT1	FED2	LOC5	EAR1	XEN1	
11:00-11:30	Coffee							
11:30-1:00		AQU2	MAT2	FED3	LOC6	EAR2	XEN2	
1:00-2:30	Lunch							
2:30-4:00		AQU3	MAT3	FED4	LOC7		XEN3	
4:00-4:30	Coffee							
4:30-6:00		AQU4	MAT4	FED5	PAL6			



Grand Foyer (posters, coffee breaks, exhibitors)

EXHIBITOR LISTING

EXHIBIT HOURS

Thursday 30 June

9:30am – 4:00pm

Friday 1 July

9:30am – 4:00pm

Saturday 2 July

9:30am – 4:00pm

American Association of Anatomists

Booth: 4

9650 Rockville Pike
Bethesda, MD 20814
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The American Association of Anatomists serves as the professional home for an international community of biomedical researchers and educators focusing on the structural foundation of health and disease, with a core mission of advancing anatomical science through research, education, and professional development.

The Anatomical Record

The Anatomical Record, an official publication of the American Association of Anatomists, publishes new discoveries in the morphological aspects of molecular, cellular, systems, and evolutionary biology. Papers are accepted dealing with functional morphology of any vertebrate organ system including those with a developmental, comparative, or evolutionary theme.

Developmental Dynamics

Developmental Dynamics provides a focus for communication among developmental biologists who study the progressive and dynamic emergence of form and function during embryonic development. The journal is an international forum for the exchange of novel and substantive information on mechanisms that control development, and is an official publication of the American Association of Anatomists.

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PROGRAM

Wednesday 29th June, 2016

1:00pm – 2:30pm PLN1

Salon E

Welcome & Plenary Session 1: Joy Reidenberg

Chairs: A Huyseune, LM Witmer

1:00pm **PLN1-1** Modifying the mammalian model: Whassup with whales? *Reidenberg J; Icahn School of Medicine at Mount Sinai*

2:30pm – 4:00pm CHA1

Salon E

Symposium: Major challenges for vertebrate morphology, evolution and development 1

Chairs: JM Hoyos, R Diogo

2:30pm	CHA1-1	An historical introduction to the major challenges in vertebrate morphology	<i>Hoyos J; Departamento de Biología, Pontificia Universidad Javeriana</i>
3:00pm	CHA1-2	Major challenges in vertebrate morphology, macroevolution, variation and human birth defects	<i>Esteve-Altava B, Molnar J, Diogo R; Royal Veterinary College, Howard University</i>
3:30pm	CHA1-3	Major challenges in vertebrate morphology and developmental biology: links with human evolution and pathology, including relations between heart and head muscle development	<i>Kelly R, Diogo R*; Aix Marseille University, Howard University</i>
3:45pm	CHA1-4	Major challenges in vertebrate morphology and theoretical biology: networks, macroevolution, and human birth defects	<i>Rasskin-Gutman D, Sánchez García J, Esteve-Altava B, Navarro Díaz A, Rasskin I, Diogo R; University of Valencia, The Royal Veterinary College, University of Montpellier, Howard University</i>

2:30pm – 4:00pm MFM1

Salon F

Symposium: Muscle functional morphology: beyond gross anatomy 1

Chairs: A Hartstone-Rose, D Marchi

2:30pm	MFM1-1	Stretch, strength, and speed: functional interpretations of muscle fiber architecture in limbs and the masticatory apparatus	<i>Hartstone-Rose A, Marchi D; University of South Carolina School of Medicine, University of Pisa</i>
2:45pm	MFM1-2	Modelling jaw muscle function in marsupials: from dissection to multibody dynamics analysis	<i>Sharp A, Graham D, Trusler P, Crompton A; University of New England, Griffith University, Monash University, Harvard University</i>
3:00pm	MFM1-3	Jaw adductor muscle fiber architecture and estimated bite force in tree shrews (Mammalia: Scandentia)	<i>Kristjansson H, Perry J; Johns Hopkins University School of Medicine</i>
3:15pm	MFM1-4	Biomechanics of the chewing musculature: osteological correlates of function and inferences from fossils	<i>Perry J, St Clair E, Hartstone-Rose A; Johns Hopkins University, University of South Carolina School of Medicine</i>
3:30pm	MFM1-5	Preliminary bite force estimations of Miocene giant mustelids (Carnivora, Mustelidae)	<i>Valenciano A, Leischner C, Grant A, Abella J, Hartstone-Rose A; Instituto de Geociencias (CSIC, UCM), Spain, Facultad de Ciencias Geológicas UCM, Spain, University of South Carolina School of Medicine, Universidad Estatal Península de Santa Elena, Universitat Autònoma de Barcelona, Spain</i>
3:45pm	MFM1-6	Functional adaptations of primate forearm muscle fiber architecture	<i>Leischner C, Allen K, Pastor F, Marchi D, Hartstone-Rose A; University of South Carolina School of Medicine, Washington University School of Medicine in St. Louis, Universidad de Valladolid, University of Pisa</i>

2:30pm – 4:00pm MIM1**Salon H****Morphological Integration & Modularity 1***Chairs: M Buchtova, W Gelnow*

2:30pm	MIM1-1	Role of FGF signaling during anterior-posterior patterning of zeugopod	<i>Buchtova M, Hampl M, Cela P, Horakova D, Krejci P; Laboratory of Molecular Morphogenesis, Institute of Animal Physiology and Genetics AS CR; Institute of Experimental Biology, Masaryk University, Czech Republic</i>
2:45pm	MIM1-2	Bodies and fins exhibit correlated evolution towards locomotor specializations in cichlid fishes	<i>Feilich K; Harvard University</i>
3:00pm	MIM1-3	How many roads lead to Rome? Phenotypic and genetic convergence in two independent lines of mice selectively bred for increases in relative limb bone length	<i>Rolian C, Yu S, Sparrow L, Farooq S, Kucka M, Beluch W, Chan Y; University of Calgary, Friedrich Miescher Lab - Max Plack Institute</i>
3:15pm	MIM1-4	Determinants of body shape and co-variation among elements of the bony torso in anthropoids (Primates: Anthroidea)	<i>Ward C, Middleton E; University of Missouri</i>
3:30pm	MIM1-5	Building blocks: functional and developmental modularity in the axial skeleton of Felidae (Mammalia)	<i>Randau M, Goswami A; University College London</i>
3:45pm	MIM1-6	Disintegrator: a new R package for evaluating phylogenetic trees while accounting for correlations between character states	<i>Gelnow W; University of Texas at Austin</i>

2:30pm – 4:00pm PAL1**Salon G****Paleontology 1***Chairs: J Mallat, AAM Mann*

2:30pm	PAL1-1	Puzzle of the earliest vertebrates: "Blessed are the meek"	<i>Mallat J; Washington State University</i>
2:45pm	PAL1-2	Osteology of the Cretaceous †Ctenothrissiformes and †Pattersonichthyiformes: clues to primitive structure in eurypterygian fishes	<i>Delbarre D, Friedman M; University of Oxford</i>
3:00pm	PAL1-3	A reconsideration of the aistopod <i>Lethiscus stocki</i> (Tetrapoda: Lepospondyli) via micro-Computed Tomography (microCT), with implications for tetrapod phylogeny	<i>Anderson J, Pardo J, Ahlberg P, Szostakiwskyj M, Germain D; University of Calgary, Uppsala University, Museum National d'Histoire Naturelle</i>
3:15pm	PAL1-4	Morphological innovations in the earliest post-Devonian tetrapods: adaptations towards increasing terrestriality?	<i>Clack J, Smithson T*; University of Cambridge</i>
3:30pm	PAL1-5	A re-description of <i>Amphibamus grandiceps</i> (Temnospondyli: Dissorophoidea) from the Francis Creek shale, Mazon Creek, Illinois	<i>Mann A, Maddin H; Carleton University</i>
3:45pm	PAL1-6	Evolution of genome size in recent and fossil salamanders	<i>Stein K, Skutchas P, Schoch R, Fröbisch N; Earth System Science - AMGC, Vrije Universiteit Brussel; Royal Belgian Institute of Natural Sciences Directorate 'Earth and History of Life', Saint Petersburg State University, Vertebrate Zoology Department, Biological Faculty, Staatliches Museum für Naturkunde, Museum für Naturkunde Berlin</i>

4:30pm – 5:45pm CHA2**Salon E****Symposium: Major challenges for vertebrate morphology, evolution and development 2***Chairs: JM Hoyos, R Diogo*

4:30pm	CHA2-1	Major challenges in vertebrate morphology, ecology and biophysics: Hummingbirds as a case study	<i>Rico-Guevara A; University of Connecticut</i>
4:45pm	CHA2-2	Major challenges in vertebrate morphology: 2D, 3D, and 4D visualization and network tools applied to study the origin and evolution of tetrapod limbs	<i>Molnar J, Esteve-Altava B, Johnston P, Diogo R; Howard University, Royal Veterinary College, University of Auckland</i>
5:00pm	CHA2-3	Major challenges in vertebrate morphology, muscle evolution and evolutionary change via heterochrony	<i>Ziermann J, Diogo R; Howard University College of Medicine</i>
5:15pm	CHA2-4	Major challenges in vertebrate morphology: bridging the gap between genotypes and musculo-skeletal phenotypes in primates using functional genomics and developmental genetics	<i>Capellini T, Dingwall H, Willen J, Wohns A; Harvard University</i>

5:30pm	CHA2-5	Biomechanics as part of the evo-devo-morphology synthesis, and the challenges of including fossil taxa	<i>Hutchinson J; The Royal Veterinary College, University London</i>
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4:30pm – 5:30pm	MFM2	Salon F
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Symposium: Muscle functional morphology: beyond gross anatomy 2

Chairs: A Hartstone-Rose, D Marchi

4:30pm	MFM2-1	Leg muscle architecture in primates and its correlation with locomotion patterns	<i>Marchi D, Mikes A, Leischner C, Pastor F, Hartstone-Rose A; University of Pisa, University of South Carolina School of Medicine, Universidad de Valladolid</i>
4:45pm	MFM2-2	From bone to behavior: reconstructing habitual activity from muscle attachment site morphology	<i>Turcotte C, Rabey K, Green D, Arbenz-Smith K, McFarlin S; George Washington University, Midwestern University</i>
5:00pm	MFM2-3	Beyond function: muscle energetic and brain evolution	<i>Hemingway H, Muchlinski M; University of Kentucky, Lexington</i>
5:15pm	MFM2-4	Old meets new: combining traditional and modern tools in the study of jaw adductor morphology and function	<i>Santana S; University of Washington</i>

4:30pm – 5:45pm	MIM2	Salon H
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Morphological Integration & Modularity 2

Chairs: SN Cobb, RN Felice

4:30pm	MIM2-1	Morphological modules within the avian skull evolve at different rates	<i>Felice R, Goswami A; University College London</i>
4:45pm	MIM2-2	The timing of cranial lateral line morphogenesis and its implications for ontogeny of sensory function	<i>Webb J; University of Rhode Island</i>
5:00pm	MIM2-3	Tempo, mode and integration in the evolution of complex morphologies	<i>Monteiro L, Nogueira M; Laboratorio de Ciencias Ambientais - UENF</i>
5:15pm	MIM2-4	Constraint and convergent evolution of diprotodonty in therian mammals	<i>Cobb S, Morris P, Cox P; Hull York Medical School, University of York, University of Hull</i>
5:30pm	MIM2-5	A maximum likelihood approach to assessing modularity with 3-D morphometric data	<i>Goswami A, Finarelli J; University College London, University College Dublin</i>
5:45pm	MIM2-6	Modularity or integration or both? 3D analysis of 21 genera of frogs demonstrates phylogenetic conservatism in skulls and lability in limbs	<i>Vidal-Garcia M, Keogh J; The Australian National University</i>

4:30pm – 6:00pm	PAL2	Salon G
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Paleontology 2

Chairs: TJD Halliday, GT Lloyd

4:30pm	PAL2-1	A new important stage in the evolution of the turtle body plan	<i>Sues H, Schoch R; Smithsonian Institution, Staatliches Museum für Naturkunde Stuttgart</i>
4:45pm	PAL2-2	Macroevolution of the crocodylomorphs	<i>Stockdale M; University of Bristol</i>
5:00pm	PAL2-3	Ornithischian dinosaur 'cheeks' are evolutionary epiphenomena of previously undescribed reorganization and enlargement of jaw musculature	<i>Nabavizadeh A; University of Chicago</i>
5:15pm	PAL2-4	Distribution of purported cursorial adaptations in Mesozoic theropod dinosaurs through phylogeny, time, and space	<i>Holtz T; University of Maryland</i>
5:30pm	PAL2-5	Measuring morphological diversity and tempo using discrete characters: advantages and disadvantages of including additional phylogenetic information	<i>Lloyd G; Macquarie University</i>
5:45pm	PAL2-6	Dynamics of morphological evolution in Cretaceous and Paleocene eutherian mammals	<i>Halliday T, Goswami A; University College London</i>

7:30pm – 9:30pm	REC1	Salons A–C
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Welcome Reception

Thursday 30th June, 2016

8:15am – 9:30am PLN2

Salon D-E

Plenary Session 2: Alexander Vargas

Chair: JE Moustakas-Verho

8:15am **PLN2-1** Embryos of living dinosaurs: A path to uncover the evolution of development *Vargas A; Universidad de Chile*

9:30am – 11:00am BON1

Salon A

Symposium: New insights into skeletal microstructure of vertebrates, extant and extinct 1

Chairs: E Rega, M Dean, T Owerkowicz

9:30am **BON1-1** Scaling of Haversian systems in a phylogenetically diverse sample of mammals is consistent with physical and physiological constraints *Middleton K, Hurtado A, Swartz S; University of Missouri, Brown University*

10:00am **BON1-2** Osteocyte mechanobiology: influence on bone modeling and remodeling and its bearing on functional interpretation of skeletal morphology *Main R; Purdue University*

10:15am **BON1-3** Bone microstructure in hibernating mammals with implications for mechanical performance *Donahue S, Wojda S, Hinrichs J, McGee-Lawrence M; Colorado State University, Georgia Regents University*

10:30am **BON1-4** Developmental mechanisms and evolutionary advantage of metatarsal elongation and fusion in bipedal jerboas (Dipodidae) *Saxena A, Gutierrez H, Cooper K*; University of California San Diego*

10:45am **BON1-5** Effects of growth rate and flight on wing bone laminarity in bats and birds *Lee A; Midwestern University*

9:30am – 11:00am GEN1

Salon C

General Morphology 1

Chairs: A Cernansky, AB Ward

9:30am **GEN1-1** Homology of the accessory elements of the hyoid arch within Gnathostomata *Bockmann F, Carvalho M, Carvalho M, Rizatto P*; Universidade de São Paulo*

9:45am **GEN1-2** Evolution of complex skull shape across the global radiation of extant bats *Shi J, Rabosky D; University of Michigan*

10:00am **GEN1-3** Mammalian neck construction between variation and constraints *Arnold P, Stark H, Werneburg I, Fischer M; Institut fuer Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, Friedrich-Schiller-Universität Jena, Germany, Senckenberg Center for Human Evolution and Palaeoenvironment (HEP) at Eberhard Karls Universität Tübingen, Germany, Fachbereich Geowissenschaften der Eberhard Karls Universität Tübingen, Germany, Museum für Naturkunde, Leibniz-Institut für Evolutions- & B*

10:15am **GEN1-4** How does the transition from lizard body to serpentiform morphology influence the atlas-axis complex in lizards? *Cernansky A; Comenius University in Bratislava*

10:30am **GEN1-5** Tinkering with the tail: variation in the vertebral column in Ophidiiformes *Ward A, Galloway K, Porter M, Mehta R; Adelphi University, University of Rhode Island, Florida Atlantic University, University of California Santa Cruz*

10:45am **GEN1-6** Body shape transformation along anatomical lines of least resistance in labyrinth fishes *Collar D, Ward A, Mehta R; Christopher Newport University, Adelphi University, University of California, Santa Cruz*

9:30am – 11:00am	LOC1	Salon G
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Locomotion 1

Chairs: A-C Fabre, AC Gibb

9:30am	LOC1-1	Comparing rodent species of different sizes for ecomorphological analyses	Verde Arregoitia L; Natural History Museum Bern
9:45am	LOC1-2	Coevolution between forelimb shape and loading regime in strepsirrhines	Fabre A, Granatosky M, Hanna J, Schmitt D; MNHN, Duke University, West Virginia School of Osteopathic Medicine
10:00am	LOC1-3	Limb specializations and adaptive diversification in Mustelidae	Kilbourne B; Museum für Naturkunde Berlin
10:15am	LOC1-4	Variation of the felid (Mammalia: Felidae) scapula and implications for felid biology	Jasinski S, Dodson P; University of Pennsylvania
10:30am	LOC1-5	Hand skeleton and wingtip shape in coraciiform and piciform birds	Hieronymus T; NEOMED
10:45am	LOC1-6	Is variation in vertebral spine morphology associated with variation in myomere morphology in the killifishes?	Minicozzi M, Gillespie S, Gibb A*; Northern Arizona University

9:30am – 11:00am	MFS1	Salon B
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Symposium: Determinants of the mammalian feeding system design 1

Chairs: O Panagiotopoulou, J Iriarte-Diaz

9:30am	MFS1-1	Not all bones are created equal: Intrinsic and extrinsic influences on phenotypic expression in the developing skull	Ravosa M, Weiss-Bilka H, Franks E, Scott J, McAbee K, Brill J, Pax K, Pasquinelli A, Mazur M, Scollan J, Eastman M; University of Notre Dame, Southern Illinois University
10:00am	MFS1-2	Tooth wear, textures, and feeding biomechanics	Schulz-Kornas E; Max Planck Weizmann Center for Integrative Archaeology and Anthropology
10:30am	MFS1-3	Performance and integration in mammalian dentitions: from blade sharpness and dental complexity to the inhibitory cascade	Evans A; Monash University

9:30am – 11:00am	PHA1	Salon H
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Symposium: The vertebrate pharynx: crossroads in evolution and development 1

Chairs: A Huyseune, A Tucker

9:30am	PHA1-1	Pharyngeal remodelling in development and evolution	Graham A; King's College London
10:00am	PHA1-2	Molecular basis of the lamprey pharyngeal development	Jandzik D, Romasek M, Square T, Cattell M, Medeiros D; University of Colorado Boulder
10:30am	PHA1-3	Tightly orchestrated epithelial transitions drive pharyngeal pouch formation in zebrafish	Choe C, Crump G*; University of Southern California

9:30am – 11:00am	SBN1	Salon F
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Sensory Biology & Neuroscience 1

Chairs: DJ Bird, AM Clement

9:30am	SBN1-1	Using the brain-neurocranial relationship in the extant Australian lungfish to interpret fossil endocasts	Clement A, Strand R, Nysjö J, Long J, Ahlberg P; Flinders University, Uppsala University
9:45am	SBN1-2	Comparative morphology of snake (Squamata) endocasts: evidence of phylogenetical and ecological signals	Allemand R, Boistel R, Blanchet Z, Cornette R, Bardet N, Vincent P, Houssaye A; Centre de Recherches sur la Paléobiodiversité et les Paléoenvironnements, Muséum National d'Histoire Naturelle, Sorbonne Universités, France, Université de Poitiers, France, Département Ecologie et Gestion de la Biodiversité, France, Institut de Systématique, Evolution, Biodiversité
10:00am	SBN1-3	The bones and genes of smell: Cribriform morphology and olfactory receptor gene repertoires	Bird D, Hayden S, Teeling E, Murphy W, Fox Rosales L, Hamid A, Van Valkenburgh B; University of California Los Angeles, University College Dublin, Texas A&M

10:15am	SBN1-4	A comparison of the fluid dynamics and odorant deposition of unsteady sniffing versus quasi-steady breathing in the nasal cavity of the coyote	Rygg A, Craven B, Van Valkenburgh B; University of California, Los Angeles, The Pennsylvania State University
10:30am	SBN1-5	Nasal morphometry and airflow dynamics in a nocturnal primate, <i>Nycticebus pygmaeus</i> (Mammalia: Primates)	Smith T, Engel S, Craven B, DeLeon V; Slippery Rock University, The Pennsylvania State University, University of Florida
10:45am	SBN1-6	Comparative morphology and histology of the nasal fossa in four mammals: gray squirrel, bobcat, coyote, and deer	Van Valkenburgh B, Yee K, Craven B, Wysocki C; UCLA, Monell Chemical Senses Center, The Pennsylvania State University

11:30am – 1:00pm **BON2**

Salon A

Symposium: New insights into skeletal microstructure of vertebrates, extant and extinct 2

Chairs: E Rega, M Dean, T Owerkowicz

11:30am	BON2-1	Functional cranial joint histology in reptiles and birds and its significance for avian cranial kinesis	Bailleul A, Horner J, Witmer L, Holliday C; University of Missouri
12:00pm	BON2-2	Atmospheric oxygen conditions do not constrain growth or biomechanical performance of limb bones in Alligatoridae: <i>Alligator mississippiensis</i>	Lujan S, Owerkowicz T, Elsey R, Hicks J, Middleton K; California State University San Bernardino, Louisiana Department of Wildlife and Fisheries, Grand Chenier LA, University of California, Irvine, University of Missouri, Columbia
12:15pm	BON2-3	Effect of embryonic calcium constraint on post-hatching growth and bone microstructure in the American alligator (<i>Alligator mississippiensis</i>)	Membreno N, Elsey R, Owerkowicz T; California State University San Bernardino, Rockefeller Wildlife Refuge, Louisiana Dept. of Wildlife and Fisheries
12:30pm	BON2-4	How's your apatite? Structure and mechanics of elasmobranch skeletal tissues	Porter M, Huber D, Seidel R, Ford J, Decker S, Dean M; Florida Atlantic University, The University of Tampa, Max Planck Institute of Colloids & Interfaces, Potsdam, Germany, University of South Florida Morsani College of Medicine, Max Planck Institute of Colloids & Interfaces, Potsdam, Germany
12:45pm	BON2-5	Evolution read in tooth and jaw: synchrotron tomography reconstructs a comparative model for dental evolution in Osteichthyes	Walten M, Cerny R, Donoghue P; University of Bristol, UK, Charles University, Czech Republic

11:30am – 1:00pm **GEN2**

Salon C

General Morphology 2

Chairs: M Boulliart, DJ Paluh

11:30am	GEN2-1	Morphology of the ovarian germinal epithelium in bony fishes: Centropomidae <i>Centropomus undecimalis</i> , Goodeidae <i>Xenotoca eiseni</i> and Chlorophthalmidae <i>Chlorophthalmus agassizi</i>	Grier H, Uribe M, Parenti L; Florida Fish and Wildlife Conservation Commission, Florida Fish and Wildlife Research Institute, National Museum of Natural History, Laboratorio de Biología de la Reproducción Animal, Universidad Nacional Autónoma de México. México
11:45am	GEN2-2	Comparison of cranial development of Siberian sturgeon, <i>Acipenser baerii</i> , and Russian sturgeon, <i>Acipenser gueldenstaedtii</i> (Acipenseriformes: Acipenseridae)	Warth P, Konstantinidis P, Hilton E, Naumann B, Olsson L; University of Jena, Virginia Institute of Marine Science
12:00pm	GEN2-3	Comparative beak morphology of two subspecies of Australian Red-tailed Black-Cockatoos: Small changes with significant functional effects as a model for macroevolutionary processes	Homberger D; Louisiana State University, Baton Rouge
12:15pm	GEN2-4	Evolution of cornification in amniotes: the case of Sauropsids	Alibardi L; Comparative Histolab, Italy
12:30pm	GEN2-5	Comparative morphology of the quadrate bone within Gekkota (Squamata): Phylogenetic and functional implications	Paluh D, Bauer A; Villanova University
12:45pm	GEN2-6	Musculoskeletal systems simplified to 2D and 3D biomechanical models: the potentials and limitations of modeling bite forces	Boulliart M, De Meyer J, Van Wassenbergh S, De Kegel B, Adriaens D; Ghent University

11:30am – 1:00pm	LOC2	Salon G
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Locomotion 2

Chairs: JL Lees, T Miyake

11:30am	LOC2-1	The transition to adhesion in geckos: evidence from <i>Gonatodes</i> (Gekkota: Sphaerodactylidae)	<i>Russell A, Higham T, Gamble T; University of Calgary, University of California Riverside, Marquette University</i>
11:45am	LOC2-2	The coordinated motion control model of tetrapod limbs with mono- and bi-articular muscles: Model, application, and evolutionary origin	<i>Miyake T, Iwata M, Sato R, Tsuji T, Tajima T, Koie H, Umemura A, Yoshimura K, Abe Y, Kumamoto M; Graduate School of Science and Technology, Japan, Marine Science Museum, Japan, Kanazawa Institute of Technology, Japan, Saitama University, Japan, Honda R&D Co., Ltd., Japan, Nihon University, Japan, Kitami Institute of Technology, Japan, Kyoto University, Japan</i>
12:00pm	LOC2-3	Rachis morphology cannot accurately predict the mechanical performance of primary feathers in extant (and therefore fossil) birds	<i>Lees J, Garner T, Cooper G, Nudds R; University of Manchester</i>
12:15pm	LOC2-4	Estimating scapular positions in extant quadrupedal tetrapods by using two different approaches: implications to forelimb posture reconstructions in extinct taxa	<i>Fujiwara S; Nagoya University Museum</i>
12:30pm	LOC2-5	Computational and experimental analysis of terrestrial locomotion in fire salamanders: insights into the evolution of walking and running in tetrapods	<i>Rankin J, Pierce S, Hutchinson J; The Royal Veterinary College, UK, Harvard University</i>
12:45pm	LOC2-6	A novel joint-based approach for studying skeletal evolution and motion	<i>Carney R; Brown University</i>

11:30am – 1:00pm	MFS2	Salon B
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Symposium: Determinants of the mammalian feeding system design 2

Chairs: O Panagiotopoulou, J Iriarte-Diaz

11:30am	MFS2-1	Variations in the material properties of mammalian and non-human primate jaws	<i>Dechow P; Texas A&M University Baylor College of Dentistry</i>
12:00pm	MFS2-2	Impact of feeding behavior on the deformations of the macaque mandible	<i>Panagiotopoulou O, Iriarte-Diaz J, Wilshin S, Dechow P, Taylor A, Grosse I, Ross C; The University of Queensland, Australia, The Royal Veterinary College, UK, University of Illinois Chicago, Texas A&M University, Baylor College of Dentistry, Duke University, University of Massachusetts, University of Chicago</i>
12:30pm	MFS2-3	What's gape got to do with it? Examining osteological correlates of jaw gape in primates	<i>Terhune C; University of Arkansas</i>

11:30am – 1:00pm	PHA2	Salon H
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Symposium: The vertebrate pharynx: crossroads in evolution and development 2

Chairs: A Huyseune, A Tucker

11:30am	PHA2-1	Endoderm out of the mouth: pre-oral gut in non-teleost fishes reveals an ancient mode of foregut development	<i>Cerny R, Metscher B, Arias Rodriguez L, Gela D, Minarik M; Charles University in Prague, Czech Republic, University of Vienna, Austria, Universidad Juárez Autónoma de Tabasco, Mexico, University of South Bohemia, Czech Republic</i>
12:00pm	PHA2-2	The first pouch in formation and evolution of the amniote middle ear	<i>Tucker A; King's College London</i>
12:30pm	PHA2-3	Evolutionary and developmental relationships between pharyngeal pouches and teeth	<i>Huyseune A, Witten P; Ghent University</i>

Sensory Biology & Neuroscience 2*Chairs: L Schmitz, A Stoessel*

11:30am	SBN2-1	Adaptive signals in the morphological evolution of vertebrate eyes	<i>Schmitz L; Claremont Colleges</i>
11:45am	SBN2-2	Drivers of visual field evolution in mammals	<i>Fraser D, Webster R, Herman A; Smithsonian National Museum of Natural History, Carleton University</i>
12:00pm	SBN2-3	Exploring the evolution of the auditory morphology of primates using <i>in-situ</i> soft-tissue visualization and geometric morphometrics	<i>Stoessel A, David R, Gunz P, Ossmann S, Hublin J, Spoor F; Max Planck Institute for Evolutionary Anthropology; Technische Universität Dresden; Klinik und Poliklinik für Hals-, Nasen- und Ohrenheilkunde</i>
12:15pm	SBN2-4	Some chameleons really do "hear it through the grapevine"	<i>Huskey S, Anderson C, Smith M, Barnett K; Western Kentucky University, Brown University, New York State Department of Environmental Conservation</i>
12:30pm	SBN2-5	The origin of ultrasonic hearing in whales: new insights from morphometric studies of the inner ear	<i>Churchill M, Geisler J, Martinez-Caceres M; New York Institute of Technology, National Museum of Natural History, Paris France</i>
12:45pm	SBN2-6	Functional morphology of mysticete sound reception: constructing the first baleen whale audiogram using finite element modeling	<i>Cranford T, Krysl P, Potter C; San Diego State University, University of California, San Diego, Smithsonian Institution</i>

Symposium: New insights into skeletal microstructure of vertebrates, extant and extinct 3*Chairs: E Rega, M Dean, T Owerkowicz*

2:30pm	BON3-1	3D virtual bone histology reveals the life history of the early tetrapod <i>Acanthostega</i>	<i>Sanchez S, Tafforeau P, Clack J, Ahlberg P; Uppsala University and SciLife Lab, European Synchrotron Radiation Facility, University of Cambridge, Uppsala University</i>
2:45pm	BON3-2	Adaptive patterns in aquatic amniote bone microanatomy: was it more complex than previously thought?	<i>Houssaye A, Klein N; CNRS/Museum National d'Histoire Naturelle Paris</i>
3:00pm	BON3-3	Bone histology of osteoderms of archosauriform diapsid reptiles (Sauropsida: Archosauriformes)	<i>Scheyer T, Desojo J, Cerda I; University of Zurich, Palaeontological Institute and Museum, CONICET, Sección Paleontología Vertebrados, Argentina y Museo Argentino de Ciencias Naturales, Argentina, CONICET, Argentina y Instituto de Investigaciones en Paleobiología y Geología, Universidad Nacional de Río Negro, Museo Carlos Ameghino, Argentina</i>
3:15pm	BON3-4	In search of the basal amniote condition of Lines of Arrested Growth (or something along those lines...)	<i>Sumida S, Segovia B, Mathew N, Rega E; California State University San Bernardino, Western University of Health Sciences</i>
3:30pm	BON3-5	Novel insight into the growth dynamics of sauropodomorph dinosaurs	<i>Cerda I, Chinsamy-Turan A*, Pol D, Apaldetti C, Otero A, Powell J, Martinez R; CONICET-Instituto de Investigaciones Paleobiología y Geología, University of Cape Town, CONICET- Instituto y Museo de Ciencias Naturales</i>
3:45pm	BON3-6	Intraskelatal growth dynamics and functional maturation in the limb bones of "dinobirds"	<i>Prondvai E, Hu D, Godefroit P, Adriaens D; Evolutionary Morphology of Vertebrates, Ghent University, Belgium, Paleontological Institute, Shenyang Normal University, China, Royal Belgian Institute of Natural Sciences, Directorate 'Earth and History of Life', Belgium</i>

2:30pm – 4:00pm	BSI1	Salon F
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Symposium: Evolution, development, and integration of the vertebrate brain and skull 1

Chairs: GS Bever, B-AS Bhullar, MR Sánchez-Villagra

2:30pm	BSI1-1	Evolution, development, and integration of the vertebrate brain and skull: Frontiers in neuroscience and paleontology	<i>Bever G; New York Institute of Technology College of Osteopathic Medicine</i>
2:45pm	BSI1-2	Deep deuterostome origins of vertebrate brain regulatory programs	<i>Lowe C, Minor P, Yao Y, Pani A, Epstein D*; Stanford University, University of Pennsylvania, University of Chicago</i>
3:15pm	BSI1-3	Geometric changes in brain and skull, and the integration and interdependence of cranial modules	<i>Marugán-Lobón J; Universidad Autónoma de Madrid</i>
3:30pm	BSI1-4	Evolution and development of the head in agnathans and fishes	<i>Kuratani S, Sugahara F, Ota K, Oisi Y; RIKEN, Academia Sinica, Yilan Marine Station, Max Planck Florida Institute for Neuroscience</i>

2:30pm – 4:00pm	GEN3	Salon C
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General Morphology 3

Chairs: M Bernardi, AA Curtis

2:30pm	GEN3-1	Primates hearing: ear morphology, functions and ecology	<i>Bernardi M, Couette S, Montuire S; EPHE/UMR uB CNRS 6282</i>
2:45pm	GEN3-2	Convergent loss of paranasal sinuses in mammals is explained by their deleterious effects on high-frequency communication	<i>Foster F, Shapiro D; Rutgers University</i>
3:00pm	GEN3-3	Evolution of the laterosensory canals of the snout in Osteognathostomata (Vertebrata: Pisces)	<i>Rizzato P, Bockmann F; LIRP-FFCLRP-USP</i>
3:15pm	GEN3-4	Coos, booms, and hoots: the evolution of closed-mouth vocal behavior in birds	<i>Riede T, Eliason C*, Miller E, Goller F, Clarke J; Midwestern University, The University of Texas at Austin, Memorial University of Newfoundland, University of Utah</i>
3:30pm	GEN3-5	The head suspension apparatus of cats and the shoulder suspension apparatus of humans: Modeling a macroevolutionary transformation with extant organisms	<i>Osborn M, Homberger D; Louisiana State University School of Veterinary Medicine</i>
3:45pm	GEN3-6	Unique turbinal morphology in echolocation specialists (Chiroptera: Rhinolophidae)	<i>Curtis A, Simmons N; American Museum of Natural History</i>

2:30pm – 4:00pm	LOC3	Salon G
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Locomotion 3

Chairs: KM Diamond, BE Flammang

2:30pm	LOC3-1	The gibbon's Achilles tendon revisited	<i>Aerts P, D'Août K, Berillon G, Thorpe S, Vereecke E; University of Antwerp, University of Liverpool, CNRS, University of Birmingham, University of Leuven</i>
2:45pm	LOC3-2	Loading distribution over the four fingers of the tapir during locomotion	<i>Nauwelaerts S, Vangeel K, MacLaren J, Aerts P; University Antwerpen</i>
3:00pm	LOC3-3	Walking with giraffes – joint angles, moments and effective mechanical advantage	<i>Basu C, Hutchinson J; Royal Veterinary College</i>
3:15pm	LOC3-4	Impacts of stream velocity and prey morphology on predator-prey interactions in Hawaiian stream fishes	<i>Diamond K, Schoenfuss H, Walker J, Blob R; Clemson University, Saint Cloud State University, University of Southern Maine</i>
3:30pm	LOC3-5	Waterfall-climbing performance of gobiid fishes from La Réunion: how conservative are novel functional behaviors?	<i>Schoenfuss H, Bertram R, Lagarde R, Ponton D, Diamond K, Offerle T, Blob R; St. Cloud State University, Hydrô Réunion, UMR Entropie, Clemson University</i>
3:45pm	LOC3-6	Tetrapod-like pelvic girdle in a walking cavefish	<i>Flammang B, Suvarnaksha A, Markiewicz J, Soares D; NJIT</i>

2:30pm – 4:00pm	MFS3		Salon B
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Symposium: Determinants of the mammalian feeding system design 3

Chairs: O Panagiotopoulou, J Iriarte-Diaz

2:30pm	MFS3-1	Functional and evolutionary relationships between jaw-muscle fiber architecture and behavior: a disturbance in the force	Taylor A, Vinyard C; Duke University School of Medicine, Northeast Ohio Medical University
3:00pm	MFS3-2	The effect of variation of the jaw adductor musculature and cranial morphology on the masticatory performance of primates	Iriarte-Diaz J, Akif Y, Deshpande R, Al-Hamawi O; University of Illinois at Chicago
3:30pm	MFS3-3	Mandibular loading, jaw-muscle activity, and symphyseal performance: elucidating the relationships among mastication, morphology, and biomechanics of the mammalian jaw	Williams S, Vinyard C, Ravosa M; Ohio University, NEOMED, University of Notre Dame

2:30pm – 4:00pm	PHA3		Salon H
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Symposium: The vertebrate pharynx: crossroads in evolution and development 3

Chairs: A Huyseune, A Tucker

2:30pm	PHA3-1	What happened to the gills during the fish-to-tetrapod transition?	Schoch R; Staatliches Museum fuer Naturkunde Stuttgart
3:00pm	PHA3-2	Lungs to gas bladders: homology, novelty and transformation	McCune A, Cass A, Longo S, Riccio M; Cornell University, North Carolina State University, University of California, Davis
3:30pm	PHA3-3	Diverse embryonic and evolutionary origins for the hypoxia-sensitive cells of the vertebrate respiratory reflex	Baker C, Hockman D, Burns A, Mongera A, Fisher S, Unlu G, Knapik E, Kelsh R, Kaufman C, Mosimann C, Zon L, Tucker A*; University of Cambridge, UCL Institute of Child Health, Max-Planck Institut für Entwicklungsbiologie, University of Pennsylvania, Vanderbilt University, University of Bath, Harvard Medical School, King's College London

4:30pm – 5:15pm	BON4		Salon A
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Symposium: New insights into skeletal microstructure of vertebrates, extant and extinct 4

Chairs: E Rega, M Dean, T Owerkowicz

4:30pm	BON4-1	Microstructure isn't enough: Additional diagnostic criteria to test among hypotheses of bone tissue identity	Werning S, Schweitzer M, Padian K; Des Moines University, North Carolina State University, University of California, Berkeley
4:45pm	BON4-2	Localized resorption spaces in femoral cortical bone of a mature <i>Tyrannosaurus rex</i> (Theropoda) are adaptive response to muscle traction	Rega E, Mathew N, Weis B, Noriega K; Western University of Health Sciences
5:00pm	BON4-3	Preliminary results on the bone histology of hadrosaurs (Ornithopoda, Dinosauria) from the Latest Cretaceous of Far Eastern Russia	Stein K, Bolotski Y, Bolotski I, Claeys P, Godefroit P; Earth System Science - AMGC, Vrije Universiteit Brussel; Royal Belgian Institute of Natural Sciences Directorate 'Earth and History of Life', Russian Academy of Sciences, Russian Federation

4:30pm – 6:00pm	BSI2		Salon F
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Symposium: Evolution, development, and integration of the vertebrate brain and skull 2

Chairs: GS Bever, B-AS Bhullar, MR Sánchez-Villagra

4:30pm	BSI2-1	Stability and flux in relationships between cranial bones and endocranial structures – paleontology and molecular development	Bhullar B-AS; Yale University
4:45pm	BSI2-2	The heads of the earliest fossil vertebrates: evolution, development and diversity	Ahlberg P; Uppsala University
5:15pm	BSI2-3	The dinosaur and bird brain: evolution, ontogeny, and function	Balanoff A; Stony Brook University
5:30pm	BSI2-4	On the interparietal and supraoccipital: the development of the mammalian skull roof and its coevolution with the brain	Koyabu D; University Museum, University of Tokyo

5:45pm	BSI2-5	Developing humanized mouse models to study human evolution	<i>Dutrow E, Reilly S, Noonan J; Kavli Institute for Neuroscience, Yale School of Medicine, Broad Institute of MIT and Harvard</i>
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4:30pm – 5:45pm **GEN4** **Salon C**

General Morphology 4

Chairs: AR Cuff, H Higashiyama

4:30pm	GEN4-1	Ventilatory rib kinematics in the savannah monitor, <i>Varanus exanthematicus</i> : an XROMM study	<i>Cieri R, Moritz S, Brainerd E; University of Utah, Brown University</i>
4:45pm	GEN4-2	Grow bigger, dig deeper? Allometric effects of size on forelimb muscle architecture in the southern brown bandicoot (<i>Isodon obesulus</i> ; Marsupialia: Peramelidae)	<i>Lane M, Warburton N, Fleming P; Murdoch University</i>
5:00pm	GEN4-3	Big cat, weak cat? The scaling of postcranial myology within Felidae	<i>Cuff A, Randau M, Pierce S, Hutchinson J, Goswami A; UCL, Harvard University, Royal Veterinary College</i>
5:15pm	GEN4-4	Transforming tails into tools: syngnathid fishes used as bio-inspiration	<i>Neutens C, De Dobbelaer B, Claes P, Praet T, Porter M, De Beule M, Christiaens J, De Kegel B, Dierick M, Boistel R, Adriaens D; Ghent University, KU Leuven, Clemson University, Université de Poitiers</i>
5:30pm	GEN4-5	On the whole-anatomy of the murine hepatobiliary system by using the transparency method	<i>Higashiyama H, Kanai Y; The University of Tokyo</i>

4:30pm – 6:00pm **LOC4** **Salon G**

Locomotion 4

Chairs: CJ Mayerl, MK O'Donnell

4:30pm	LOC4-1	Functional pelvic anatomy of the red-legged running frog (Anura: Hyperoliidae, <i>Kassina maculata</i>)	<i>Collings A, Porro L, Richards C; The Royal Veterinary College</i>
4:45pm	LOC4-2	The importance of good posture: clinging in climbing and non-climbing salamanders	<i>O'Donnell M, Deban S; University of South Florida</i>
5:00pm	LOC4-3	Scaling of morphology and performance in elastically powered systems	<i>Olberding J, Deban S; University of South Florida</i>
5:15pm	LOC4-4	Hind limb muscle function in turtles: is novel skeletal design correlated with novel muscle function?	<i>Mayerl C, Pruett J, Rivera A, Blob R; Clemson University, Creighton University</i>
5:30pm	LOC4-5	One foot out the door: limb function during swimming in a recently evolved, terrestrial lineage of turtles	<i>Young V, Vest K, Rivera A, Espinoza N, Blob R; Clemson University, Creighton University</i>
5:45pm	LOC4-6	The effects of differential function in the limbs of turtles on patterns of symmetry: an examination of fore- and hindlimb propelled species	<i>Rivera G; Creighton University</i>

4:30pm – 5:30pm **MFS4** **Salon B**

Symposium: Determinants of the mammalian feeding system design 4

Chairs: O Panagiotopoulou, J Iriarte-Diaz

4:30pm	MFS4-1	Modulation of feeding energetic costs in primates: the impact of morphology and behavior across body size	<i>Wall C, Hanna J, O'Neill M, Toler M; Duke University, West Virginia School of Osteopathic Medicine, University of Arizona College of Medicine, Johns Hopkins University</i>
5:00pm	MFS4-2	Symposium discussion	<i>Ross CF, University of Chicago</i>

Symposium: The vertebrate pharynx: crossroads in evolution and development 4

Chairs: A Huyseune, A Tucker

4:30pm	PHA4-1	Neural crest-pharyngeal interactions that underlie the evolution of jaw size	Fish J, Vavrušová Z, Chakrabarti D, Gambino K, Rose N, Schneider R*; University of Massachusetts Lowell, University of California San Francisco
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7:30pm – 9:30pm POS1**Grand Foyer****Poster session & reception 1****Sensory Biology and Neuroscience (SBN)**

POS1-1	Structural changes in the olfactory organs of <i>Taricha granulosa</i> , the rough-skinned newt, between aquatic and terrestrial phases	Bronson A, Snee E*, Cummings A, Reiss J; Humboldt State University
POS1-3	Location specific protein expression and cell proliferation in the central nervous system following tail loss in the gecko (Reptilia: Squamata)	Gilbert E, McDonald R, Vickaryous M*; University of Guelph
POS1-5	Subterranean specialization of the ear morphology in <i>Eospalax fontanierii</i> (Rodentia: Spalacidae)	Plestilova L, Hrouzkova E, Hua L, Burda H, Sumner R; University of South Bohemia, Czech Republic, Lanzhou University and Gansu Grassland Ecological Research Institute, China, University of Duisburg-Essen, Germany
POS1-7	Vomeroneasal organ development in the sand lizard (Reptilia: Squamata: Lacertidae: <i>Lacerta agilis</i>)	Tytiuk O, Hruby V*, Yaryhin O, Stepanyuk Y; Lesya Ukrainka Eastern European National University, I. I. Schmalhausen Institute of Zoology National Academy of Science of Ukraine
POS1-9	Gross Anatomical Brain Region Approximation (GABRA): a new landmark-based approach for estimating brain regions in archosaurs	Morhardt A, Ridgely R, Witmer L; Ohio University
POS1-11	The skull and endocranial anatomy of the extinct giant moa <i>Dinornis robustus</i> (Aves: Palaeognathae) and implications for the behavioral role of vision in moa	Early C, Ridgely R, Porter W, Cerio D, Witmer L; Ohio University
POS1-13	Neuroanatomy of the extinct terror birds (Aves: Phorusrhacidae): implications for a predatory mode of life	Degrange F, Tambussi C, Ridgely R, Witmer L*; CONICET-Universidad Nacional de Córdoba, Argentina, Ohio University

Locomotion (LOC)

POS1-15	Muscle function in rainbow smelt, <i>Osmerus mordax</i> , during winter	Coughlin D, Bradley M, Shuman J; Widener University
POS1-17	Scaling of burial mechanics in the English sole, <i>Parophrys vetulus</i> (Actinopterygii: Pleuronectiformes)	Corn K, Farina S, Gibb A, Summers A; Cornell University, Harvard University, Northern Arizona University, University of Washington
POS1-19	How to modify a fin into a limb: Insights from anglerfish	Dickson B, Pierce S; Museum of Comparative Zoology and Department of Organismic and Evolutionary Biology, Harvard
POS1-21	Simulating movement in early tetrapods: inputs from limb muscle physiology	Pierce S, West T, Hutchinson J; Harvard University, Structure and Motion Lab, The Royal Veterinary College, UK
POS1-23	Why are long bones curved?	Milne N; University of Western Australia
POS1-25	Tendinous system in <i>Leptodactylus</i> (Amphibia, Anura, Leptodactylidae): Morphological diversity and its relation to habitat and locomotion	Fratani J, Ponssa M, Abdala V; CONICET-Fundación Miguel Lillo, Instituto de Biodiversidad Neotropical UNT-CONICET
POS1-27	Does crocodilian ankle morphology relate to ankle kinematics?	Suzuki D; Sapporo Medical University
POS1-29	Investigating inter-limb evolutionary linkages in avian limb proportions	Proffitt J; The University of Texas at Austin
POS1-31	Sciuriform limb bones: morphological correlates to different locomotor behaviors	Woelfer J, Nyakatura J; Humboldt U. Berlin
POS1-33	Kinematics of arboreal descent in primates	Perchalski B; Duke University
POS1-35	Form-function relationships and the evolution of arboreal locomotion in mammals	Herrel A, Böhmer C, Fabre A, Herbin M, Cornette R, Peigné S; MNHN Paris
POS1-37	Functional implications of manual grasping strength in marmosets (Primates: <i>Callithrix jacchus</i>) and squirrel monkeys (Primates: <i>Saimiri boliviensis</i>)	Young J, Chadwell B, O'Neill T, Patel B; Northeast Ohio Medical University (NEOMED), University of Southern California

POS1-39	Functional anatomy of the nasal muscles in Japanese badger <i>Meles anakuma</i> (Mammalia: Mustelidae)	<i>Kobayashi M, Hosomi H; Okayama University of Science</i>
POS1-41	Thoracic strengths a new indicator of life reconstruction in extinct secondary aquatic mammals	<i>Ando K, Fujiwara S*; Graduate School of Environmental Studies, Nagoya University, Nagoya University Museum</i>
Paleontology (PAL)		
POS1-43	Anatomy and diversity of the earliest fossil vertebrates (Chengjiang Biota, Cambrian, China): new evidence from experimental taphonomy	<i>Murdock D, Gabbott S, Cong P, Purnell M; University of Leicester, UK, Yunnan Key Laboratory for Palaeobiology, Yunnan University, China</i>
POS1-45	Morphology of two early fossils aligned with the specialized deep-sea predatory fish groups Gempylidae and Trichiuridae assessed using micro-computed tomography	<i>Beckett H, Johanson Z, Friedman M; University of Oxford, Natural History Museum, London</i>
POS1-47	Early Permian amphibamid <i>Pasawioops</i> (Amphibamidae, Dissorophoidea): An ontogenetic series	<i>Atkins J, Reisz R, Maddin H; Carleton University, University of Toronto Mississauga</i>
POS1-49	Phylogeny, ecology, and time: 2D outline analysis of anuran skulls from the Early Cretaceous to Recent	<i>Bardua C, Evans S, Goswami A; University College London</i>
POS1-51	New skull material of the Early Permian <i>Eryops</i> from Brushy Creek (Wichita Group, Texas) showing the morphological variability of foramina and canals in the quadratojugal of basal tetrapods	<i>Klembara J, Cernansky A, Witzmann F, van Heteren A; Comenius University in Bratislava, Museum für Naturkunde Berlin, Universität Bonn, Germany</i>
POS1-53	The description of the axial osteology of a juvenile plesiosaur, and revision of polycotylid systematics	<i>Morgan D, O'Keefe F; Marshall University</i>
POS1-55	Body size evolution in glyptosaurine lizards (Squamata: Anguidae) accurately models paleoclimates for the interior of North America	<i>ElShafie S, Head J; University of California, Berkeley, University of Cambridge</i>
POS1-57	Constraints in crocodylomorph body size evolution	<i>Godoy P, Benson R, Bronzati M, Butler R; University of Birmingham, United Kingdom, University of Oxford, United Kingdom, Bayerische Staatssammlung für Paläontologie und Geologie, Germany</i>
POS1-59	Predicting skull size in Breviostres using cranial pit depth	<i>Lynch L, Lynch E, Schubert B; Oklahoma State University Center for Health Sciences, Don Sundquist Center of Excellence in Paleontology, East Tennessee State University</i>
POS1-61	The mechanical origin and morphology of the labial (horizontal) shelf in Leptoceratopsia demonstrates it is now a synapomorphy of Neoceratopsia (Dinosauria: Ornithischia)	<i>Varriale F, Morschhauser E*; King's College, Drexel University</i>
POS1-63	The visual apparatus of archosaurs: correlates of orbital anatomy, eye size, and behavior	<i>Cerio D, Witmer L; Ohio University Department of Biological Sciences, Ohio University Heritage College of Osteopathic Medicine</i>
POS1-65	A novel method to estimate cranial muscle strain in fossil and extant vertebrates using digital modelling and visualisation	<i>Lautenschlager S; School of Earth Sciences, University of Bristol</i>
POS1-67	The morphology of motion: sub-surface foot trajectories and fossil tracks	<i>Turner M, Falkingham P, Gatesy S; Brown University, Liverpool John Moores University</i>
POS1-69	One foot, many footprints: the origin of track morphological diversity	<i>Gatesy S, Falkingham P; Brown University, Liverpool John Moores University</i>
POS1-71	A total-evidence, time-calibrated phylogeny of the 'waterbird' assemblage (Tetrapoda, Aves)	<i>Moore A; The George Washington University</i>
POS1-73	Dental microwear and macrowear morphology of the Japanese dormice (Mammals: Gliridae <i>Glirulus japonicus</i>)	<i>Tomohiko H; Tokyo Gas Technology Research Institute</i>
POS1-75	Occipital condyle width predicts body mass in proboscideans	<i>Jukar A; George Mason University</i>
POS1-77	A complete description and phylogenetic analysis of <i>Puijila darwini</i> , (Mammalia: Carnivora) and inferences on the plesiomorphic swimming condition of pinnipeds	<i>Paterson R, Rybczynski N, Kohno N, Maddin H; Carleton University, Canadian Museum of Nature, National Museum of Nature and Science</i>
POS1-79	Macroevolutionary responses to invasion in terrestrial carnivorans from the early Miocene of North America	<i>Soul L; Smithsonian NMNH</i>
POS1-81	A well-preserved malleus in a juvenile specimen of the extinct family Nimravidae	<i>Spearing K, Boyd C, Welsh E; Morningside College, North Dakota Geological Survey, Badlands National Park</i>
POS1-83	Histological analysis of morphological integration and development in the Weberian apparatus of the zebrafish	<i>Bird N; University of Northern Iowa</i>

Morphological Integration & Modularity (MIM)

- POS1-85** A refined system of vertebral column subdivision in Chinook salmon, *Oncorhynchus tshawytscha* (Actinopterygii: Salmonidae) *De Clercq A, Perrott M, Davie P, Preece M, Wybourn B, Ruff N, Huysseune A, Witten P; Institute of Veterinary, Animal and Biomedical Sciences, Massey University, New Zealand, New Zealand King Salmon, Skretting Australia, Ghent University, Belgium*
- POS1-87** Chemical manipulation of axolotl regeneration and angiogenesis *Dickie R, Wilkins D, Ritenour A; Towson University*
- POS1-89** Ontogenetic integration and modularity in the dermatocranium of the Greater Short-horned lizard, *Phrynosoma hernandesi* *Powell G, Russell A, Jamniczky H, Hallgrímsson B; University of Calgary*

Evo-Devo (EVD)

- POS1-91** Comparative study of hexose transporters in ostrich small intestine *Hussar P, Kärner M, Järveots T, Duritis I; University of Tartu, Estonian University of Life Sciences, Latvian University of Agriculture*
- POS1-93** Fetal membrane morphology in oviparous lampropeltine snakes (Colubridae) *Kim Y, Blackburn D; Trinity College*
- POS1-95** Placental morphology in viviparous North American water snakes (Colubridae) *Blackburn D, Johnson A, Anderson K, Marquez E, Callard I; Trinity College, Cornell University, Boston University*
- POS1-97** A novel pattern of yolk mobilization in developing squamate reptiles *Powers K, Blackburn D; Trinity College*
- POS1-99** Endocrine control of limb development in the direct-developing frog *Eleutherodactylus coqui* (Anura: Eleutherodactylidae) *Laslo M, Hanken J; Harvard University, Museum of Comparative Zoology*
- POS1-101** A survey of morphological and heterochronal variations during early ontogeny in six families of Leptodactyliformes (Anura: Hyloides) *Grosso J, Vera Candiotti M, Barraso D, Nogueira Costa P, Barrionuevo S, Natale G, Baldo J; UEL-CONICET, IDEAus-CONICET, Museu Nacional, Universidade Federal do Rio de Janeiro, Museo Argentino de Ciencias Naturales – CONICET, CIMA-CONICET, IBS, CONICET-UNaM*
- POS1-103** Evolutionary and developmental mechanisms underlying craniofacial variation in Neotropical bats *Camacho J, Heyde A, Abzhanov A; Harvard University, Imperial College London*
- POS1-105** *Hoxa11* and *Hoxd11* loss-of-function mutations alter pisiform growth plate organization *Kjosness K, Hines J, Reno P; The Pennsylvania State University*
- POS1-107** Evolution of fetal skeletogenesis in mammals: patterns, diversity, and modularity *Koyabu D, Sánchez-Villagra M; University Museum, University of Tokyo, Palaeontological Institute and Museum, University of Zürich*
- POS1-109** Linking morphometrics with 3D analysis of gene expression patterns of early limb development in an Apert syndrome mouse model *Sastre J, Mateu R, Russo L, Richtsmeier J, Sharpe J, Martínez-Abadías N*; Centre for Genomic Regulation, Universitat de Barcelona, Pennsylvania State University*
- POS1-111** Expression of a set of cranial neural crest regulatory genes in the dental mesenchyme during mouse tooth development *Woodruff E, Mangino A, Bloch J, Cohn M; University of Florida, Florida Museum of Natural History*
- POS1-113** Fetal growth in mysticete and odontocete skulls: the developmental origins of the highly divergent skulls of cetaceans *Roston R, Yamato M, Roth V; Duke University, National Museum of Natural History*
- POS1-115** Testing a model of scute patterning in chelonid sea turtles *Moustakas-Verho J, Wyneken J*; Institute of Biotechnology, University of Helsinki, Florida Atlantic University*
- POS1-117** Functional characterization of enhancer variants driving human evolution *Ryu A, Pollen A, Kircher M, Martin B, Shendure J, Pollard K, Ahituv N; UCSF, University of Washington*

Hard-tissue Biology (HRD)

- POS1-119** Evidence of hyperostosis in the oarfish (Actinopterygii: *Regalecus russellii*) *Paig-Tran E, Barrios A*, Ferry L; CSU Fullerton, Arizona State University West*
- POS1-121** Bone growth and bone morphology in Atlantic salmon under conditions of severe phosphorus deficiency: The uncoupling of bone formation and bone mineralisation *Witten P, Fontanillas R, Soenens M, McGurk C, Obach A; Ghent University, Skretting Aquaculture Research Centre*
- POS1-123** Ligaments that push and cartilage that bends: Diverse connective tissue morphology in teleost fishes is associated with diverse functions *Staab K; McDaniel College*
- POS1-125** High-resolution study of salamander braincase morphology using micro-CT reveals novel phylogenetic information *Szostakiwskyj M, Anderson J; University of Calgary*

POS1-127	The overlooked cranial sesamoids of squamate reptiles	Montero R, Daza J, Bauer A, Abdala V; Universidad Nacional de Tucumán, Argentina, Sam Houston State University, Villanova University
POS1-129	Integration of histology and morphology to assess the skeletal maturity of early-diverging dinosauromorphs	Bano L, Griffin C; Virginia Polytechnic Institute and State University
POS1-131	Body mass estimation of juvenile individuals: towards a better understanding of extinct animal growth	Chiba K, Evans D, Campione N; University of Toronto, Royal Ontario Museum, Uppsala University
POS1-133	The calcar: a novel hindlimb structure in bats	Stanchak K, Santana S; University of Washington
POS1-135	Compressive behavior of vertebral bodies in cetaceans (<i>Delphinidae</i>) and Sirenians (<i>Trichechidae</i>)	Ingle D, Porter M; Florida Atlantic University
POS1-137	Bone architecture in the rabbit (<i>Oryctolagus cuniculus</i>) mandible as a function of load and age	Rafferty K, Salamati A, Cunningham C, Shin D, Herring S; University of Washington
POS1-139	Bone microstructure of <i>Bathyergus suillus</i> (Rodentia: Bathyergidae): cortical bone thickening and sexual dimorphism	Montoya-Sanhueza G, Anusuya Chinsamy A; University of Cape Town, South Africa
POS1-141	Effects of selection for high wheel running on femoral nutrient foramen dimensions	Schwartz N, Horner A, Garland T, Patel B; California State University San Bernardino, University California Riverside, University Southern California
POS1-143	Comparison of impact loading and wheel running on femoral cross-section morphology in young outbred mice	Smolinsky A, Middleton K; University of Missouri, Columbia
POS1-145	Effects of disrupting the dental lamina and mandibular nerve on tooth replacement in the green iguana (Squamata: <i>Iguana iguana</i>): A reanalysis of historic radiograph data	Brink K, Richman J; University of British Columbia
POS1-147	Comparative assessment of enamel tufts	Kelly M, Kempainen A, Ledue N, Constantino P; Saint Michael's College
POS1-149	Enamel decussation patterns in carnivorans	Kempainen A, Ledue N, Kelly M, Constantino P; Saint Michael's College
POS1-151	The role of enamel thickness in carnivoran dietary adaptation	Ledue N, Kelly M, Kempainen A, Constantino P; Saint Michael's College

Friday 1st July, 2016

8:15am – 9:30am **PLN3** **Salon D-E**

Plenary Session 3: Zerina Johanson

Chair: AP Summers

8:15am	PLN3-1	Developmental origin of the synsacral in jawed vertebrates: implications for vertebral development and fusion	Johanson Z, Boisvert C, Trinajstić K; Natural History Museum, Curtin University
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9:30am – 11:00am **ECO1** **Salon B**

Symposium: Past, present and future of ecological morphology 1

Chairs: LD McBrayer, EJ McElroy, R Wilson

9:30am	ECO1-1	Introduction to the symposium	McElroy EJ, McBrayer LD, Wilson R
9:45am	ECO1-2	Ecomorphology: Insights into adaptation from the analysis of form-function complexes to the dynamics of species diversification	Miles D; Ohio University
10:00am	ECO1-3	Adaptations, innovations, and diversification	Wainwright P; University of California, Davis
10:15am	ECO1-4	Life-history of the multivariate performance phenotype	Lailvaux S; University of New Orleans
10:30am	ECO1-5	Trajectories of insight in ecological morphology: phenotypic integration, speciation, and the Anthropocene	Langerhans R; North Carolina State University
10:45am	ECO1-6	Ecomorphological adaptations to an invasive predator: insights from lizards and fire ants	Langkilde T, Thawley C; Pennsylvania State University

9:30am – 11:00am **GMM1** **Salon C**

Geometric Morphometrics 1

Chairs: ME Kirchner-Smith, A Tinus

9:30am	GMM1-1	Morphological responses of the scapula and os coxae to selection for high voluntary locomotor activity in laboratory mice (<i>Mus musculus domesticus</i> , Rodentia: Muridae)	Schutz H, Jamniczky H, Asplund C, Braaten-Fierros K, Higginbotham C, Donovan E, Garland T; Pacific Lutheran University, Cumming School of Medicine, University of Calgary, University of California, Riverside
9:45am	GMM1-2	Using 3D geometric morphometrics to study interspecific variation in the forelimb of modern tapirs (Perissodactyla: <i>Tapirus</i>)	MacLaren J, Aerts P, Nauwelaerts S; Universiteit Antwerpen
10:00am	GMM1-3	3-D geometric morphometric exploration of pelvic girdle configuration in four ecomorphs of Greater Antillean anoles (Squamata: Dactyloidae)	Tinus A, Russell A; University of Calgary
10:15am	GMM1-4	How good is the tarsometatarsus for species identification? 3D Geometric Morphometrics in living and extinct foot-propelled diving birds	Kirchner-Smith M; University of California, Berkeley
10:30am	GMM1-5	Femoral neck bone density and morpho-functional feature in chimpanzees	Matsumura A, Okada M; National Defense Medical College, Tsukuba University
10:45am	GMM1-6	Ontogenetic changes in muscle architectural properties in the Eastern cottontail rabbit (<i>Sylvilagus floridanus</i>)	Butcher M, Rose J, Glenn Z, Tatomirovich N, Foster A, Smith G, Young J; Youngstown State University, NEOMED, Kent State University at Stark

9:30am – 11:00am **HAL1** **Salon A**

Symposium: The many faces of the skeleton: a tribute to the achievements of Brian K. Hall 1

Chairs: PE Witten, M Vickaryous

9:30am	HAL1-1	Facing plasticity in the skeleton of teleosts	Witten P, Huysseune A; Ghent University
10:00am	HAL1-2	Dermal skeletal plasticity and evolution of the chondrichthyan dentition	Meredith Smith M, Johanson Z, Underwood; Kings College London, Natural History Museum London, Birkbeck College London
10:30am	HAL1-3	A neural crest origin of trunk dermal denticles in the little skate, <i>Leucoraja erinacea</i>	Gillis J, Alsema E; University of Cambridge
10:45am	HAL1-4	Evolution and development of scleral ossicles	Franz-Odenaal T; Mount Saint Vincent University

9:30am – 11:00am	NPL1		Salon H
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Symposium: Fundamental aspects of the spatial associations, development, and birth defects of the muscles and skeleton in non-pentadactyl limbs 1

Chairs: V Abdala, T Kohlsdorf, R Diogo

9:30am	NPL1-1	Non-pentadactyly, soft and hard tissue associations, birth defects, and implications for medicine	Smith C, Diogo R; Howard University
10:00am	NPL1-2	The genetic basis of mammalian limb diversification	Sears K, Maier J, Rivas-Astroza M, Cao X, Zhong S, Zhao K, Sinha S, Ma J, Behringer R, Cretekos C, Rasweiler J; University of Illinois
10:30am	NPL1-3	What determines the identity of the distal limb muscles? A myological analysis of mammals with digit reduction/digit loss	Bello-Hellegouarch G, Diogo R, Abdala V, Kohlsdorf T; University of São Paulo, Brazil, Howard University College of Medicine, Instituto de Biodiversidad Neotropical, Argentina

9:30am – 11:00am	PAL3		Salon F
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Paleontology 3

Chairs: C Griffin, J Moustakas-Verho

9:30am	PAL3-1	Intraspecific variation and the evolution of the ancestral dinosaurian growth condition	Griffin C; Virginia Tech
9:45am	PAL3-2	Wing-bone thickness and bending resistance in pterosaurs	Martin-Silverstone E; University of Southampton/ University of Bristol
10:00am	PAL3-3	Evolutionary increases in vertebral regionalization within the mammalian lineage: evidence from fossil synapsids	Jones K, Polly P, Head J, Angielczyk K, Pierce S; Harvard University, Indiana University, University of Nebraska-Lincoln, Field Museum of Natural History
10:15am	PAL3-4	The cave bear story: integrating paleontological and developmental evidence	Moustakas-Verho J, Jernvall J; Institute of Biotechnology, University of Helsinki
10:30am	PAL3-5	Morphometry and behavioural biology: As seen in the humerus of Pleistocene tiger (<i>Panthera cf. tigris</i> Pocock 1929) from Manjra Valley, India	Sathe V, Chakraborty P; Deccan College Post Graduate and Research Institute
10:45am	PAL3-6	Evolution and function of the angular process in early mammalian jaws	Grossnickle D; University of Chicago

9:30am – 11:00am	PLT1		Salon G
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Symposium: Palate development, function and evolution 1

Chairs: J Richman, CM Holliday, J Abramyan

9:30am	PLT1-1	Molecular patterning of the hard palate during mammalian palatogenesis	Ye W, Huang Z, Chen Y; Tulane University, Fujian Normal University
10:00am	PLT1-2	Differing effects of Fgfr mutations on palate morphology in non-cleft mouse models	Martinez-Abadias N, Motch Perrine S, Melkonian F, Pankratz T, Rhodes K, Wang Y, Zhou X, Wang Jabs E, Richtsmeier J; Center for Genomic Regulation, Pennsylvania State University, Universitat de Barcelona, Icahn School of Medicine at Mount Sinai
10:15am	PLT1-3	An open and shut case; Variation in morphogenesis of the secondary palate in amniotes	Richman J, Higashihori N, Abramyan J; University of British Columbia, Tokyo Medical and Dental School
10:30am	PLT1-4	Mechanisms of crocodilian palate formation	Abramyan J, Richman J; University of British Columbia
10:45am	PLT1-5	Morphology and development of secondary palate in chameleon	Hampl M, Dosedelova H, Zahradnické O, Pyszkó M, Zikmund T, Buchtova M; Institute of Animal Physiology and Genetics, Masaryk University, Czech Republic, University of Veterinary and Pharmaceutical Sciences, Czech Republic, Academy of Sciences of the Czech Republic, Czech Republic, CEITEC BUT, Czech Republic

11:30am – 1:00pm	GMM2		Salon C
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Geometric Morphometrics 2

Chairs: C Fruciano, CT Stayton

11:30am	GMM2-1	Quantitative morphological convergence and divergence of carnivorous rodents from the Indo-Pacific	<i>Fabre P, Rowe K, Achmadi A, Esselstyn J; Institut des Sciences de l'Evolution de Montpellier, Museum Victoria, LIPI, Museum Zoologicum Bogoriense, Louisiana State University, Museum of Natural Science</i>
11:45am	GMM2-2	Morphometric models for estimating bite force in murid rodents: empirical versus analytical models	<i>Ginot S, Hautier L, Herrel A, Claude J; ISE-M, MNHN</i>
12:00pm	GMM2-3	Darwin's Niata - an anatomical, morphometric, and genetic study of an extinct cattle breed: expanding morphological boundaries through selective breeding	<i>Veitschegger K, Wilson L, Camenisch G, Keller L, Sánchez-Villagra M; University of Zürich, Switzerland, University of New South Wales, Australia</i>
12:15pm	GMM2-4	Physical media influence the rate and pattern of turtle carapace shape evolution	<i>Djurakic M, Herrel A; University of Novi Sad, Faculty of Sciences, Department of Biology and Ecology, UMR 7179 CNRS/MNHN Département d'Ecologie et de Gestion de la Biodiversité</i>
12:30pm	GMM2-5	Patterns of morphological and mechanical evolution in the turtle shell	<i>Stayton C; Bucknell University</i>
12:45pm	GMM2-6	A look at measurement error in geometric morphometrics	<i>Fruciano C, Weisbecker V, Phillips M; Queensland University of Technology, University of Queensland</i>

11:30am – 1:00pm	HAL2		Salon A
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Symposium: The many faces of the skeleton: a tribute to the achievements of Brian K. Hall 2

Chairs: PE Witten, M Vickaryous

11:30am	HAL2-1	Ontogeny and homology of the vertebrate skull	<i>Hanken J; Harvard University</i>
12:00pm	HAL2-2	Cranial morphology in the earliest shark-like fishes (Chondrichthyes)	<i>Maisey J; American Museum of Natural History</i>
12:30pm	HAL2-3	Cartilage regeneration and diversity in lizards	<i>Subramaniam N, McDonald R, Jacyniak K, Vickaryous M*; University of Guelph</i>
12:45pm	HAL2-4	Integrative biology, evo-devo, and Brian Hall	<i>Wake M; University of California, Berkeley</i>

11:30am – 12:45pm	NPL2		Salon H
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Symposium: Fundamental aspects of the spatial associations, development, and birth defects of the muscles and skeleton in non-pentadactyl limbs 2

Chairs: V Abdala, T Kohlsdorf, R Diogo

11:30am	NPL2-1	Adapting the vertebrate limb neuromuscular system to changes in dactyly	<i>Tschopp P, Young J, Speziale D, Zeller R, Diogo R, Tabin C; Harvard Medical School, University of Basel, Howard University</i>
12:00pm	NPL2-2	Ecomorphology and biomechanics of digit reduction	<i>Nauwelaerts S, MacLaren J, Kaashoek M, Aerts P; University Antwerpen</i>
12:15pm	NPL2-3	Chameleon hand/foot clefting, a tweak on the pentadactyl design and a challenge to limb congenital malformations	<i>Diaz R; La Sierra University</i>
12:30pm	NPL2-4	Patterning and post-patterning modes of evolutionary digit loss in mammals	<i>Cooper K, Sears K, Uygun A, Maier J, Baczkowski K, Brosnahan M, Antczak D, Skidmore J, Tabin C; University of California San Diego, University of Illinois Urbana-Champaign, Harvard Medical School, Ecole Normale Supérieure de Lyon, Cornell University, The Camel Reproduction Centre</i>

11:30am – 1:00pm	PAL4	Salon F
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Paleontology 4

Chairs: JD Marcot, MR McCurry

11:30am	PAL4-1	Extreme longirostry in Miocene odontocetes: the ecomorphology and biomechanics underlying the repeated evolution of a superlative snout	<i>McCurry M, Pyenson N; National Museum of Natural History, Smithsonian Institution</i>
11:45am	PAL4-2	Morphological consequences of tooth loss: A comparison of the course of the mandibular canal in mysticete cetaceans using 3D models	<i>Peredo C, Pyenson N, Uhen M; George Mason University, Smithsonian National Museum of Natural History</i>
12:00pm	PAL4-3	The diversity and evolution of supraorbital crests in Platanistoidea (Cetacea: Odontoceti), and their implications for echolocation	<i>Boersma A, Pyenson N; Smithsonian National Museum of Natural History</i>
12:15pm	PAL4-4	Digital reduction patterns in terrestrial artiodactyls: how many mechanisms?	<i>Theodor J; University of Calgary</i>
12:30pm	PAL4-5	Beam mechanics of digit reduction in fossil horses	<i>McHorse B, Pierce S, Biewener A; Harvard University</i>
12:45pm	PAL4-6	Limb evolution of North American Equidae	<i>Marcot J, Maier J, Kozak K; University of Illinois</i>

11:30am – 12:45pm	PLT2	Salon G
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Symposium: Palate development, function and evolution 2

Chairs: J Richman, CM Holliday, J Abramyan

11:30am	PLT2-1	Structure and strain in the chondrichthyan palatoquadrate	<i>Wilga C, Diniz S, Tutu E, Summers A; University of Alaska Anchorage, University of Rhode Island, University of Washington</i>
12:00pm	PLT2-2	Relative kinetic competency in the palatal complexes of birds and other diapsids	<i>Cost I, Spates A, Sellers K, Davis J, Middleton K, Witmer L, Holliday C; University of Missouri, University of Southern Indiana, Ohio University</i>
12:15pm	PLT2-3	The significance of novel palatal joints in the adaptive radiations of archosaurs	<i>Holliday C, Bailleul A, Cost I, Sellers K, Witmer L, Vickaryous M; University of Missouri, Ohio University, University of Guelph</i>
12:30pm	PLT2-4	Why (and how) the long face? The evolutionary and developmental bases of Anolis facial diversity	<i>Sanger T, Johnson M, Sherratt E; Loyola University in Chicago, Trinity University, Australian National University</i>

12:45pm – 1:00pm	ECO2	Salon B
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Symposium: Past, present and future of ecological morphology 2

Chairs: LD McBrayer, EJ McElroy, R Wilson

11:30am	ECO2-1	Ecometric patterning in hind limb morphology of North American carnivorans (Carnivora, Mammalia): community-level functional morphology and evolutionary ecology	<i>Polly P; Indiana University</i>
11:45am	ECO2-2	500 million years of form and function in fishes: perspectives from Deep Time	<i>Friedman M, Close R, Delbarre D, Dobson C, Giles S, Johanson Z; University of Oxford, University College London, Natural History Museum, London</i>
12:00pm	ECO2-3	Reciprocal illumination of body shape on predator-prey interactions and trophic morphology	<i>Mehta R, Baliga V, Diluzio A, Higgins B, Harrison J; University of California, Santa Cruz</i>
12:15pm	ECO2-4	Ecological morphology in neotropical lizards: is Tropiduridae a key biological system?	<i>Kohlsdorf T, Barros F, Lofeu L, Rothier P, Brandt R; University of São Paulo</i>
12:30pm	ECO2-5	Success in nature and sport: exploring the biological basis of excellence in physical activities?	<i>Wilson R; The University of Queensland</i>
12:45pm	ECO2-6	Symposium roundtable discussion	<i>McElroy EJ, McBrayer LD, Wilson R</i>

2:30pm – 4:00pm	EVD1	Salon G
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Evo-Devo - Evolution of developmental processes 1

Chairs: M Debais-Thibaud, EJ Rayfield

2:30pm	EVD1-1	The evolution of collagen and SPARC secretion during tooth development in vertebrates	Debais-Thibaud M, Enault S, Munoz D, Ventéo S, Sire J, Marcellini S; Montpellier University, France, University of Concepción, Chili, INSERM U1051, Montpellier, France, CNRS UMR7138, Paris, France
2:45pm	EVD1-2	Reduction in tooth site regeneration underlies morphological novelty during pufferfish dental regeneration	Thiery A, Fraser G*; University of Sheffield
3:00pm	EVD1-3	Tammar wallaby <i>Macropus eugenii</i> (Macropodidae) as a model for tooth evolution, development, and replacement in mammals	Nasrullah Q, Renfree M, Evans A; Monash University, The University of Melbourne
3:15pm	EVD1-4	Developmental mechanism and genetic basis of the unique morphological characters of non-model organisms: investigation in bear molars as an example	Asahara M, Kishida T; Mie University, Kyoto University
3:30pm	EVD1-5	Morphology and function of the tooththrow in a rodent knockout model and implications for mammalian tooth evolution	Zurowski C, Jamniczky H, Graf D, Theodor J; University of Calgary, University of Alberta
3:45pm	EVD1-6	The influence of mechanical loading on jaw joint morphology during development	Rayfield E, Brunt L, Bright J, Roddy K, Hammond C; University of Bristol, University of Sheffield

2:30pm – 4:00pm	FED1	Salon A
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Feeding 1

Chairs: LP Hernandez, FR O'Keefe

2:30pm	FED1-1	Assessing the role of the rostrum in skull variation and feeding performance among billfishes: a 3-D Geometric Morphometric approach	Habegger M, Motta P, Lajeunesse M, Ford J, Decker S; University of South Florida
2:45pm	FED1-2	Evolution of mysticete-like filter feeding in plesiosaurs of the austral Late Cretaceous	O'Keefe F, Otero R, Soto-Acuna S; Marshall University, Huntington, WV, USA, Museo Nacional de Historia Natural, Santiago, Chile
3:00pm	FED1-3	Bioinspired design: A novel mechanism of filtration based on manta ray feeding	Paig-Tran E, Bolla V, Summers A; CSU Fullerton, U Washington
3:15pm	FED1-4	Ontogeny of a cypriniform filter-feeding novelty	Hernandez L, McCalley M, Cohen K; George Washington University
3:30pm	FED1-5	Forelimb morphology determines prey processing style in pinnipeds (Mammalia, Carnivora)	Hocking D, Fitzgerald E, Evans A; Monash University, Museum Victoria
3:45pm	FED1-6	Independent transitions to a more goose-like beak in waterfowl (Aves: Anseriformes) correlate with a performance trade-off between terrestrial and aquatic feeding	Olsen A; University of Chicago

2:30pm – 3:45pm	GEN5	Salon B
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General Morphology 5: Climate Change, Environmental Drivers, & Morphological Change

Chairs: BP Bentley, J Wyneken

2:30pm	GEN5-1	Predicting the effect of climate change on sea turtle embryos in North West Australia	Bentley B, Mitchell N, Whiting S, Berry O; The University of Western Australia, WA Department of Parks and Wildlife, Commonwealth Scientific and Industrial Research Organisation (CSIRO)
2:45pm	GEN5-2	Environmental impacts on reptilian nests and offspring: differential embryonic success and neonate growth	Wyneken J, Lolavar A*, Tezak B; Florida Atlantic University
3:00pm	GEN5-3	Virtual fish gills: Computational modeling of gills to quantify hydrodynamic trade-offs in actinopterygian fishes from diverse habitats	Farina S; Harvard University
3:15pm	GEN5-4	Pattern of habitat use of the parasitic nematode <i>Crassicauda</i> within its host, the pygmy sperm whale (<i>Kogia breviceps</i>)	Keenan-Bateman T, McLellan W, Costidis A, Harms C, Rotstein D, Rommel S, Potter C, Pabst D; University of North Carolina Wilmington, North Carolina State University, Marine Mammal Pathology Services, Smithsonian Institution

3:30pm	GEN5-5	Identification and characterization of ionocytes in branchial epithelium of catfish <i>Heteropneustes fossilis</i> and the effect of salinity on their morphometry	<i>Abidi S, Parwez I; Aligarh Muslim University, India</i>
2:30pm – 4:00pm GMM3			Salon C
Geometric Morphometrics 3			
<i>Chairs: JA Bright, RA Close</i>			
2:30pm	GMM3-1	Morphospace occupation and subclade disparity through time in monitor lizards	<i>Ferrer E; American Museum of Natural History</i>
2:45pm	GMM3-2	Interspecific and intersexual morphometric variation in <i>Darevskia</i> lizards based on anal scale shape	<i>Gabelaia M, Adriaens D, Tarkhnishvili D; Ghent University, Ilia State University</i>
3:00pm	GMM3-3	Assessing levels of variation among parthenogenetic and bisexual whiptail lizard using geometric morphometrics	<i>Tulga S, Ferrer E; University of Chicago, American Museum of Natural History</i>
3:15pm	GMM3-4	The relationship between feeding ecology and phylogeny for Weberian ossicle and otolith morphology in the piranha and pacu family (Actinopterygii: Serrasalminidae)	<i>Boyle K, Botton-Divet L, Couillaud P, Herrel A; Muséum National d'Histoire Naturelle, UMR7179 Paris, France</i>
3:30pm	GMM3-5	Probing the third dimension: are morphospaces of 2D and 3D fossil fish crania congruent?	<i>Close R, Friedman M; University of Birmingham, University of Oxford</i>
3:45pm	GMM3-6	Diversification of the avian bill revealed with crowdsourced 3D geometric morphometrics	<i>Bright J, Cooney C, Capp E, Hughes E, Moody C, Nouri L, Varley Z, Thomas G; University of Sheffield</i>
2:30pm – 3:10pm LTG			Salon H
Lightning Session – 5-minute talks			
<i>Chairs: J Fortuny, A Hardin</i>			
2:30pm	LTG-1	Exploring integument mass properties in extant archosaurs and implications for digital volumetric modelling of centre of mass	<i>Macaulay S, Brophy P, Allen V, Hone D, Bates K, Hutchinson J; University of Liverpool, University College Dublin, Royal Veterinary College, Queen Mary University of London</i>
2:35pm	LTG-2	A survey of tooth character data amongst iguanian lizards reveals patterns related to size and taxonomy	<i>Gray J, Hutchinson M, Jones M; University of Adelaide, South Australian Museum</i>
2:40pm	LTG-3	Homologies in forelimb structure between moles and Early Paleogene insectivore mammals	<i>Perepelova A; Zoological Institute RAS</i>
2:45pm	LTG-4	Hunting in the Late Triassic: insights on the ambush strategy of the metoposaurs (Temnospondyli: Stereospondyli)	<i>Fortuny J, Marcé-Nogué J, Konietzko-Meier D; ICP - MNHN, Centrum für Naturkunde - University of Hamburg, Opole University</i>
2:50pm	LTG-5	Genome assembly and annotation of <i>Mastomys coucha</i> , a murid with an extreme mammary phenotype	<i>Hardin A, Carbone L, Ahituv N; University of California, San Francisco, Oregon Health & Science University</i>
2:55pm	LTG-6	Body shape vs. osteology in the fish superfamily Cottoidea	<i>Buser T, Summers A; Oregon State University, University of Washington</i>
3:00pm	LTG-7	Physical properties of the sub-dermal fibrous layers in cetacean tail flukes	<i>Gough W, Fish F, Bart-Smith H; West Chester University, University of Virginia</i>
3:05pm	LTG-8	Seasonal skin anatomy changes in three sympatric anuran species from the Midwestern United States	<i>VanBuren C; University of Cambridge</i>
2:30pm – 4:00pm PAL5			Salon F
Paleontology 5			
<i>Chairs: M Lambertz, HP Tsai</i>			
2:30pm	PAL5-1	The cartilage cone of archosauromorphs: biomechanical implications for hip joint loading and femoral ossification	<i>Tsai H, Middleton K, Holliday C; Brown University, University of Missouri</i>
2:45pm	PAL5-2	Developmental trajectories of convergence, recapitulation, and evolutionary novelty in the crocodylian skull	<i>Morris Z, Abzhanov A, Pierce S; Harvard University, Imperial College London</i>
3:00pm	PAL5-3	Evolution of the flexible avian neck: insights from 3D cervical joint kinematics in wild turkeys	<i>Kambic R, Biewener A, Pierce S; Harvard University</i>

3:15pm	PAL5-4	Paleobiology of caseids (Synapsida: Caseidae) and the functional morphology of their respiratory apparatus: implications for the evolutionary origin of the mammalian diaphragm	Lambertz M, Shelton C, Spindler F, Perry S; <i>Sektion Herpetologie, Zoologisches Forschungsmuseum Alexander Koenig; Institut für Zoologie, Rheinische Friedrich-Wilhelms-Universität Bonn, Steinmann-Institut für Geologie, Mineralogie und Paläontologie, Technische Universität Bergakademie Freiberg</i>
3:30pm	PAL5-5	Functional morphology of the pectoral girdle and forelimbs of a new burrowing cistecephalid dicynodont (Therapsida: Anomodontia)	Lungmus J, Angielczyk K; <i>University of Chicago, Field Museum of Natural History</i>
3:45pm	PAL5-6	Triassic wheelbarrow race: revisiting cynodont forelimb posture with a musculoskeletal model	Lai P, Biewener A, Pierce S; <i>Harvard University</i>

4:30pm – 6:30pm POS2

Grand Foyer

Poster session & reception 2

Geometric Morphometrics (GMM)

POS2-4	Phylogenies from shapes: using shell landmarks to infer the phylogeny of geoemydid turtles	Ascarrunz E; <i>University of Fribourg, Switzerland</i>
POS2-6	Sources of shape change in the testudine skull: A 3D geometric morphometric analysis	Croghan J; <i>Ohio University</i>
POS2-8	The influence of phylogeny and diet in the skull morphology of representatives of Dipsadidae (Squamata: Serpentes)	Murta-Fonseca R, Fernandes D; <i>Museu Nacional, Universidade Federal do Rio de Janeiro, Instituto de Biologia</i>
POS2-10	Beak shape is a poor predictor of trophic ecology in extant birds	Navalón G, Marugán-Lobón J, Bright J, Rayfield E; <i>University of Bristol, Universidad Autónoma de Madrid, University of Sheffield</i>
POS2-12	Growth orientations of rhamphothecae in extant beaked animals with implications to the reconstruction of the beaks in extinct taxa	Urano Y, Matsumoto R, Kawabe S, Tanoue K, Ohashi T, Fujiwara S; <i>Nagoya University, Kanagawa Prefectural Museum of Natural History, Gifu Prefectural Museum, Fukuoka University, Kitakyushu Museum of Natural History & Human History, Nagoya University Museum</i>
POS2-14	Novel analyses estimating evolutionary rates using ancestral state reconstruction suggest recent stasis in the cranium of the dwarf lemur <i>Cheirogaleus</i> (Primates: Cheirogaleidae)	Fulwood E, Cunningham C, Boyer D, Groeneveld L; <i>Duke University, University of Göttingen</i>
POS2-16	Comparative shape analysis of koalas and wombats	Mehari Abraha H, Weisbecker V, Terhune C, Morrison R, Wailan M, Mullins C, Sharp A, Johnston S, Panagiotopoulou O; <i>The University of Queensland, Australia, University of Arkansas, University of New England, Australia</i>
POS2-18	Analyzing the association between platyrrhine locomotor mode percentages and talar shape	Püschel T, Sellers W; <i>University of Manchester</i>
POS2-20	Musculoskeletal fitness in small mammals: are captive-bred individuals fit for the wild?	Foreman C, Stott P, Norris R*; <i>The University of Adelaide, City University of Hong Kong</i>
POS2-22	Reconstruction of muscle fascicle architecture from digital images: a combined texture mapping and streamline approach	Stark H, Mundry R, Neininger F, Heidlauf T, Röhrle O, Kupczik K; <i>Friedrich-Schiller-University Jena, Max Planck Institute for Evolutionary Anthropology, Leipzig, Universität Stuttgart</i>

Feeding (FED)

POS2-24	Measuring bite force in the domestic dog (<i>Canis lupus f. familiaris</i>): A novel experimental approach for recording predatory bites <i>in vivo</i>	Bemmann M, Helbig T, Kupczik K; <i>Max Planck Institute for Evolutionary Anthropology, Technische Universität Ilmenau</i>
POS2-26	Biting mechanics of raccoons (Carnivora: <i>Procyon lotor</i>) and skunks (Carnivora: <i>Mephitis mephitis</i>): exploring the link between cranial morphology and infectious disease control	Klimovich C, Williams S; <i>Ohio University</i>
POS2-28	The evolution of insectivory in freshwater stingrays	Kolmann M, Welch K, Summers A, Lovejoy N; <i>University of Toronto Scarborough, University of Washington</i>
POS2-30	Strange from the start: Ontogeny of the filtering mechanism in Silver Carp	Cohen K, Hernandez LP; <i>George Washington University</i>
POS2-32	The role of the chondrocranium and sutures in a biomechanical model of <i>Tupinambis</i> (Lepidosauria)	Jones M, Groening F, Crumpton N*, Fagan M, Evans S; <i>The University of Adelaide, South Australia, University of Aberdeen, UK, University College London, UK, University of Hull, UK</i>

POS2-34	Functional aspects of the interpterygoid vacuities in the palate of early tetrapods and a reconstruction of the associated cranial muscles	Witzmann F, Lautenschlager S, Werneburg I*; Brown University, University of Bristol, United Kingdom, Eberhard Karls Universität, Germany
POS2-36	Inferring the diets of pterosaurs and extant analogues using quantitative 3D textural analysis of tooth microwear	Bestwick J, Unwin D, Purnell M; University of Leicester
POS2-38	Morphology of the pterygoid musculature in pleurodire turtles	Ferreira G, Werneburg I; University of São Paulo, Eberhard Karls Universität; Museum für Naturkunde - Leibniz-Institut für Evolutions- & Biodiversitätsforschung

General Morphology (GEN)

POS2-40	Domestication effect on skull morphology and biting performance in rats	Becerra F, Bemmann M, Cagan A, Konoshenko M, Kozhemyakina R, Kupczik K; Max Planck Weizmann Center for Integrative Archaeology and Anthropology, Max Planck Institute for Evolutionary Anthropology, Institute of Cytology and Genetics, Siberian Branch of the Russian Academy of Sciences
POS2-42	Finite element analysis of maxillary alveolar bone in rats under dental occlusal changes	Prado F, Freire A, Okamoto R, Rossi A; Piracicaba Dental School - University of Campinas, Araçatuba Dental School - Paulista State University
POS2-44	Feeding in Testudines: A finite element and parametric analysis of a tortoise skull	Luján A, Marcé-Nogué J, Delfino M, Alba D, Fortuny J; Institut Català de Paleontologia M. Crusafont, Centrum für Naturkunde - University of Hamburg, ICP-UNITO, ICP-MNHN
POS2-46	The utility of polymorphic characters in reconstructing the phylogeny of geoemydid turtles	Garbin R, Ascarrunz E; University of Fribourg
POS2-48	Evolutionary associations between body shape and climate in tree frogs (Amphibia: Anura: Hylidae)	Clozel M, Kohlsdorf T; University of São Paulo
POS2-50	Musculoskeletal development of the only matrotrophic viviparous anuran, <i>Nimbaphrynoides occidentalis</i> (Amphibia: Anura: Bufonidae)	Penske S, Mueller H; Institut für Spezielle Zoologie und Evolutionsbiologie, Friedrich-Schiller-Universität Jena, Germany
POS2-52	Diversification of pectoral girdle muscles within frogs (Amphibia: Anura)	Engelkes K, Kleinteich T, Haas A; Universität Hamburg, Kiel University
POS2-54	Tipping the scale: Muscle mass distribution and its effect on center of mass position in the wild and modern domestic turkey	Stover K, Roberts T, Brainerd E; Brown University
POS2-56	Three-dimensional analysis of rib kinematics during lung ventilation in the Argentine black and white tegu, <i>Salvator merianae</i> (Reptilia: Teiidae)	Capano J, Moritz S, Brainerd E; Brown University
POS2-58	The effect of craniokinesis on the middle ear of domestic chickens (<i>Gallus gallus domesticus</i>)	Claes R, Muyschondt P, Van Hoorebeke L, Dhaene J, Dirckx J, Aerts P*; University of Antwerp, University of Ghent
POS2-60	The role of cervical air sacs in the vocalization of songbirds	Cozic A, Homberger D; Louisiana State University
POS2-62	Virtual reconstruction of the skull of a large parrot (Aves: Psittaciformes: <i>Ara macao</i>), highlighting the anatomy of the brain endocast, inner ear, ramphotheca, and kinetic apparatus	Nassif J, Ridgely R, Witmer L; Ohio University
POS2-64	Turbinal variation in high and low altitude populations of <i>Peromyscus maniculatus</i>	Pang B, Mayo K, Van Valkenburgh B; University of California, Los Angeles
POS2-66	Functional anatomy of the hind limb in Japanese cormorants (Aves: Phalacrocoracidae)	Ichikawa M; Okayama University of Science
POS2-68	Morphological disparity, growth and life history variation in domesticated horses	Heck L, Sánchez-Villagra M; Paleontological Institute and Museum, University of Zurich
POS2-70	Morphology and mechanics of remora adhesion	Flammang B, Beckert M, Anderson E, Nadler J; NJIT
POS2-72	Structure and motion over the fin-to-limb transition	Molnar J, Esteve-Altava B, Pierce S, Hutchinson J; Howard University, Royal Veterinary College
POS2-74	Ontogeny of the West African caecilian <i>Idiocranium russeli</i> (Lissamphibia: Gymnophiona: Indotyphlidae)	Theska T, Mueller H*; Department of Comparative Zoology, Jena University
POS2-76	Modeling the skeleto-muscular system in Sea Lampreys (<i>Petromyzon marinus</i>): An integrative approach from microdissection, 3D imaging, and field observations	Wood B, Kynard B, Homberger D; Louisiana State University, Baton Rouge, University of Massachusetts at Amherst
POS2-78	Ultrastructural study of the skin of three caecilians (<i>Ichthyophis tricolor</i> , <i>Uraeotyphlus oxyurus</i> , and <i>Gegeneophis ramaswami</i>) from Western Ghats, India	Damodaran A, Ramachandran K, Akbarshah M, Oommen V, Divya L; Central University of Kerala, India, Government College Madappally, India, Bharathidasan University, Tamil Nadu, Kerala State Biodiversity Board, India

POS2-80	Flow sensing in the deep sea: Novel observations on the mechanosensory lateral line system in stomiiform fishes	Marranzino A, Webb J; University of Rhode Island
POS2-82	Morphophysiology of the gonoduct of the viviparous fish: Poeciliidae <i>Poeciliopsis gracilis</i>	Campuzano Caballero J, Uribe M, Grier J; Universidad Nacional Autónoma de México, National Museum of Natural History, Florida Fish and Wildlife Research Institute
POS2-84	Comparative anatomy of the facial muscles in <i>Myocastor coypus</i> (Mammalia: Myocastoridae)	Taketani M; Okayama University of Science
POS2-86	Preliminary investigations of cranial morphology in the Paradoxurinae (Mammalia, Carnivora, Vivveridae)	Beery S, McAfee R; Ohio Northern University
POS2-88	Comparative anatomy of the subscapularis, teres major, and latissimus dorsi muscles from salamanders to humans	Koizumi M; Tokyo Ariake University of Medical and Health Sciences
POS2-90	The Myosin Heavy Chain specific A4.1025 antibody discriminates different cardiac segments in ancient groups of gnathostomes: Morphological and evolutionary implications	López-Unzu M, Lorenzale M, Soto M, Durán A, Sans-Coma V, Fernández B; University of Málaga
POS2-92	Comparative morphology of <i>Horadandia</i> Deraniyagala and <i>Rasboroides</i> Brittan (Teleostei: Cyprinidae)	Batuwita S, Udugampala S, Athauda S, Edirisinghe U; Postgraduate Institute of Agriculture, University of Peradeniya, Society for the Biodiversity Conservation
POS2-94	Anatomical, histochemical and immunohistochemical characterization of the outflow tract of ray hearts (Rajiformes; Chondrichthyes)	Lorenzale M, López-Unzu M, Rodríguez C, Soto M, Sans-Coma V, Fernández B, Durán A; University of Málaga
POS2-96	Additional articulations on the cervical and thoracic vertebrae and fossoriality in armadillos (Mammalia, Xenarthra)	Castro M, Gallari F; Universidade de São Paulo, Universidad Nacional de La Plata
POS2-98	Evolution of spinal process shape and vertebral immobility in hominoids	Machnicki A, Reno P; Pennsylvania State University
Contrast-enhanced CT (DCT)		
POS2-100	Physiological examination of ratite orthopedic disorders and soft-tissue visualization via micro-CT	Green T, De Miranda Jr. M, Larson A, Bonitz S, Gignac P, Kley N, Kanatous S; Oklahoma State University Center for Health Sciences, Colorado State University, Stony Brook University
POS2-102	Contrast-enhanced versus phase-contrast imaging: costs and benefits of different methods	Herrel A, Boistel R, Adriaens D; CNRS/MNHN, Université de Poitiers, Ghent University
POS2-104	DiceCT and its applications for understanding the reptile musculoskeletal system	Holliday C, Tsai H, Cost I, Sellers K, Lautenschlager S, Witmer L; University of Missouri, Brown University, Bristol University, Ohio University
Ecological Morphology (ECO)		
POS2-106	Substrate and limb evolution: a global ecomorphological analysis of ruminant unguals	Bormet A, Polly P; Indiana University
POS2-108	Ecomorphology of the hind limb long bones in Mustelidae (Mammalia: Carnivora)	Botton-Divet L, Fabre A, Houssaye A, Herrel A, Cornette R; UMR 7179 MNHN/CNRS, Mecadev, Paris, UMR 7205 MNHN/CNRS/UPMC/EPHE, ISYEB, Paris
POS2-110	The evolution of median fin shape and its implications for swimming performance in the fish superfamily Balistoidea (Order Tetraodontiformes)	George A, Westneat M; University of Chicago
POS2-112	A functional role for bipedal locomotion in lizards	McBrayer L; Georgia Southern University
POS2-114	Do parasites have a place in ecomorphology?	McElroy E, de Buron I; College of Charleston
Fossoriality (FOS)		
POS2-116	Digging for clues: Methodological review of subterranean lifestyle inferences in fossil mammals	Selva C, Ladeveze S, Peigne S, Germain D; Centre de recherche sur la Paleobiodiversité et les Paleoenvironnements - Museum national d'Histoire naturelle - UPMC - CNRS
Inner and Middle Ear (EAR)		
POS2-118	The bony labyrinth morphology helps to recalibrate the Cervidae tree	Mennecart B, Costeur L, Bibi F, Métais G, Rössner G, DeMiguel D, Schultz G, Müller B; Natural History Museum, Switzerland, Museum für Naturkunde Berlin, Leibniz Institute for Evolution and Biodiversity Science, Germany, CNRS-Museum National d'Histoire Naturelle, Paris, Bayerische Staatssammlung für Paläontologie und Geologie, Germany, Catalan Institute of Palaeontology Miquel Crusafont, Spain, University of Basel, Switzerland

POS2-120	Sound transmission pathway in protocetids (Mammalia: Cetacea)	Mourlam M, Orliac M; Institut des Sciences de l'Évolution de Montpellier (ISEM - UMR 5554 UM-CNRS-IRD)
POS2-122	Inner ear orientation shows head posture in extant rhinos (Perissodactyla: Rhinocerotidae)	Schellhorn R; Steinmann-Institut, Paläontologie, Universität Bonn
POS2-124	Digging into mammal inner ear morphology: new insights into subterranean lifestyle determination using 3D landmarks inference model	Selva C, Germain D, Peigne S, Ladeveze S; Centre de recherche sur la Paleobiodiversité et les Paléoenvironnements - Museum national d'Histoire naturelle - UPMC - CNRS

Muscle Functional Morphology (MFM)

POS2-126	Comparative myology and adductor leverage in phalangeriform possum jaws	Harper T, Perry J; Johns Hopkins University, SOM
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Secondary adaptation to aquatic life (AQU)

POS2-128	Ontogenetic development and intraspecific variability of bone microstructure in the king penguin <i>Aptenodytes patagonicus</i> : considerations for paleoecological inferences in Sphenisciformes	Canoville A, de Buffrénil V; Steinmann Institute for Geology, Mineralogy and Paleontology, University of Bonn, Germany, CR2P, Centre de Recherche sur la Paléobiodiversité et les Paléoenvironnements, Sorbonne Universités, CNRS/MNHN/UPMC, Muséum National d'Histoire Naturelle, France
POS2-130	Biomechanical and physiological signals in the vascular system of Squamata in the context of secondary adaptation to an aquatic life	Dumont M, Houssaye A; UMR CNRS/MNHN 7179, Mecadev Adaptive mechanisms and evolution
POS2-132	Dietary transitions and the evolutionary origin of whales: 3D texture analysis of tooth microwear in archaeocetes and extant analogues	Goodall R, Purnell*; University of Leicester
POS2-134	Water as a driver of evolution: the example of aquatic snakes	Segall M, Cornette R, Fabre A, Godoy-Diana R, Herrel A; MECADEV (MNHN) - PMMH (ESPCI), ISYEB (MNHN)

Xenarthra (XEN)

POS2-136	Advantages and limitations in the use of extant xenarthrans (Mammalia) as morphological analogues for paleobiological reconstruction	Vizcaíno S; Museo de La Plata, Argentina
POS2-138	An isolated petrosal of the pampathere <i>Holmesina floridans</i> (Mammalia, Xenarthra, Cingulata) from the Blancan NALMA of Florida	Gaudin T; University of Tennessee at Chattanooga
POS2-140	Pedolateralization, foot anatomy, and weight support in extinct sloths (Xenarthra, Folivora)	Toledo N, Racco A, Bargo M, Vizcaíno S, Fernicola J; División Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, CONICET, Sección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", CONICET
POS2-142	Species delimitation and morphological variation in the skull of long-nosed armadillos (<i>Dasypus</i>)	Billet G, Hautier L, de Thoisy B, Delsuc F; CR2P, Museum National d'Histoire Naturelle, France, ISEM, University of Montpellier, France, Institut Pasteur de Guyane, France
POS2-144	Feeding ecology in Oligocene mylodontoid sloths (Mammalia, Xenarthra) as revealed by orthodontine microwear analysis	Kalthoff D, Green J; Swedish Museum of Natural History, Kent State University at Tuscarawas
POS2-146	Tarsal morphology and weight support in the evolution of glyptodonts (Mammalia, Xenarthra, Cingulata)	Fernicola J, Toledo N, Bargo M, Vizcaíno S; CONICET-Sección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"; Universidad Nacional de Luján, CIC; División Paleontología Vertebrados, Unidades de Investigación Anexo Museo, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata
POS2-148	3D finite element analysis of lower jaws in glyptodonts	Tambusso P, Marcé-Nogué J, Fortuny J, Varela L, Fariña R; Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay, Centrum für Naturkunde, University of Hamburg, Hamburg, Germany, C2RP, CNRS-MNHN-UPMC, Paris, France; Institut Català de Paleontologia Miquel Crusafont, Cerdanyola del Vallès, Spain.
POS2-150	Inner and middle ear 3D reconstruction of the extinct giant sloth <i>Lestodon armatus</i>	Varela L, Tambusso P, Fariña R*; Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay

6:30pm – 7:30pm

BUS

Salon D-E

ISVM Business Meeting

Chair: A Huyseune

Saturday 2nd July, 2016

8:15am – 9:30am **PLN4** **Salon D-E**

Plenary Session 4: Luis Chiappe

Chairs: A Chinsamy-Turan

8:15am	PLN4-1	Assembling the bird: morphological evidence from Mesozoic fossils elucidates the evolution of the avian body plan and systems	<i>Chiappe L; Natural History Museum of Los Angeles County</i>
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9:30am – 11:00am **DCT1** **Salon A**

Symposium: Diffusible iodine-based contrast-enhanced computed tomography (diceCT) and related imaging techniques for evolutionary morphology 1

Chairs: PM Gignac, AN Herdina, NJ Kley, A Morhardt, JA Clarke, M Colbert

9:30am	DCT1-1	DiceCTing the future: new horizons for 3-D visualization of vertebrate morphology	<i>Gignac P, Herdina A, Kley N, Morhardt A, Colbert M, Clarke J; Oklahoma State University Center for Health Sciences, Karolinska Institutet, Stony Brook University, Ohio University, The University of Texas at Austin</i>
10:00am	DCT1-2	Using the STABILITY protocol prior to IKI staining to provide the first accurate, in situ quantification of mammalian brain proportion scaling using marsupials	<i>Weisbecker V, Carlisle A, Hinds L, Selwood L, Whish S; School of Biological Sciences, University of Queensland, CSIRO Health and Biosecurity Flagship, University of Melbourne</i>
10:15am	DCT1-3	Mind the gap: ontogenetic shape differences between brains and endocasts in archosaurs	<i>Watanabe A, Gignac P, Norell M; American Museum of Natural History, Oklahoma State University Center for Health Sciences</i>
10:30am	DCT1-4	Incorporating diceCT into multi-scale structural studies of the brain for highly divergent lineages of acrodont lizards: validation of preservation methods conducted in the field	<i>Hughes D, Walker E, Gignac P, Khan A; University of Texas at El Paso, Oklahoma State University Center for Health Sciences</i>
10:45am	DCT1-5	Applying diceCT to PET: new tools for correlating morphology to function in living animals	<i>Gold M, Schulz D, Budassi M, Gignac P, Vaska P, Norell M; Stony Brook University, Yeditepe University, Oklahoma State University Center for Health Sciences, American Museum of Natural History</i>

9:30am – 11:00am **DEN1** **Salon B**

Symposium: Mechanisms of whole dentition patterning in extant and extinct amniotes 1

Chairs: J Richman, L Hlusko, T Grieco

9:30am	DEN1-1	Asymmetry and developmental integration in the replacing leopard gecko dentition (Squamata: <i>Eublepharis macularius</i>) provide evidence for <i>in ovo</i> jaw patterning maintained throughout life	<i>Grieco T, Richman J; University of British Columbia</i>
10:00am	DEN1-2	Early dental development and the origins of toothlessness in amniotes	<i>Lainoff A, Moustakas-Verho J, Hu D, Kallonen A, Marcucio R, Hlusko L; University of California, San Francisco, University of Helsinki, University of California, Berkeley</i>
10:15am	DEN1-3	Crocodyles as perfect models to investigate the mechanisms of continuous dental replacement as it functioned in mammalian ancestors	<i>Thivichon-Prince B, Bertin B, Tafforeau P, Richman J, Viriot L; IGFL, UMRCNRS 5242, ENS, University Lyon1, HCL, France, European Synchrotron Radiation Facility, Grenoble, France, Life Sciences Institute, UBC, Vancouver, Canada</i>
10:30am	DEN1-4	Stem cells and molecular circuits in alligator tooth renewal	<i>Wu P, Tsai S, Abdelhamid A, Widelitz R, Chuong C; Keck School of Medicine, University of Southern California, Qassim University, Saudi Arabia</i>

9:30am – 11:00am	EVD2	Salon C
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Evo-Devo - Evolution of developmental processes 2

Chairs: SJ Rehorek, RG Souza

9:30am	EVD2-1	The development and evolution of cranial nerves and head muscles in two actinopterygian taxa, the longnose gar (<i>Lepisosteus osseus</i>) and the turquoise killifish (<i>Nothobranchius furzeri</i>)	Naumann B, Konstantinidis P, Warth P, Hartmann N, Englert C, Hilton E, Metscher B, Olsson L; Institute of Special Zoology and Evolutionary Biology
9:45am	EVD2-2	Embryonic derivation of the bony skull and cranial musculature in the axolotl (<i>Ambystoma mexicanum</i>)	Sefton E, Hanken J; Harvard University
10:00am	EVD2-3	Correlation between <i>Hox</i> code and vertebral morphology in archosaurs	Böhmer C, Rauhut O, Wörheide G; MNHN Paris, SNSB-BSPG München, LMU München
10:15am	EVD2-4	Comparative anatomy of the nasolacrimal duct: different origins but same end point	Rehorek S, Bly K, Flethcher Q, Rock J, Smith T, Hillenius W; Slippery Rock University, College of Charleston
10:30am	EVD2-5	An earful of jaw, then and now: using marsupial evo-devo to understand a major evolutionary transition in the paleontological record	Urban D, Anthwal N, Tucker A, Sears K; University of Illinois at Urbana-Champaign, King's College London
10:45am	EVD2-6	Revisiting the homologues hypotheses: are we really testing it?	Souza R; Museu Nacional/UFRJ

9:30am – 11:00am	FOS1	Salon F
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Symposium: Life Underground: Morphological Consequences of Fossoriality 1

Chairs: CA Hipsley, E Sherratt, HC Maddin

9:30am	FOS1-1	Introduction to the Symposium	Maddin H; Carleton University
9:45am	FOS1-2	The influence of fossoriality on cranial architecture in caecilian amphibians (Gymnophiona)	Brenning M, Kleinteich T, Wake M, Maddin H; Carleton University, Kiel University, University of California Berkeley
10:00am	FOS1-3	Eyes underground: The degradation of vision genes in subterranean environments	Emerling C, Springer M; University of California Berkeley, University of California Riverside
10:15am	FOS1-4	Ontogenetic allometry constrains cranial shape of the head-first burrowing worm lizard <i>Cynisca leucura</i> (Reptilia: Squamata: Amphisbaenidae)	Hipsley C, Rentinck M, Roedel M, Mueller J; University of Melbourne, Museum für Naturkunde Berlin
10:30am	FOS1-5	Cranial and postcranial specializations for fossoriality in the Permian dicynodont family Cistecephalidae	Kammerer C, Froebisch J; Museum fuer Naturkunde Berlin
10:45am	FOS1-6	Morphological specialization and kinematic flexibility in mole burrowing (Mammalia: Talpidae)	Lin Y, Konow N, Dumont E; UMass, Amherst, Brown University

9:30am – 11:00am	HRD1	Salon G
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Hard-Tissue Biology 1

Chairs: JC Boughner, O Yaryhin

9:30am	HRD1-1	Development of the basal chondrocranial elements in lizards	Yaryhin O, Werneburg I; I. I. Schmalhausen institute of zoology NAS of Ukraine, Senckenberg Center for Human Evolution and Palaeoenvironment (HEP) at Eberhard Karls Universität
9:45am	HRD1-2	Body size and parafrontal bones in the Sphaerodactylidae (Reptilia: Squamata: Gekkota)	Griffing A, Bauer A; Villanova University
10:00am	HRD1-3	Evolution, development, and function of the elaborate frontal sinuses of porcupines	Krentzel D, Angielczyk K; University of Chicago, Field Museum
10:15am	HRD1-4	Predicting calvarial growth in normal and craniosynostotic mice using finite element analysis	Marghoub A, Libby J, Babbs C, Wilkie A, Fagan M, Moazen M; University College London, University of Hull, University of Oxford
10:30am	HRD1-5	The developmental genetics of mammalian tooth and jaw morphological integration and evolution	Boughner J, Raj M, Phen A, Uppal J, Greer J, Paradis M; University of Saskatchewan
10:45am	HRD1-6	Aberrant amelogenesis and osteogenesis in DSPP mutant mice	Cusack B, Kang R, Chong R, Yang X, Beniash E, Verdelis K, Szabo-Rogers H*; University of Pittsburgh

9:30am – 11:00am	SEG1	Salon H
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Symposium: Segmentation and serial homology: surprising new insights for long-standing central questions in vertebrate morphology 1

Chairs: R Diogo, G Wagner, F Galis

9:30am	SEG1-1	Serial homology: how does it fit into the picture?	<i>Wagner G; Yale University</i>
10:00am	SEG1-2	Serial homology vs derived similarity of pectoral and pelvic appendages: comparative, genetic, evo-devo and network studies in fish, tetrapods, and human birth defects	<i>Diogo R, Esteve-Altava B, Molnar J; Howard University</i>
10:30am	SEG1-3	The evolution of head segmentation in the Phylum Chordata	<i>Holland L, Gilland E; University of California San Diego, Howard University</i>

11:30am – 1:00pm	DCT2	Salon A
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Symposium: Diffusible iodine-based contrast-enhanced computed tomography (diceCT) and related imaging techniques for evolutionary morphology 2

Chairs: PM Gignac, AN Herdina, NJ Kley, A Morhardt, JA Clarke, M Colbert

11:30am	DCT2-1	Musculoskeletal modelling and simulations of the mouse hindlimb during locomotion: the role of high-resolution scanning and contrast imaging	<i>Charles J, Cappellari O, Spence A, Wells D, Hutchinson J; Royal Veterinary College, Temple University</i>
11:45am	DCT2-2	The evolution of the mammalian jaw adductor musculature— inferences from soft-tissue imaging of extant taxa	<i>Lautenschlager S, Gill P, Fagan M, Rayfield E; University of Bristol, University of Hull</i>
12:00pm	DCT2-3	Masticatory muscle anatomy of African mole-rats revealed by diceCT	<i>Cox P; University of York</i>
12:15pm	DCT2-4	Integration of diceCT with XROMM and fluoromicrometry enhances functional morphology and biomechanics research: a case study of the macaque (Mammalia: Primates) feeding apparatus	<i>Orsbon C, Gidmark N, Ross C; University of Chicago</i>
12:30pm	DCT2-5	Contrast-enhanced CT provides insight into amphibian lingual morphology	<i>Stanley E, Blackburn D; Florida Museum of Natural History</i>
12:45pm	DCT2-6	Studying metamorphosis of the cranial musculoskeletal system in the axolotl using contrast-enhanced μ CT	<i>Pardo J, Shipclark R, Szostakiwskyj M, Anderson J; University of Calgary</i>

11:30am – 1:00pm	DEN2	Salon B
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Symposium: Mechanisms of whole dentition patterning in extant and extinct amniotes 2

Chairs: J Richman, L Hlusko, T Grieco

11:30am	DEN2-1	Osr2 patterns the mammalian dentition through modulation of Wnt signaling	<i>Kwon H, Jia S, Lan Y, Zhou J, Liu H, Jiang R*; Cincinnati Children's Hospital Medical Center</i>
12:00pm	DEN2-2	Development of the diphyodont dentition in minipigs	<i>Buchtova M, Dosedelova H, Popa E, Putnova I, Stembirek J, Tucker A; Institute of Animal Physiology and Genetics, Czech Republic, King's College London, Guy's Hospital London, UK</i>
12:15pm	DEN2-3	Genetic and phenotypic modularity in the mammalian dental arcade	<i>Hlusko L, Brasil M, Clay S, Hoehna S, Huelsenbeck J, Huffman M, Monson T, Takenaka R, Schmitt C, Yoo S, Mahaney M; University of California Berkeley, Boston University, University of Texas Rio Grande Valley</i>
12:45pm	DEN2-4	Discerning genetic architecture from phenotypic covariance in human dentitions	<i>Huffman M, Brasil M, Monson T, Hlusko L; University of California, Berkeley</i>

11:30am – 1:00pm	EVD3	Salon C
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Evo-Devo - Evolution of developmental processes 3

Chairs: A Arenas Rodríguez, SK Sessions

11:30am	EVD3-1	Sample size artifacts in analyses of ontogenetic sequences	Colbert M, Morris Z; The University of Texas at Austin, Harvard University
11:45am	EVD3-2	Variation in onset of ossification and conserved regions of bone contact in the bony skull development of marsupial mammals	Spiekman S, Werneburg I; Paläontologisches Institut und Museum der Universität Zürich, Senckenberg Center for Human Evolution and Palaeoenvironment at Eberhard Karls Universität
12:00pm	EVD3-3	Description and comparison of ossification sequences in Colombian species of frogs	Arenas Rodríguez A, Hoyos Hoyos J; Pontificia Universidad Javeriana
12:15pm	EVD3-4	Breeding with and without water: What are the consequences of terrestrialization for embryonic morphology in anuran development?	Schweiger S, Mueller H; Department of Zoology and Evolutionary Biology
12:30pm	EVD3-5	Testis-ova and male gonad variability in the European blind cave salamander, <i>Proteus anguinus</i> (Amphibia: Urodela): consequence of sex-chromosome turnover?	Bizjak Mali L, Sessions S; University of Ljubljana, Hartwick College
12:45pm	EVD3-6	The phoenix rises: reversal of cave adaptations in the blind cave salamander, <i>Proteus anguinus</i> (Amphibia: Urodela: Proteidae)	Sessions S, Bizjak Mali L; Hartwick College, University of Ljubljana

11:30am – 1:00pm	FOS2	Salon F
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Symposium: Life Underground: Morphological Consequences of Fossoriality 2

Chairs: CA Hipsley, E Sherratt, HC Maddin

11:30am	FOS2-1	Ontogeny of a burrowing morphology - examples from anurans and caecilians (Lissamphibia: Anura and Gymnophiona)	Mueller H; Jena University
11:45am	FOS2-2	Morphological diversity of the pectoral girdle and anterior body axis in Amphisbaenia	Mueller J, Camey S, Hipsley C; Museum fuer Naturkunde Berlin
12:00pm	FOS2-3	Evolution of cranial features associated with the "freight-train" burrowing of uropeltid snakes	Olori J, Brown L; SUNY Oswego
12:15pm	FOS2-4	Blind, naked, and feeling no pain: sensory neurobiology of the naked mole-rat (Mammalia: Bathyergidae)	Park T, Browe B*; University of Illinois at Chicago
12:30pm	FOS2-5	Climate change impacts on the fossorial herpetofauna of the globe: integrating models across paleo, contemporary and future timeframes	Sinervo B, Miles D; UC Santa Cruz, Ohio University
12:45pm	FOS2-6	Comparative morphology of the shoulder muscles of Amphisbaenia (Reptilia, Squamata) using iodine-staining and computed tomography	Westphal N, Mueller J, Mahlow K; Museum fuer Naturkunde, Berlin

11:30am – 1:00pm	HRD2	Salon G
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Hard-Tissue Biology 2

Chairs: A Canoville, SM Kuhn-Hendricks

11:30am	HRD2-1	Environmental change, resource availability and the evolution of dental eruption patterns in artiodactyls (Mammalia: Artiodactyla)	Monson T, Hlusko L; UC Berkeley
11:45am	HRD2-2	Convergent dental dynamics between extinct rodent-like mammals and rodents	Gomes Rodrigues H, Billet G; CR2P, MECADEV, Muséum National d'Histoire Naturelle, PARIS
12:00pm	HRD2-3	The effects of dental wear on hard object food breakdown	Fitton L, Swan K, Cobb S; Hull York Medical School
12:15pm	HRD2-4	A biomechanical explanation for the ampullae of tyrannosaurid teeth based upon fracture mechanics	Kuhn-Hendricks S, Erickson G; Florida State University
12:30pm	HRD2-5	Microanatomical diversity of amniote ribs	Canoville A, de Buffrénil V, Laurin M; University of Bonn, Germany, CR2P, Sorbonne Universités, CNRS/MNHN/UPMC, Muséum National d'Histoire Naturelle, France
12:45pm	HRD2-6	Mechanical loading and lifestyle adaption response in secondary bone tissue: A quantitative assessment of secondary osteon geometry	Mitchell J, Sander P; University of Bonn

11:30am – 12:45pm SEG2**Salon H****Symposium: Segmentation and serial homology: surprising new insights for long-standing central questions in vertebrate morphology 2***Chairs: R Diogo, G Wagner, F Galis*

11:30am	SEG2-1	Medial-lateral aspects of anterior-posterior patterning in the vertebrate body plan	Burke A; Wesleyan University
12:00pm	SEG2-2	Acquisition of serial patterning and the making of a 'segment' across the evolutionary origin of the vertebrate jaw	Miyashita T; University of Alberta
12:15pm	SEG2-3	Serial homology of paired appendages and sexual organs: studies in early gnathostome fossils	Trinajstić K, Long J, Johanson Z; Curtin University, Flinders University, Natural History Museum
12:30pm	SEG2-4	There may be more to the Hox Code than you thought. The "Distal Phase" HoxA/D expression pattern is an ancient module that is deployed in a variety of novel features in vertebrates	Crow K; San Francisco State University

2:30pm – 4:00pm ANA1**Forest Glen****Workshop: Anatomical network analysis (AnNA): A new tool to quantify morphological complexity, integration, and modularity in vertebrate evolution and development 1***Chairs: B Esteve-Altava, D Rasskin-Gutman, R Diogo***2:30pm – 4:00pm DCT3****Salon A****Symposium: Diffusible iodine-based contrast-enhanced computed tomography (diceCT) and related imaging techniques for evolutionary morphology 3***Chairs: PM Gignac, AN Herdina, NJ Kley, A Morhardt, JA Clarke, M Colbert*

2:30pm	DCT3-1	Contrast-enhanced micro-CT imaging of fish and frogs: digital dissections and biomechanical applications	Porro L, Brocklehurst R, Adriaens D, Herrel A, Rayfield E; Royal Veterinary College, University of London, University of Manchester, Ghent University, CNRS/Museum National d'Histoire Naturelle, University of Bristol
2:45pm	DCT3-2	The curious case of the vomeronasal organ in bats: genetics asks questions only anatomy can answer	Yohe L, Curtis A, Rosenthal H, Hoffmann S, Martin K, Davalos-Alvarez L; Stony Brook University, American Museum of Natural History, Smithtown High School West
3:00pm	DCT3-3	Comparative morphology of bat cranial muscles using contrast-enhanced micro-CT imaging	Vander Linden A, Santana S; University of Massachusetts Amherst, University of Washington
3:15pm	DCT3-4	Advantages and difficulties of alcoholic iodine staining for correlative 2D and 3D microCT imaging and histomorphology in bat developmental studies	Herdina* A, Nugraha T, Semiadi G, Großschmidt K, Haase A, Lina P, Godlevska L, Vlaschenko A, Metscher B; University of Vienna, Austria, Indonesian Institute of Sciences, Indonesia, Medical University of Vienna, Austria, Naturalis Biodiversity Center, Netherlands, National Academy of Sciences of Ukraine, Ukraine, Feldman Ecopark Bat Rehabilitation Center, Ukraine, Karolinska Institutet, Sweden
3:30pm	DCT3-5	DiceCT and the staining of old museum specimens, exemplified by the analysis of venom glands in viperid snakes	Mahlow K, Mueller J; Museum für Naturkunde Berlin
3:45pm	DCT3-6	Diffusible iodine-based contrast enhancement of large, post-embryonic, intact vertebrates for CT scanning: staining, destaining, and long-term storage	Morhardt A, Ridgely R, Witmer L; Ohio University

2:30pm – 4:00pm	DEN3	Salon B
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Symposium: Mechanisms of whole dentition patterning in extant and extinct amniotes 3

Chairs: J Richman, L Hlusko, T Grieco

2:30pm	DEN3-1	Embryonic tooth development in an Early Jurassic dinosaur	<i>Reisz R, LeBlanc A, Maddin H; University of Toronto Mississauga, Carleton University</i>
3:00pm	DEN3-2	The simplification of sauropod teeth as an adaptation to herbivory	<i>Whitlock J; Mount Aloysius College</i>
3:30pm	DEN3-3	The evolution of dental batteries: new insights from extinct reptiles	<i>LeBlanc A, Reisz R; University of Toronto Mississauga</i>

2:30pm – 4:00pm	EVD4	Salon C
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Symposium: Mechanisms of whole dentition patterning in extant and extinct amniotes 3

Chairs: TR Dial, T Hirasawa

2:30pm	EVD4-1	The domestication of the neural crest – A developmental perspective on the origins of morphological variation in mammalian breeds and land races	<i>Sánchez-Villagra M, Geiger M, Schneider R; University of Zurich, University of California San Francisco</i>
2:45pm	EVD4-2	Developmental basis behind the evolutionary origin of the diaphragm	<i>Hirasawa T, Fujimoto S, Kuratani S; Evolutionary Morphology Laboratory, RIKEN</i>
3:00pm	EVD4-3	A cryptic sacral series that varies in count but not size defines the modular organization of the vertebral column in odontocete cetaceans	<i>Buchholtz E; Wellesley College</i>
3:15pm	EVD4-4	Anatomical tests of Hox gene function in a derived vertebrate body form: "Deregionalization" and the role of <i>Hox10</i> in the evolution of snakes	<i>Head J, Royle S; University of Cambridge</i>
3:30pm	EVD4-5	Size, not age, predicts feeding morphology and kinematics among guppy offspring and juveniles	<i>Dial T, Hernandez LP, Brainerd E; Brown University, George Washington University</i>
3:45pm	EVD4-6	Modelling human skull development	<i>Libby J, Marghoub A, Khonsari R, Fagan M, Moazen M; University of Hull, University College London, Hopital Universitaire Necker, Paris</i>

2:30pm – 4:00pm	HRD3	Salon G
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Hard-Tissue Biology 3

Chairs: S Regnault, J Sartori

2:30pm	HRD3-1	Walking with giants: is the cortical bone structure and vascularization adapted to load bearing in large terrestrial vertebrates?	<i>Dumont M, Herrel A, Tafforeau P, Sanchez S; Uppsala University EBC</i>
2:45pm	HRD3-2	Patelloid and patellar sulcus: clues to kneecap evolution?	<i>Regnault S, Pitsillides A, Hutchinson J; Royal Veterinary College</i>
3:00pm	HRD3-3	The micro-structure, composition and mechanical properties of bones of the Olm (<i>Proteus anguinus</i>)	<i>Haggag L, Jelic D, Shahar R*; The Hebrew University of Jerusalem, Croatian Institute of Biodiversity, Croatia</i>
3:15pm	HRD3-4	Variation in limb bone stiffness between aquatic and terrestrial salamanders	<i>Taft N, Kawano S; University of Wisconsin-Parkside, National Institute for Mathematical and Biological Synthesis</i>
3:30pm	HRD3-5	Fiber courses of the Achilles tendon enthesis in the mouse (<i>Mus musculus</i>) as test for biomechanical hypotheses	<i>Sartori J, Köhring S, Schilling C, Witte H, Löffler M, Fischer M; Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, Friedrich-Schiller-Universität Jena, Fachgebiet Biomechatronik, Fakultät für Maschinenbau, TU Ilmenau, Dresden Center for Nanoanalysis, TU Dresden</i>
3:45pm	HRD3-6	The remarkable armor of poachers	<i>Summers A; University of Washington</i>

2:30pm – 4:00pm	PHY1	Salon F
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Symposium: New insights into the functional relationship between anatomy and physiology of extinct and extant vertebrates 1

Chairs: WR Porter, G Tattersall

2:30pm	PHY1-1	Vascular anatomy and thermophysiological strategies in the heads of extinct and extant dinosaurs	<i>Porter W, Witmer L; Ohio University Heritage College of Osteopathic Medicine</i>
2:45pm	PHY1-2	Avian bills as thermoregulatory structures	<i>Tattersall G; Brock University</i>
3:00pm	PHY1-3	Mathematical models and bone histology shed light on maximal aerobic capacities of both extinct and extant tetrapods	<i>Farmer C, Huttenlocker A, Davis C; University of Utah, Pepperdine University</i>
3:30pm	PHY1-4	Insular dwarfism and the distinct physiology in island deer: bone histology of Japanese extinct island cervids indicates interrupted growth	<i>Hayashi S, Kubo M, Fujita M, Taruno H, Oshiro I; Osaka Museum of Natural History, The University of Tokyo, Okinawa Prefectural Museum & Art Museum, Okinawa-ishi-no-kai</i>

4:30pm – 6:00pm	ANA2	Forest Glen
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Workshop: Anatomical network analysis (AnNA): A new tool to quantify morphological complexity, integration, and modularity in vertebrate evolution and development 2

Chairs: B Esteve-Altava, D Rasskin-Gutman, R Diogo

4:30pm – 5:00pm	DCT4	Salon A
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Symposium: Diffusible iodine-based contrast-enhanced computed tomography (diceCT) and related imaging techniques for evolutionary morphology 4

Chairs: PM Gignac, AN Herdina, NJ Kley, A Morhardt, JA Clarke, M Colbert

4:30pm	DCT4-1	An evaluation of the efficacy and mechanism of contrast-enhanced X-ray Computed Tomography for avian cranial material utilizing iodine through experimental and simulation approaches	<i>Li Z, Clarke J, Ketcham R, Colbert M, Yan F; The University of Texas at Austin, Rice University</i>
4:45pm	DCT4-2	Microscopic anatomy of the animals—a project in integrative publishing	<i>Starck J, Haug J; University of Munich (LMU)</i>

4:30pm – 6:00pm	DEN4	Salon B
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Symposium: Mechanisms of whole dentition patterning in extant and extinct amniotes 4

Chairs: J Richman, L Hlusko, T Grieco

4:30pm	DEN4-1	Tissue-level analysis of ziphodont teeth in terrestrial animals	<i>Brink K, Reisz R; University of British Columbia, University of Toronto Mississauga</i>
5:00pm	DEN4-2	Morphological integration of deciduous and permanent dentitions in carnivorans	<i>Tomiya S, Reuter D, Sulser R; Field Museum of Natural History, University of Oregon, University of Chicago</i>
5:30pm	DEN4-3	Voies, molars, and molecules: integrating quantitative morphology, genetics, and evo-devo to study evolutionary processes	<i>Burroughs R; University of Chicago</i>

4:30pm – 6:00pm	EVD5	Salon C
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Evo-Devo - Evolution of Developmental Processes 5

Chairs: LJ Ekstrom, M Marchini

4:30pm	EVD5-1	Divergence and elaboration of skeletal musculature in early vertebrates	<i>Kusakabe R, Kuratani S; Evolutionary Morphology Laboratory, RIKEN</i>
4:45pm	EVD5-2	A single mutation reveals latent capacity for limb-like development in the zebrafish	<i>Hawkins M, Henke K, Harris M; Harvard University, Harvard Medical School Department of Genetics, Orthopaedic Research Boston Children's Hospital</i>
5:00pm	EVD5-3	Establishing proportion: a hypothesis for the role of the vasculature in zebrafish fin length mutants	<i>Ekstrom L, Fitzgerald E, Henrikson K, Shi A, Harris M, Lanni J; Wheaton College, Harvard Medical School, Children's Hospital Boston</i>

5:15pm	EVD5-4	How is preaxial polarity established in limb development? A comparison of larval and direct developing salamanders to other tetrapods	<i>Triepel S, Müller H, Mitgutsch C, Fröbisch N; Museum für Naturkunde Berlin, Friedrich-Schiller-Universität Jena</i>
5:30pm	EVD5-5	Probing the cellular and genetic mechanisms involved in producing bone length variation using the Longshanks mouse	<i>Marchini M, Rolian C; University of Calgary</i>
5:45pm	EVD5-6	The role of <i>Hox</i> in pisiform and calcaneus ossification and the nature of the zeugopod/autopod boundary	<i>Reno P, Kjosness K, Hines J; Pennsylvania State University</i>

4:30pm – 6:00pm	PHY2	Salon F
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Symposium: New insights into the functional relationship between anatomy and physiology of extinct and extant vertebrates 2

Chairs: WR Porter, G Tattersall

4:30pm	PHY2-1	The function of the carotid rete - the unique "wonderful net" of the Cetartiodactyla	<i>Strauss W, Hetem R, Mitchell D, Maloney S, Meyer L, Fuller A; University of the Witwatersrand (WITS), University of Western Australia</i>
5:00pm	PHY2-2	Complicated noses keep cool heads: the thermoregulatory effects of nasal passage shape in extant birds and reptiles, with implications for dinosaurs	<i>Bourke J, Witmer L, Porter W; North Carolina Museum of Natural Sciences, Ohio University</i>
5:30pm	PHY2-3	Macroevolutionary impact of selective brain cooling on artiodactyl diversity patterns throughout the Cenozoic	<i>O'Brien H; Ohio University</i>

7:30pm – 9:30pm	REC2	Grand Ballroom
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Closing Reception

Sunday 3rd July, 2016

8:15am – 9:30am		PLN5	Salon D-E
Plenary Session 5: Stephanie Pierce <i>Chairs: J Wyneken</i>			
8:15am	PLN5-1	Form, function, and fossils: modern twists on ancient evolutionary transitions	<i>Pierce S; Museum of Comparative Zoology and Department of Organismic and Evolutionary Biology, Harvard University</i>
9:30am – 11:00am		AQU1	Salon A
Symposium: Functional (secondary) adaptation to an aquatic life in vertebrates 1 <i>Chairs: A Houssaye, F Fish</i>			
9:30am	AQU1-1	Primary and secondary adaptations to aquatic feeding in salamanders	<i>Heiss E; Institute of Systematic Zoology and Evolutionary Biology</i>
10:00am	AQU1-2	Feeding modes in Sirenia (Mammalia): more of them than you probably thought!	<i>Domning D; Howard University</i>
10:30am	AQU1-3	Evolutionary innovation and ecology in mysticete cetaceans: transition from teeth to baleen and raptorial to bulk filter feeding	<i>Berta A, Lanzetti A*, Ekdale E, Deméré T; San Diego State University, San Diego Natural History Museum</i>
9:30am – 11:00am		EAR1	Salon G
Symposium: Show me your ear - The inner and middle ear in vertebrates 1 <i>Chairs: C Pfaff, JA Schultz, R Schellhorn</i>			
9:30am	EAR1-1	The utility of the shark inner ear as a 'landmark' for hyoid arch position	<i>Bronson A, Hutchins R, Denton J, Maisey J; American Museum of Natural History, University of Montana</i>
9:45am	EAR1-2	Inner ear morphology in early neopterygian fishes (Actinopterygii: Neopterygii)	<i>Giles S, Rogers M, Friedman M; University of Oxford</i>
10:00am	EAR1-3	<i>Mesosuchus browni</i> (Rhynchosauria: Archosauromorpha) and the early evolution of the archosaur ear	<i>Sobral G, Butler R, Müller J; Museu Nacional do Rio de Janeiro, University of Birmingham, Museum für Naturkunde Berlin</i>
10:15am	EAR1-4	Ear ossicle morphology of the Jurassic euharamiyidan <i>Arboroharamiya</i> and evolution of mammalian middle ear	<i>Meng J, Bi S, Zheng X, Wang X; American Museum of Natural History, Indiana University of Pennsylvania, Shandong Tianyu Museum of Nature, China, Linyi University, China</i>
10:30am	EAR1-5	Inner ear morphology in gondwanatherian mammals and implications for ear evolution in mammaliaforms	<i>Hoffmann S; Stony Brook University</i>
10:45am	EAR1-6	New study of the membranous labyrinth of monotremes and comparative morphology of mammalian inner ears	<i>Schultz J, Zeller U, Luo Z; University of Chicago, Humboldt Universität zu Berlin, Germany</i>
9:30am – 11:00am		FED2	Salon C
Feeding 2 <i>Chairs: LA Ferry, CJ Moran</i>			
9:30am	FED2-1	XROMM and VROMM studies of suction feeding in fishes	<i>Brainerd E, Camp A, Wilga C, Scott B, Olsen A, Jimenez Y, Laurence-Chasen J, Knörlein B; Brown University, University of Alaska Anchorage, University of Rhode Island, University of Chicago</i>
9:45am	FED2-2	Comparative biomechanics of biting vs. suction feeding in fish	<i>Brocklehurst R, Porro L, Herrel A, Adriaens D, Standen E, Rayfield E; University of Bristol, UK, Royal Veterinary College, UK, Muséum National d'Histoire Naturelle, France, Ghent University, Belgium, University of Ottawa, Canada</i>
10:00am	FED2-3	Feeding behavior variation in polyphenic bluegill	<i>Moran C, Neubauer D, Rzcudlo C, Gerry S; Fairfield University</i>

10:15am	FED2-4	Where does the vertebral column bend during suction feeding in fishes? A comparative study of axial bending during cranial elevation	<i>Jimenez Y, Camp A, Brainerd E; Brown University</i>
10:30am	FED2-5	Built to bite? Bite performance based on 3D-reconstructions in European glass eels (Teleostei: Anguilliformes)	<i>De Meyer J, Boulliart M, Dhaene J, Adriaens D; Ghent University</i>
10:45am	FED2-6	Premaxillary protrusion in Lampriformes: innovations and radiations	<i>Ferry L, Paig-Tran E, Summers A; Arizona State University, California State University Fullerton, University of Washington</i>

9:30am – 10:45am **LOC5** **Salon F**

Locomotion 5

Chairs: MF Bonnan, A Klinkhamer

9:30am	LOC5-1	Digital musculoskeletal modelling of an Australian sauropod dinosaur	<i>Klinkhamer A; University of New England</i>
9:45am	LOC5-2	How the largest known flying animal, the pterosaur <i>Quetzalcoatlus</i> , walked on land	<i>Padian K, Cunningham J, Langston W, Conway J, Manafzadeh A*; University of California, Berkeley, Cunningham Engineering Associates, University of Texas</i>
10:00am	LOC5-3	Forelimb kinematics of rats using XROMM, with implications for small eutherians and their fossil relatives	<i>Bonnan M, Shulman J, Horner A, Brainerd E; Stockton University, California State University San Bernardino, Brown University</i>
10:15am	LOC5-4	Ontogenetic changes in effective mechanical advantage in the Eastern cottontail rabbit (<i>Sylvilagus floridanus</i>)	<i>Foster A, Butcher M, Smith G, Young J; NEOMED, Youngstown State University, Kent State University at Stark</i>
10:30am	LOC5-5	Jumping performance in the Longshanks mouse	<i>Bradley M, Hou L*, Sparrow L, Rolian C; University of Calgary</i>

9:30am – 11:00am **MAT1** **Salon B**

Symposium: Interdisciplinary and evolutionary approaches to vertebrate biological materials 1

Chairs: M Dean, AJ Crosby, D Irschick, L Li

9:30am	MAT1-1	From physical to digital and back: How 3D modeling and additive manufacturing reveal nature's design rules	<i>Seidel R, Hosny A, Weaver J, Adriaens D, Porter M, Dean M; Max Planck Institute of Colloids and Interfaces, Wyss Institute for Biologically Inspired Engineering, Ghent University, Clemson University</i>
10:00am	MAT1-2	Additive manufacturing of composites inspired by vertebrates	<i>Stuart A; ETH Zurich</i>
10:30am	MAT1-3	Bioinspired design and mechanical characterizations: a case for soft/flexible systems and living tissues	<i>Li L, Crosby A*; Harvard University, University of Massachusetts Amherst</i>

9:30am – 11:00am **XEN1** **Salon H**

Symposium: Morphology & evolution of the Xenarthra 1

Chairs: S Bargo, J Nyakatura

9:30am	XEN1-1	Recent progress and future prospects in fossil xenarthran studies	<i>De Iuliis G; University of Toronto</i>
10:00am	XEN1-2	Potential distribution of fossil xenarthrans during the late Pleistocene	<i>Varela L, Tambusso P, Di Giacomo M, Patiño S, Fariña R*; Universidad de la República, Uruguay, University of Delaware</i>
10:15am	XEN1-3	Phylogeny and historical biology of sloths	<i>Tambusso P, Varela L, Patiño S, McDonald H, Fariña R; Universidad de la República, Uruguay</i>
10:30am	XEN1-4	Osteoderms in ground sloths: plesiomorphic or apomorphic?	<i>McDonald H; Bureau of Land Management</i>
10:45am	XEN1-5	When development and paleontology meet: novel developmental data shed new light on the evolutionary history of the Xenarthra	<i>Hautier L, Billet G, Gomes Rodrigues H, Oliver J, Pierce S; Université Montpellier, CNRS, Sorbonne Universités, CR2P, UMR CNRS 7207, Univ Paris 06, Muséum National d'Histoire Naturelle, Harvard University, Museum of Comparative Zoology</i>

11:30am – 1:00pm	AQU2	Salon A
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Symposium: Functional (secondary) adaptation to an aquatic life in vertebrates 2

Chairs: A Houssaye, F Fish

11:30am	AQU2-1	Acoustic fatheads: Parallels in the functional anatomy of underwater sound reception mechanisms in dolphins, seals, turtles, and sea birds	Ketten D; Harvard Medical School/WHOI
12:00pm	AQU2-2	Hypernatremia in marine snakes: implications for the evolution of a euryhaline physiology	Brischoux F; Centre d'Etudes Biologiques de Chizé - CNRS
12:30pm	AQU2-3	"On the fence" versus "all in": insights from turtles for functional transitions in the aquatic locomotion of amniotes	Blob R, Mayerl C, Rivera A, Rivera G, Young V; Clemson University, Creighton University

11:30am – 1:00pm	EAR2	Salon G
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Symposium: Show me your ear - The inner and middle ear in vertebrates 2

Chairs: C Pfaff, JA Schultz, R Schellhorn

11:30am	EAR2-1	Functional morphological adaptations of the bony labyrinth in marsupials (Mammalia: Theria)	Pfaff C, Kaineder G, Czerny S, Nagel D, Kriwet J; University of Vienna, Austria
11:45am	EAR2-2	Head posture and orientation of the lateral semicircular canal in xenarthrans (Mammalia)	Coutier F, Hautier L, Cornette R, Amson E, Billet G*; CR2P, Museum National d'Histoire Naturelle, France, ISEM, University of Montpellier, France, ISYEB, Humboldt-Universitaet, Berlin, Germany
12:00pm	EAR2-3	Bony labyrinth of Carnivora (Mammalia): the significance of phylogeny and the sensorial adaptation to aquatic environments	Grohe C, Tseng Z, Lebrun R, Boistel R, Flynn J; American Museum of Natural History, Institut des Sciences de l'Evolution de Montpellier, Université de Poitiers
12:15pm	EAR2-4	Morphological diversity among the inner ears of extinct and extant baleen whales (Cetacea: Mysticeti)	Ekdale E; San Diego State University
12:30pm	EAR2-5	Hooves on the roof: the ear region of <i>Diplobune minor</i> , an arboreal artiodactyl from the Early Oligocene of France	Orliac M, Brualla N, Assemet A, Guignard M, Lihoreau F; Institut des Sciences de l'Evolution
12:45pm	EAR2-6	3D geometric morphometrics and cladistics analyses of the tragulid bony labyrinth: morphological variability and implications for ruminant phylogeny	Costeur L, Mennecart B; Natural History Museum Basel, Switzerland

11:30am – 1:00pm	FED3	Salon C
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Feeding 3

Chairs: SB Crofts, KC Sellers

11:30am	FED3-1	Functional diversity and evolution of dicynodont (Therapsida: Anomodontia) jaw mechanics	Angielczyk K, Nabavizadeh A, Krentzel D; Field Museum of Natural History, University of Chicago
11:45am	FED3-2	Modelling microscopic tooth wear using finite elements: indicating how abrasive particles interact with enamel surfaces	Berthaume M, Kupczik K, Schulz-Kornas E; Max Planck Weizmann Center for Integrative Archaeology and Anthropology
12:00pm	FED3-3	Tooth form and function of extinct durophagous reptiles, the Placodontia	Crofts S, Summers A; New Jersey Institute of Technology, University of Washington, Friday Harbor Labs
12:15pm	FED3-4	Quantifying textures of tooth wear for dietary analysis of fishes, sharks and whales	Purnell M; University of Leicester
12:30pm	FED3-5	Ecomorphological relationships between tooth morphology and diet in varanid lizards (Squamata: Varanidae)	Larson D, Evans D; Philip J. Currie Dinosaur Museum, Royal Ontario Museum
12:45pm	FED3-6	A high-fidelity, 3D model of the skull of <i>Alligator mississippiensis</i> (Archosauria: Crocodylia) and its significance for vertebrate feeding biomechanics	Sellers K, Davis J, Middleton K, Holliday C; University of Missouri, University of Southern Indiana

11:30am – 1:00pm	LOC6	Salon F
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Locomotion 6

Chairs: D Shapiro, EE Vereecke

11:30am	LOC6-1	The biological role of carpal sinus hair sensing on the body posture during locomotion of rats (<i>Rattus norvegicus</i> , Rodentia)	Niederschuh S, Thomas H, Danja V, Witte H, Schmidt M; Institute of Systematic Zoology and Evolutionary Biology, FSU Jena, Department of Biomechanics, Ilmenau University of Technology
11:45am	LOC6-2	3D dynamics of burrowing in pocket gophers	Moore Crisp A, Lee D; UNLV
12:00pm	LOC6-3	The kinematics of grooming: How mammals clean their coat	Schmidt M, van Beesel J, Dargel L, Fischer M; Friedrich Schiller University Jena
12:15pm	LOC6-4	Out on a limb: effects of substrate compliance on the gait mechanics of common marmosets (Primates: <i>Callithrix jacchus</i>)	Chadwell B, Stricklen B, Young J; Northeast Ohio Medical University (NEOMED), Kent State University
12:30pm	LOC6-5	Quantifying trabecular bone density and anisotropy in the primate lower ilium with implications for reconstructing locomotor loading	Shapiro D; Rutgers, The State University of New Jersey
12:45pm	LOC6-6	The stability-mobility conflict in the primate thumb	Vereecke E, Vanhoof M, Szu-Ching L, Kerkhof F; University of Leuven, University of Kent

11:30am – 1:00pm	MAT2	Salon B
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Symposium: Interdisciplinary and evolutionary approaches to vertebrate biological materials 2

Chairs: M Dean, AJ Crosby, D Irschick, L Li

11:30am	MAT2-1	Material perspectives on the evolution of bone across fishes and tetrapods	Kawano S, Shahar R; National Institute for Mathematical and Biological Synthesis, Hebrew University of Jerusalem
12:00pm	MAT2-2	Contractile and connective tissue interactions in skeletal muscles	Azizi E, Balaban J, Holt N; University of California, Irvine
12:30pm	MAT2-3	Evolution of crystal form and mineralization control in vertebrates	Omelson S, Habraken W; University of Ottawa, Max Planck Institute of Colloids and Interfaces

11:30am – 1:00pm	XEN2	Salon H
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Symposium: Morphology & evolution of the Xenarthra 2

Chairs: S Bargo, J Nyakatura

11:30am	XEN2-1	Expanded diagnosis of the ground sloth <i>Myodon darwini</i> (Mammalia: Xenarthra: Pilosa) and the functional implications	McAfee R; Ohio Northern University
11:45am	XEN2-2	Biomechanical study in claws of extinct sloths and extant xenarthrans	Patiño S, Fariña R; Facultad de Ciencias, Universidad de la República
12:00pm	XEN2-3	Early dietary, jaw shape and biomechanical performance differentiation in the evolution of armadillos (Xenarthra: Cingulata)	De Esteban-Trivigno S, Cantalapiedra J, Marcé-Nogué J, Fortuny J; Institut Català de Paleontologia Miquel Crusafont / Transmitting Science, Museum für Naturkunde, Leibniz-Institut für Evolutions und Biodiversitätsforschung, Universität Hamburg, Muséum National d'Histoire Naturelle
12:15pm	XEN2-4	Conceptual and methodological approaches for a paleobiological integration: the Santacrucian sloths (early Miocene of Patagonia) as a study case	Toledo N, Vizcaíno S, Bargo M, Cassini G; División Paleontología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, CONICET, División Mastozoología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", CONICET
12:30pm	XEN2-5	Bend it like an armadillo: An investigation into the bending mechanics of the xenarthran vertebral column	Oliver J, Hautier L, Pierce S; Museum of Comparative Zoology, Harvard, University of Montpellier II
12:45pm	XEN2-6	Bone internal microstructure of the forelimb of xenarthrans (Mammalia) – functional implications	Amson E, Arnold P, Nyakatura J; AG Morphologie und Formengeschichte, Bild Wissen Gestaltung - ein interdisziplinäres Labor & Institut fuer Biologie, Humboldt-Universität, University of Jena, Germany

2:30pm – 3:30pm	AQU3	Salon A
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Symposium: Functional (secondary) adaptation to an aquatic life in vertebrates 3

Chairs: A Houssaye, F Fish

2:30pm	AQU3-1	How to become aquatic with the mustelid toolkit? A morphometric insight into aquatic mustelid long bone evolution	Botton-Divet L, Fabre A, Herrel A, Cornette R, Houssaye A; UMR 7179 MNHN/CNRS, Mecadev, Paris, UMR 7205 MNHN/CNRS/UPMC/EPHE, ISYEB, Paris
3:00pm	AQU3-2	Secondary evolution of aquatic propulsion in higher vertebrates: Validation and prospect	Fish F; West Chester University

2:30pm – 3:45pm	FED4	Salon C
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Feeding 4

Chairs: J Marcé-Nogué, S Pineda-Munoz

2:30pm	FED4-1	Hierarchical variation in EMG signal in oral vs. pharyngeal muscles	German R, Gould F, Ohlemacher J, Vinyard C; NEOMED
2:45pm	FED4-2	The relationship between kinematics and performance in mammalian swallowing	Ohlemacher J, Gould F, German R; Northeast Ohio Medical University
3:00pm	FED4-3	Variation in tongue and bolus shape and its relationship to airway protection in infant mammals	Gould F, Ohlemacher J, German R; Northeast Ohio Medical University
3:15pm	FED4-4	Dental morphology, diet and the dynamics of morphological evolution across marsupials and placentals	Pineda-Munoz S, Alroy J, Evans A; NMNH Smithsonian Institution, Macquarie University, Monash University
3:30pm	FED4-5	Primate chewing biomechanics revisited using Finite Element Analysis of the mandible	Marcé-Nogué J, de Esteban-Trivigno S, González P, Kaiser T; University of Hamburg, Germany, Universitat Autònoma de Barcelona, Spain, Instituto de Genética Veterinaria

2:30pm – 4:00pm	LOC7	Salon F
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Locomotion 7

Chairs: A Abourachid, V Allen

2:30pm	LOC7-1	Does exaggerated morphology constrain locomotor performance in the peacock, <i>Pavo cristatus</i> (Aves: Galliformes)	Thavarajah N, Codd J; Manchester University
2:45pm	LOC7-2	Fifty ways to measure a moment arm: cadaveric analysis of emu toe joints using XROMM	Sustaita D, Roberts T, Gatesy S; Brown University
3:00pm	LOC7-3	Patella mechanics in avian terrestrial locomotion	Allen V, Kambic R, Gatesy S, Hutchinson J; Royal Veterinary College, Harvard University, Brown University
3:15pm	LOC7-4	The locomotion of the Hoatzin chick	Abourachid A, Herrel A, Garcia Amado M, Decamps T; Museum National d'Histoire Naturelle CNRS, Instituto Venezolano de Investigaciones Cientificas
3:30pm	LOC7-5	Rapid growth backfires: Biomechanical simulations of broiler chicken gait reveal the effects of intrinsic pelvic limb muscle weakness on locomotion	Paxton H, Rankin J, Hutchinson J; The Royal Veterinary College
3:45pm	LOC7-6	Intraspecific scaling of the minimum metabolic cost of transport in leghorn chickens (<i>Gallus gallus domesticus</i>): links with limb kinematics, morphometrics and posture	Rose K, Nudds R, Codd J; University of Manchester

2:30pm – 4:00pm	MAT3	Salon B
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Symposium: Interdisciplinary and evolutionary approaches to vertebrate biological materials 3

Chairs: M Dean, AJ Crosby, D Irschick, L Li

2:30pm	MAT3-1	Co-evolution of teeth and food: Probing the interplay between tooth materials, tooth structures and foods	<i>van Casteren A, Crofts S; Max Planck Institute for Evolutionary Anthropology, New Jersey Institute of Technology</i>
3:00pm	MAT3-2	Structure and mechanics of natural scales: inspiration for novel flexible protective systems	<i>Martini R, Van Zyl D, Barthelat F*; McGill University</i>
3:30pm	MAT3-3	Vertebrate skin in interaction with the environment: evolutionary solutions	<i>Spinner M; Kiel University, Zoological Institute</i>

2:30pm – 3:15pm	XEN3	Salon H
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Symposium: Morphology & evolution of the Xenarthra 3

Chairs: S Bargo, J Nyakatura

2:30pm	XEN3-1	Architecture of dorsovertebral muscles corresponds with derived function of the vertebral column during suspensory locomotion in two toed sloths (Mammalia: Xenarthra)	<i>Nyakatura J, Stark H; Humboldt U. Berlin, FSU Jena</i>
2:45pm	XEN3-2	Architectural specializations of the forelimb musculature of the three-toed sloth (Xenarthra: <i>Bradypus variegatus</i>)	<i>Olson R, Cliffe R, Glenn Z, Thomas D, Kennedy S, Butcher M; Ohio University, Swansea University, Youngstown State University</i>
3:00pm	XEN3-3	Diagnostic imaging in Linnaeus's two-toed sloth (<i>Choloepus didactylus</i>)—pregnancy diagnosis and fetometry	<i>Thielebein J, Wujciak D, Kiefer I; Martin-Luther-University Halle-Wittenberg, Radiological Community Practice, University of Leipzig</i>

4:30pm – 5:30pm	AQU4	Salon A
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Symposium: Functional (secondary) adaptation to an aquatic life in vertebrates 4

Chairs: A Houssaye, F Fish

4:30pm	AQU4-1	How to build a deep diver	<i>Pabst D, McLellan W, Rommel S; UNC Wilmington</i>
5:00pm	AQU4-2	Aquatic habits in the ancestors of cetaceans: integrating stable isotopes and bone cross-sectional morphology	<i>Cooper L, Clementz M, Usip S, Bajpai S, Hieronymus T, Hussain S, Thewissen J; NEOMED, University of Wyoming, Birbal Sahni Institute of Palaeobotany, Howard University</i>

4:30pm – 6:00pm	FED5	Salon C
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Feeding 5

Chairs: JS Davis, K Kupczik

4:30pm	FED5-1	Loss of a tongue muscle improves prey-capture performance in salamanders	<i>Bloom S, Deban S; University of South Florida</i>
4:45pm	FED5-2	Robust hyobranchial apparatus yields increased aquatic feeding performance in newts	<i>Stinson C, Deban S; University of South Florida</i>
5:00pm	FED5-3	Aquatic prey capture in snakes: the link between morphology, behavior and hydrodynamics	<i>Segall M, Godoy-Diana R, Herrel A; MNHN - ESPCI</i>
5:15pm	FED5-4	Masticatory jaw movements in two species of musteloid carnivorans with divergent dietary specializations: an XROMM and EMG study	<i>Davis J, Klimovich C, Williams S; High Point University, Ohio University</i>
5:30pm	FED5-5	Fibre type composition in the masticatory muscles of wolves (Carnivora: <i>Canis lupus</i>) and domestic dogs: implications for canine chewing efficiency and feeding ecology	<i>Kupczik K, Unterhitzberger G, Szentiks C, Fischer M; Max Planck Institute for Evolutionary Anthropology, Germany, Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, Friedrich-Schiller-Universität Jena, Leibniz Institute for Zoo and Wildlife Research, Germany</i>

5:45pm	FED5-6	Exploring the value of anatomy ontologies: testing the Mammalian Feeding Muscle Ontology	<i>Druzinsky R, German R, Haendel M, Herring S, Lapp H, Muller H, Mungall C, Sternberg P, Van Auken K, Vinyard C, Williams S, Wall C; U. of Illinois at Chicago, Northeast Ohio Medical University, Oregon Health and Science University, University of Washington, Duke University, California Institute of Technology, Lawrence Berkeley National Laboratory, Ohio University</i>
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4:30pm – 5:30pm	MAT4	Salon B
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Symposium: Interdisciplinary and evolutionary approaches to vertebrate biological materials 4

Chairs: M Dean, AJ Crosby, D Irschick, L Li

4:30pm	MAT4-1	Biological attachment mechanisms; from dry to wet: Examples and Applications	<i>Ditsche P, Stark A, Irschick D; University of Washington, University of Louisville, University of Massachusetts at Amherst</i>
5:00pm	MAT4-2	Mechanisms, evolution and biomimicry of color-producing nanostructures in birds and other dinosaurs	<i>Shawkey M; University of Ghent</i>

4:30pm – 5:30pm	PAL6	Salon F
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Paleontology 6

Chairs: DM Henderson, A Manafzadeh

4:30pm	PAL6-1	Testing the buoyancy of an immersed <i>Spinosaurus</i> (Dinosauria: Theropoda) with a digital model	<i>Henderson D; Royal Tyrrell Museum of Palaeontology</i>
4:45pm	PAL6-2	Correlated and stepwise evolution of tail weaponry in mammals, turtles, and dinosaurs	<i>Arbour V, Zanno L; North Carolina Museum of Natural Sciences</i>
5:00pm	PAL6-3	Modeling fragmentary dentaries as beams to test hypotheses of differing diets	<i>Manafzadeh A, Holroyd P, Rankin B; UC Berkeley</i>
5:15pm	PAL6-4	Specialized wear facets in mammalian dentitions	<i>Koenigswald W; Steinmann Institut (Paläontologie) der Universität Bonn</i>

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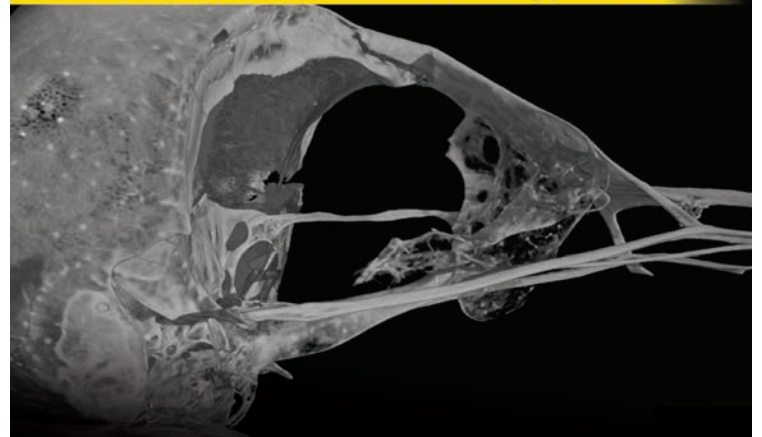
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


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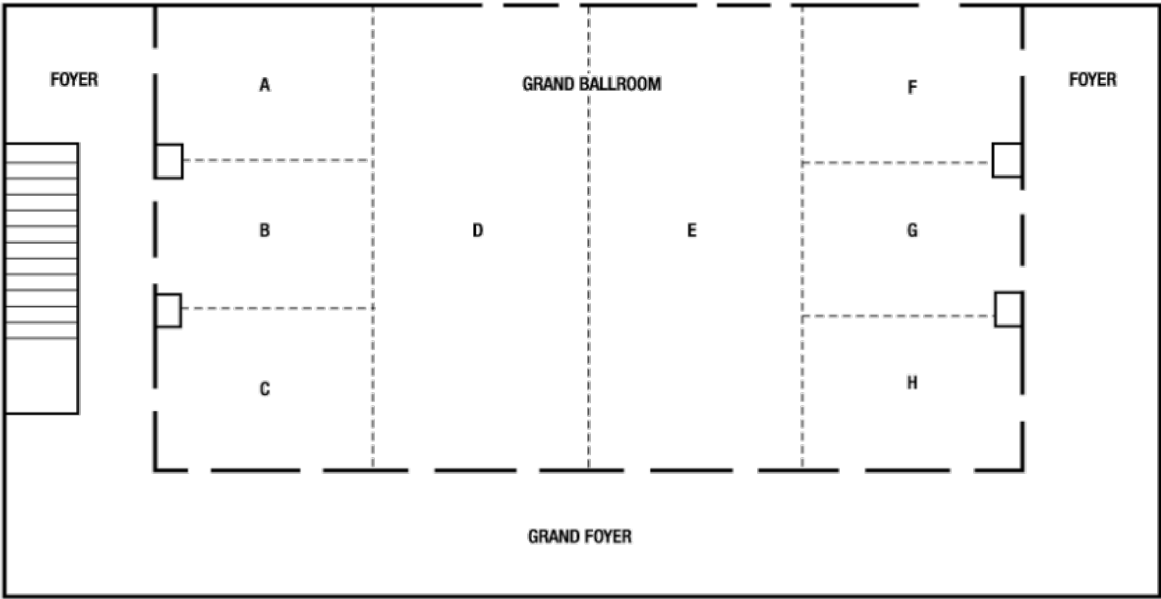
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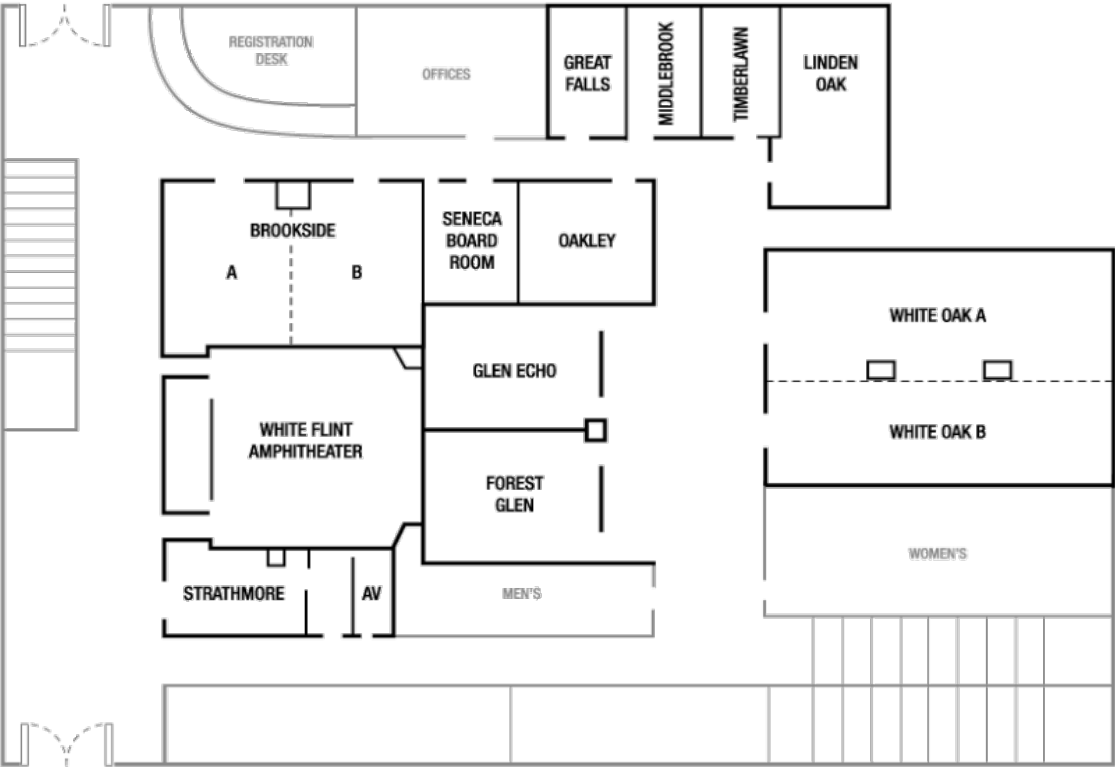
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MAIN LEVEL



LOWER LEVEL



Abstracts of the 11th International Congress of Vertebrate Morphology

PLENARY LECTURES

PLN1-1 1:00 pm

Modifying the mammalian model: Whassup with whales?

Reidenberg JS*, *Icahn School of Medicine at Mount Sinai* joy.reidenberg@mssm.edu

Abstract: Whales (including dolphins and porpoises) have unusual anatomy by any standard. Nearly every system of the typical mammalian body was dramatically transformed. This talk will dive into the wild world of their weird anatomy, wacky evolutionary story, and wonderful adaptations. The body shape became hydrodynamic, including smooth and deforming skin, yet they retain hairs. Fins emerged to stabilize position in 3-D space, yet the semicircular canals are reduced. Flippers evolved from front limbs to regulate locomotion, yet each flipper retains the complete skeleton of an upper extremity. Lower extremities disappeared, but the remnants of a pelvis can be found. The tail elongated and evolved flukes for powerful propulsion, yet the up-and-down motion of the vertebral column is reminiscent of galloping on the land. External genitalia are withdrawn into slits during locomotion, but can be extruded to enable internal fertilization and lactation. The diet changed from herbivorous to carnivorous, although the stomach retains multiple chambers similar to that of ruminants. Oral modifications enable prey capture, but vary greatly between toothed and baleen whales. External pinnae are gone, but mandibular fat pads now catch and channel sounds from the jaws to the ears. Nostrils migrated caudally to allow efficient breathing while swimming and protection from water intrusion, but reveal a dependence on breathing air. Nasal and laryngeal modifications enable sound production and transmission, although whales still generate sounds pneumatically. Diving adaptations include increased muscle myoglobin, reduced heart rate, extreme breath holding, and collapsible/expandable lungs, but whales are still susceptible to decompression sickness. Although bone necrosis indicates accumulated damage from diving, vascular specializations may limit decompression sickness. Mimicking these adaptations may lead to developing better medical treatments, new protective devices, or improved technologies.

PLN2-1 8:15 am

Embryos of living dinosaurs: A path to uncover the evolution of development.

Vargas AO*, *Universidad de Chile* thearchosaur@gmail.com

Abstract: Several historical debates on the evolution of birds demonstrate that combining developmental and paleontological data can be quite challenging. Paleontologists and embryologists may provide different identifications for the same avian body parts, and claims have been made that the development of the wing and ankle of birds does not support a dinosaur ancestor. New techniques have revealed many debated structures actually show dinosaur-like development, but in some cases, both paleontology and development provide sound data, that nevertheless appears contradictory. Given the accumulated evidence the dinosaur-bird link, these cases are now interpreted as pointing to previously unsuspected evolutionary changes in developmental pathways. A well-known case is the likely occurrence of a homeotic transformation of digit identity in the evolution from dinosaur hands to bird wings. The wrist provides another example. Dinosaurs most closely related to birds ("raptors") did not have a pisiform bone in their wrist, yet birds have added a large bone with unmistakable pisiform-like development. Past arguments against the dinosaur-bird link have included "Dollo's law", the alleged impossibility of re-evolving structures once lost in evolution. The case of the pisiform would urge us to revise this law, but even today, evolutionary reversions are controversial and subject to high demands of evidence. Differences to ancient structures are argued to show that "reversion" is actually neomorphism, and any ancestral resemblance is coincidental. Evidence of ancient molecular-genetic mechanisms can also be demanded as ultimate proof of reversion. I will discuss cases in birds (both natural and experimental) to argue that reversion need not be absolute: differences may evolve, but resemblances to ancestors involve the co-option of ancient developmental systems. Further, these ancient developmental systems can be largely epigenetic, leaving little or no molecular-genetic signature.

PLN3-1 8:15 am

Developmental origin of the synsacral in jawed vertebrates: implications for vertebral development and fusion.

Johanson Z*, *Natural History Museum; Boisvert CA, Curtin University; Trinajstić K, Curtin University* z.johanson@nhm.ac.uk

Abstract: The vertebrate axial skeleton is composed of vertebrae developing antero-posteriorly, comprising dorsal, central, and ventral elements in various combinations. Dorsal and ventral vertebral elements occur in jawless vertebrates (e.g., lamprey, hagfish), although axial skeleton fusion appears restricted to jawed vertebrates. This fusion can occur normally during development, or abnormally, as in certain human disorders, or due to external factors like high temperatures or stress. Examples of fusion during regular development include the tetrapod sacrum, the synsacrum in birds, and the fusion of the anterior vertebral column known as the synsacral. The synsacral forms immediately posterior to the cranium and occurs convergently in jawed vertebrates like fossil placoderms and chondrichthyans. Comparable fusion in the neck region in human disorders can be due to failure of somites to segment properly during development (Klippel-Feil syndrome) or to transformation of tissues between the vertebrae into cartilage and bone (FOP), the latter also characterizing vertebral fusion in farmed fishes (salmon). Here, vertebral

fusion has important implications for human health and food production, but cannot be examined experimentally (humans) or results from often variable and non-standardized conditions (farmed salmon). In the chondrichthyan *Callorhynchus*, the synarcual forms consistently in normal development. Regular vertebral segmentation occurs, with subsequent fusion into the synarcual. Vertebrae directly behind the synarcual continue to be incorporated through growth. This appears to be a common pattern, occurring in three major groups of early jawed vertebrates; fusion involves transformation of intervertebral tissues into cartilage and bone/mineralised cartilage. We suggest chondrichthyans have potential as ideal extant models to better understand fundamentals of vertebral fusion for application to abnormal fusion in humans and important food animals such as the salmon.

PLN4-1 8:15 am

Assembling the bird: morphological evidence from Mesozoic fossils elucidates the evolution of the avian body plan and systems.

Chiappe LM*, *Natural History Museum of Los Angeles County* lchiappe@nhm.org

Abstract: Worldwide discoveries of Mesozoic fossils provide unprecedented anatomical information for understanding when and how key traits related to the life history, physiology, ecology, and locomotion of birds first evolved. Bone microstructural studies reveal the evolution of growth patterns and other life history traits. These studies show how early in their evolution, birds transitioned from interrupted to uninterrupted growth, thereby revealing how birds that ancestrally grew over multiple years evolved modern patterns in which somatic maturity is reached within the first year. These studies also document that sexual maturity predated somatic maturity in early birds and how the opposite pattern, typical of modern birds, originated later in the group's evolution. Fossils preserving soft tissues and intestinal contents clarify the evolution of the digestive and reproductive systems of birds. They demonstrate that the bauplan of the digestive tract of present-day birds evolved at least 125 million years ago. They also illustrate how the avian pattern of sequential maturation of follicles and ovulation was acquired early in their evolution and in a piecemeal fashion. The diversity of body plans and ecomorphological traits of Mesozoic birds alludes to the evolution of many different lifestyles, some resembling those of their modern counterparts. Fossils preserving plumage allow for the characterization of aerodynamic parameters (wing surface area, aspect ratio, and others) that, together with quantitative predictions from extant birds, provide information about the basic flight modes of primitive birds, thus rendering evidence of when modern flight modes first appeared. In all, a wealth of Mesozoic fossils clarifies how unique adaptations of the avian body—rapid growth, large egg volume, endothermy, and flight modalities, among others—developed through variably complex and stepwise patterns during the early stages of the evolutionary history of birds.

PLN5-1 8:15 am

Form, function, and fossils: modern twists on ancient evolutionary transitions.

Pierce SE*, *Museum of Comparative Zoology and Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, USA* spierce@oeb.harvard.edu

Abstract: The vertebrate tree of life is filled with weird and wonderful animals that recount an evolutionary journey that has fascinated us for generations. Of particular interest, are the extensive morphological, functional, and environmental transformations that resulted in vertebrate biodiversity as we know it today. Our knowledge and understanding of major events in vertebrate evolution continues to be remodeled by new discoveries, both paleontological and neontological, and with the advent of new technologies and analytical toolkits. My research team investigates ancient evolutionary transitions, focusing on interpreting functional shifts through the fossil record. To achieve this, we study extant and extinct animals, utilizing state-of-the-art methodologies that allow us to capture, explore, and interpret morphology and function from various perspectives. Here I will introduce a selection of active research endeavors in my lab, the questions we seek to answer and the techniques we are using in the process. I'll tackle three classic vertebrate transitions: 1) the fish-tetrapod transition and the evolution of terrestrial locomotion; 2) the dinosaur-bird transition and the acquisition of the flexible avian neck; and 3) the "reptile"-mammal transition and the origin of mammalian gaits. Although these projects appear unrelated, all are designed to investigate the hidden complexities of musculoskeletal form and function in order to elucidate the underlying principles governing vertebrate movement. We accomplish this by building comparative data sets from extant animals—to uncover trends and to validate techniques—and use these to make informed decisions about the fossil taxa under study. The ultimate goal is to reanimate the fossil remains of extinct animals bridging transitional boundaries and reveal how adaptive/functional complexes are assembled and transformed with greater precision and clarity.

SYMPOSIA, WORKSHOPS, & CONTRIBUTED SESSIONS

Note 1: Listed alphabetically by session abbreviation (e.g., AQU, BON, BSI, CHA, etc.)

Note 2: Some of the symposia and all of the Contributed Sessions have associated posters

Symposium – Functional (secondary) adaptation to an aquatic life in vertebrates (AQU)

Organizers: Alexandra Houssaye, Frank Fish

AQU1-1 9:30 am

Primary and secondary adaptations to aquatic feeding in salamanders.

Heiss Egon, Institute of Systematic Zoology and Evolutionary Biology*

Abstract: Salamanders exhibit a primary bimodal lifestyle with an aquatic larva that metamorphoses to a more or less terrestrial postmetamorphic stage. All free swimming larval salamanders bear gills and are primarily adapted to aquatic suction feeding where a unidirectional water flow enters the mouth and leaves the pharyngeal area through gill slits—a system strikingly similar to fish-like vertebrates. During metamorphosis, gill slits are closed and the larval "gill system" is transformed into a "tongue system". The tongue is a key innovation that allows food uptake on land. The general mechanics of the tongue and its function in capturing prey is roughly similar amongst all metamorphosed salamanders, though some salamander groups forego metamorphosis and become adult with no or only little changes from the larval somatic condition and might be regarded as primary aquatic forms. Consequently, the feeding apparatus of metamorphosed salamanders can be viewed as primary adaptation to terrestrial feeding but the ability to employ a suction feeding mechanism, slightly modified from the larval condition, was maintained in some salamander groups and is found in many salamandrids and ambystomatids. Other salamanders, such as most plethodontids, have changed their life-history to direct development and as a consequence, have lost their free larval stage and have freed themselves from an obligatory aquatic phase. The specialized tongues in plethodontids are amongst the most efficient tools for terrestrial prey capture in salamanders but prevent suction feeding in water, though some plethodontids show secondary adaptations to aquatic feeding by using their jaws or their tongue to capture prey.

AQU1-2 10:00 am

Feeding modes in Sirenia (Mammalia): more of them than you probably thought!

Domning Daryl, Howard University ddomning@howard.edu*

Abstract: From their first appearance in the Eocene, sirenians have been feeding on aquatic plants, especially seagrasses. Although this may not seem complicated, they have in fact tried and refined several, surprisingly diverse approaches to this task: 1) selective browsing, with narrow rostra and mandibular symphyses, as seen in prorastomids; 2) progressively less selective grazing, with broader symphyses and loss of incisors, canines, and premolars, as in protosirenids and dugongids; 3) rhizivory, with progressively enlarged, bladelike I1 tusks, as in dugongines (paralleled in a protosirenid and one or two halitheriines); 4) degenerate rhizivory, with loss of enamel, in *Dugong dugon*; 5) algivory, with total loss of teeth, in *Hydrodamalis*; 6) grazing on freshwater true grasses, with polydonta and unlimited horizontal tooth replacement, in trichechines; 7) durophagy (possibly on shellfish and/or calcareous algae) in miosirenines. Mode 1 was the primitive condition; modes 2 and 3 comprise the majority of known fossil species. Mode 3 characterized the striking Oligocene-Pliocene adaptive radiation of dugongines, with several lineages independently achieving the most extreme morphology; this appears to have been a risky specialization that consistently ended in extinction. The three genera that survived into Recent times each displayed divergent and unique specializations: modes 4 in *Dugong*, 5 in *Hydrodamalis*, and 6 in *Trichechus*. Finally, the Miosireninae, a short-lived clade in northwestern Europe, evolved massively reinforced palates, evidently for crushing some sort of hard food. Mode 2, the most conservative adaptation, was the safest over the long haul, characterizing ecologically-generalist seagrass eaters from Eocene to Pliocene—yet it was not represented in the Quaternary fauna. Apparently, the radical environmental changes of the last 3 million years exceeded the tolerances of that adaptation, which was optimized for the most stable sirenian niches of the Tertiary.

AQU1-3 10:30 am

Evolutionary innovation and ecology in mysticete cetaceans: transition from teeth to baleen and raptorial to bulk filter feeding.

Berta A, San Diego State University; Lanzetti A, San Diego State University; Ekdale EG, San Diego State University; Deméré TA, San Diego Natural History Museum*

Abstract: The origin of baleen and filter feeding in mysticete cetaceans occurred approximately 28-24 million years ago and represents a major macroevolutionary transition in cetacean morphology (teeth to baleen) and ecology (raptorial to filter feeding). We explore this dramatic change in feeding strategy by employing a diversity of tools and approaches: morphology, molecules, and isotopes. Adaptations for raptorial feeding in extinct toothed mysticetes provide the phylogenetic context for evaluating morphological apomorphies preserved in the skeletons of stem and crown edentulous mysticetes. In this light, the presence of novel vascular structures on the palates of Oligocene toothed mysticetes is interpreted as the earliest evidence of baleen and points to an intermediate condition between

an ancestral condition with teeth only and a derived condition with baleen only. Supporting this step-wise evolutionary transition, isotopic evidence shows how changes in dental chemistry in early toothed mysticetes tracked the modification in diet and environment. Recent discoveries also demonstrate how this transition was made possible by radical changes in cranial ontogeny. In addition, genetic mutations and the possession of dental pseudogenes in extant baleen whales support the fact of a toothed ancestry for mysticetes. Based on genetic and morphologic data, we provide a hypothesis that reconstructs the dramatic shifts that take place in extant baleen whales before birth, in skull development, resorption of a fetal dentition and growth of baleen. Comparisons are also made with filter feeding Mesozoic bony fishes and marine reptiles to define common themes in this striking example of convergent evolution. The mechanisms involved in this complex evolutionary transition that entails multiple, integrated aspects of anatomy and ecology are only beginning to be understood, and future work will further clarify the processes and the development underlying this macroevolutionary pattern.

AQU2-1 11:30 am

Acoustic fatheads: Parallels in the functional anatomy of underwater sound reception mechanisms in dolphins, seals, turtles, and sea birds.

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Abstract: Cetaceans lack conventional external ears. They have no evident pinnae and it is thought that the occluded residual external auditory canals are likely dysfunctional. Even more remarkable is that the auditory tympano-periotic bullar complex is extra-cranial, residing in a peribullar sinus bordered by the squamosal, occipital, and temporal bones. Pinnipeds, by contrast, have distinct, well-developed sinusoidal, external auditory canals but also valves and tissues that may operate to occlude the canals underwater. Sound conduction mechanisms in diving sea birds and sea turtles are virtually untested and the anatomy minimally investigated. In this study, computerized tomography (CT) and magnetic resonance imaging (MRI) were used to map densities of tissues associated with the outer, middle, and inner ears of five odontocete, two mysticete, two pinniped, three sea turtle, and two sea bird species. Three-dimensional reconstructions of scan data were used to determine species-specific geometry of tissue groups connected to the middle ear or surrounding the ear canal. The analyses show bundles of coherent fatty tissues in contact with the tympanum in all species examined. Densities of these fats are similar across species and are consistent with sound speeds near that of sea water. In seals and birds, these fats sheathed the external auditory canal. In turtles, the fats formed a discrete column communicating with plates on the lateral surface of the head. In odontocetes, the fats formed three distinct bundles: two directed anteriorly along the lower jaw with a third projecting laterally. In mysticetes examined to date, the fats form a single, large, ovoid lateral lobe. These findings suggest that all four marine groups evolved parallel soft tissue mechanisms that act as the primary low impedance channels for underwater sound conveyance to the middle and then inner ear. [Supported by the Mellon Foundation; Seaver Institute; Office of Naval Research; NIH]

AQU2-2 12:00 pm

Hypernatremia in marine snakes: implications for the evolution of a euryhaline physiology.

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Abstract: Secondary transitions from terrestrial to marine life provide remarkable examples of evolutionary change. Although the maintenance of osmotic balance poses a major challenge to secondarily marine vertebrates, its potential role during evolutionary transitions has not been assessed. However, the widespread relationship between salt excreting structures (e.g., salt glands) and marine life strongly suggests that the ability to regulate salt balance has been crucial during the transition to marine life in tetrapods. In the current presentation, I review the role of oceanic salinity as a proximate physiological challenge for snakes during the phylogenetic transition from the land to the sea. A review of osmoregulatory physiology in species situated along a continuum of habitat use between fresh- and seawater shows that snake species display a concomitant tolerance toward hypernatremia, even in species lacking salt glands. Free-ranging marine snake species usually display hypernatremia despite having functional salt glands. Overall, sea snakes exhibit a marked tolerance to salt load compared to other marine tetrapods and apparently trigger substantial salt excretion only once natremia exceeds a high threshold. Collectively, these data suggest that a physiological tolerance toward hypernatremia has been critical during the evolution of a euryhaline physiology, and may well have preceded the evolution of salt glands.

AQU2-3 12:30 pm

"On the fence" versus "all in": insights from turtles for functional transitions in the aquatic locomotion of amniotes.

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Abstract: Though ultimately descended from terrestrial amniotes, turtles have deep roots as an aquatic lineage and are quite diverse in the extent of their aquatic specializations. Many taxa can be viewed as "on the fence" between aquatic and terrestrial realms, whereas others have independently hyperspecialized and moved "all in" to aquatic habitats. Such differences in specialization are reflected strongly in the locomotor system, and we have conducted several studies to evaluate the performance consequences of such variation in design, as well as the mechanisms

through which both locomotor specialization and the use of multiple habitats are facilitated in turtles. One path to aquatic hyperspecialization has involved the evolutionary transformation of the forelimbs from rowing, tubular limbs with distal paddles into flapping, flattened flippers, as in sea turtles. Hydrodynamically advantageous for sustained, long-distance swimming, the evolution of such flippers may have been enabled by a reduction in twisting loads on proximal limb bones that accompanied swimming in rowing ancestors, facilitating a shift from tubular to flattened limbs. Moreover, the control of flapping movements appears related primarily to shifts in the activity of a single forelimb muscle, the deltoid. Despite some performance advantages, flapping may entail a locomotor cost in terms of decreased locomotor stability. However, other morphological specializations among rowing species may enhance swimming stability. For example, among highly aquatic pleurodiran turtles, fusion of the pelvis to the shell appears to dramatically reduce motions of the pelvis compared to freshwater cryptodiran species. This could contribute to advantageous increases in aquatic stability among the predominantly aquatic pleurodires. Thus, even within the potential constraints of a body design encased by a shell, turtles exhibit diverse locomotor capacities that have enabled diversification into a wide range of aquatic habitats.

AQU3-1 2:30 pm

How to become aquatic with the mustelid toolkit? A morphometric insight into aquatic mustelid long bone evolution.

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Abstract: The locomotor apparatus at least partially reflects where and how an animal moves. Biological structures are shaped by functional demands, yet are constrained by phylogenetic history as well as architectural and developmental constraints. As the locomotor apparatus can be used for locomotion through media with different mechanical properties, it is exposed to often diverging selective pressures. This is especially the case for semi-aquatic species that have to cope with the dramatic differences in density and viscosity in water versus land. Mustelids (Carnivora) display a large range of locomotor behaviors with several specializations ranging from arboreal to semi-aquatic. Semi-aquatic mustelids including otters (Lutrinae) and minks (Mustelinae) present many degrees of adaptation to the aquatic environment. This diversity is associated with a diversity in the modes of swimming that can involve one or both limb pairs. Moreover, the axial skeleton and tail may be used for propulsion too depending on the species and swimming speed. Here we examine the adaptations of semi-aquatic mustelids to locomotion in both environments and test whether minks present traits that are convergent on those observed in otters. To do so we use 3D geometric morphometrics to describe the shape of the long bones of both the fore- and hind limbs in five species of otters, two species of mink and closely related terrestrial Mustelinae. We test for convergence between minks and otters in long bone shape and explore whether swimming mode impacts long bone shape in otters.

AQU3-2 3:00 pm

Secondary evolution of aquatic propulsion in higher vertebrates: Validation and prospect.

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Abstract: Re-invasion of the aquatic environment by terrestrial vertebrates resulted in the evolution of species expressing a suite of adaptations for high performance swimming. Examination of swimming by secondarily aquatic vertebrates provides opportunities to understand potential selection pressures and mechanical constraints, which may have directed the evolution of these aquatic species. Mammals and birds realigned the body and limbs for cursorial movements and flight, respectively, from the primitive tetrapod configuration. This realignment produced multiple solutions for aquatic specializations and swimming modes. Initially in the evolution of aquatic mammals and birds, swimming was accomplished by using paired appendages in a low efficiency, drag-based paddling mode. This mode of swimming arose from the modification of neuromotor patterns, associated with gaits characteristic of terrestrial and aerial locomotion. The evolution of advanced swimming modes occurred in concert with changes in buoyancy control for submerged swimming, and a need for increased aquatic performance. Aquatic mammals evolved three specialized lift-based modes of swimming that included caudal oscillation, pectoral oscillation, and pelvic oscillation. Based on modern analogs, a biomechanical model was developed to explain the evolution of the specialized aquatic mammals and their transitional forms. Subsequently, fossil aquatic mammals were described that validated much of the model. However for birds, which were adapted for aerial flight, fossil evidence has been less forthcoming to explain the transition to aquatic capabilities. A biomechanical model is proposed for birds to describe the evolution of specialized lift-based foot and wing swimming. For both birds and mammals, convergence in morphology and propulsive mechanics is dictated by the need to increase speed, reduce drag, improve thrust output, enhance efficiency and control maneuverability in the aquatic environment.

AQU4-1 4:30 pm

How to build a deep diver.

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Abstract: Mesoplodonts are extreme divers, diving for over 45 minutes and to depths of over 800m (Tyack et al. 2006). These dives are of similar depth and duration to those of *Physeter macrocephalus*, whose body mass can

be over 50 times greater (Watwood *et al.* 2006). Velten *et al.* (2103) suggested that the deep dives of mesoplodonts can remain aerobic if diving metabolic rate is low. We present body composition data that support the hypothesis of low metabolic rates in mesoplodonts. We utilized a mass dissection protocol to systematically dissect six mesoplodonts (one *Mesoplodon bidens*, one *M. europaeus*, two *M. densirostris*, and two *M. mirus*) into discrete anatomical compartments, including integument and individual muscles, organs, and bones. These component masses, as a percent total body mass (%TBM), were compared to those of shallow-diving species investigated using similar techniques - *Phocoena phocoena* (McLellan *et al.* 2001) and *Tursiops truncatus* (Mallette *et al.* 2016). The %TBM represented by integument (20-26%) and bone (9-11%) were similar across all species. Relative brain mass was smaller in mesoplodonts (0.2%) than in *Tursiops* (0.7%) or *Phocoena* (1%), as was combined thoracic and abdominal viscera (4-5% in mesoplodonts vs. 15% in *Tursiops* and 13% in *Phocoena*). In contrast, mesoplodonts invest a substantially larger %TBM (48-49%) in locomotor muscle than does *Tursiops* (31%) or *Phocoena* (26%). This locomotor muscle is composed of 80% large, fast-twitch glycolytic muscle fibers with low mitochondrial volume densities (Velten *et al.* 2013). This muscle fiber profile, apparently unique to beaked whales, suggests low rates of oxygen usage in this extremely large body compartment. The large investment in musculoskeletal tissues and small investment in brain and viscera likely contribute to low metabolic rates in diving mesoplodonts.

AQU4-2 5:00 pm

Aquatic habits in the ancestors of cetaceans: integrating stable isotopes and bone cross-sectional morphology.

Cooper L.N.*, NEOMED; Clementz M.T., University of Wyoming; Usip S., NEOMED; Bajpai S., Birbal Sahni Institute of Palaeobotany; Hieronymus T.L., NEOMED; Hussain S.T., Howard University; Thewissen J.G.M., NEOMED lcooper@neomed.edu

Abstract: The first 15 million years of cetacean evolution is one of the best case-studies in macroevolutionary transitions. The earliest cetaceans were interpreted as semi-aquatic based on the presence of thickened bones and stable oxygen isotope values in tooth enamel, relative to coeval, land-dwelling taxa. However, the origin of aquatic habits in cetacean ancestors remains unclear. This study reconstructed the origins of aquatic habits in this group based on CT scans of long bones of a large sample of extant and fossil cetartiodactylans. In agreement with isotopic evidence, the common ancestor of anthracotheres, hippopotamids, raoellids and cetaceans may have spent a great deal of time in the water. Some modern taxa (e.g., tragulids) are capable of submerging for long periods of time, but probably utilize a different, non-skeletal, solution to counteract body buoyancy. Results also showed bone cross-sectional phenotype is not a reliable stand-alone proxy for aquatic behaviors, and is best combined with other lines of information, like stable isotopes. Morphology was, however, an accurate indicator of a semi-aquatic lifestyle as taxa that spent the majority of their lives in water displayed extreme hyperostosis. This study extends our understanding of the progression of skeletal phenotypes associated with habitat shifts among mammals.

Symposium — New insights into skeletal microstructure of vertebrates, extant and extinct (BON)

Organizers: Elizabeth Rega, Mason Dean, Tomasz Owerkowicz

BON1-1 9:30 am

Scaling of Haversian systems in a phylogenetically diverse sample of mammals is consistent with physical and physiological constraints.

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Abstract: Haversian systems (HS) or secondary osteons are the hallmarks of bone remodeling, resulting from the resorption of older bone via osteoclast activity and deposition of new bone by osteoblasts. The outer edge of each HS is marked by a cement line, where the HS intersects with either primary bone or another, older, HS that it is replacing. Although some canaliculi, the cytoplasm-containing channels connecting osteocytes, cross the cement line, the vast majority of osteocytes within a single HS are supplied via the HS's central canal. The requirement for nutrients and oxygen to diffuse from the central canal out to the cement line means that the size of a single HS might be constrained either by the laws of physics or physiology. We tested the hypothesis that the size of a single HS might scale either isometrically, suggesting a diffusion-limited process, or following basal metabolic rate (BMR), in a phylogenetically diverse range of mammals across over four orders of magnitude in body mass. Using an historical sample of femoral mid-diaphyseal cross-sections, we estimated cortical area, counted total number of HS and calculated mean HS diameter and percent remodeled bone. Contrary to the conventional view that remodeling is absent or rare in small mammals, we found strong phylogenetic signal in HS count, with evidence for both HS in small mammals and large mammals with relatively few HS. Phylogenetically informed reduced major axis regression of mean HS area on body mass revealed a scaling exponent of 0.68 (95% CI 0.59-0.76). The 95% CI included both isometry and the often-cited mass-specific scaling relationship for BMR, 0.75. We conclude that HS size in mammals is likely limited by either diffusion or scaling, with evidence for each currently equivocal. Based on the finding of significant phylogenetic signal in HS counts, we propose that this trait may track phylogenetic patterns in basal metabolic rate, however this hypothesis remains to be tested.

BON1-2 10:00 am

Osteocyte mechanobiology: influence on bone modeling and remodeling and its bearing on functional interpretation of skeletal morphology.

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Abstract: The bony skeleton displays a high degree of phenotypic plasticity during development and adulthood in response to environmental, dietary, and mechanical stimuli. The influence of mechanical stimuli on bone morphology is hypothesized to be mediated by matrix-bound osteocytes regulating bone formation and resorption. The skeletons of all major amniote groups respond to differential physical stimuli, suggesting a plesiomorphic function for osteocytes in mechanosensitive anabolic pathways. In this talk, I review our current understanding of the fundamental cellular mechanisms by which the skeleton senses and responds to mechanical stimuli, current in vivo and in vitro models for studying adaptive plasticity in the skeleton, and the extent to which we can use skeletal histomorphology to infer functional skeletal adaptation. While much has been learned in the past thirty years about vertebrate skeletal mechanobiology using model taxa, fundamental questions remain regarding how taxonomic variation in the osteocyte lacunar-canalicular network might affect the potential for different groups to adapt to physical stimuli, the role metabolic rate may play in skeletal plasticity, and finally, how the skeletons of vertebrate taxa lacking osteocytes (e.g. many teleosts, chondrichthyans) respond to changes in physical demands on the skeleton.

BON1-3 10:15 am

Bone microstructure in hibernating mammals with implications for mechanical performance.

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Abstract: Physical inactivity leads to increased bone resorption, elevated serum and urinary calcium concentrations, bone loss, bone mechanical property loss, and increased fracture risk in humans and the experimental menagerie (e.g., mice, rats, turkey, dogs, sheep). Grizzly and black bears, yellow-bellied marmots, arctic ground squirrels, and 13-lined ground squirrels do not lose bone mass or mechanical properties during prolonged (4-8 months) hibernation. Bone remodeling (i.e., bone resorption and formation) continues during hibernation, although at significantly reduced levels compared to summer levels in bears and marmots. These changes in bone remodeling during hibernation leave histological signatures in bone such as the density of secondary osteons and lines of arrested growth (LAG). Hibernating bears are anuric, yet serum calcium concentration remains at homeostatic levels throughout the entire year. These findings suggest that hibernating bears and rodents have biological mechanisms to preserve bone tissue integrity when challenged with prolonged physical inactivity. Reduced bone remodeling in hibernators likely contributes to the conservation of metabolic energy. Neural signals and circulating factors (e.g., calcium regulatory hormones) likely contribute to the changes at the bone cell level that are involved in bone tissue preservation. Normal balance between bone resorbing osteoclasts and bone forming osteoblasts is likely maintained to preserve normal serum calcium concentrations during anuria. Identification of the molecular mechanisms that regulate bone cell function during hibernation may contribute to the development of new therapies for osteoporosis and inform our understanding of how hibernators have adapted to survive extreme environmental conditions. Funding from NIH (NIAMS AR050420).

BON1-4 10:30 am

Developmental mechanisms and evolutionary advantage of metatarsal elongation and fusion in bipedal jerboas (Dipodidae).

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Abstract: Throughout the radiation of vertebrates, alterations to the size and shape of skeletal elements have transformed the ancestral body plan and allowed species to expand into niches in all three-dimensions. For example, extreme hindlimb modifications in the bipedal jerboas enable ricochet locomotion at high speeds over long distances in an open desert environment. The disproportionately elongated metatarsals shift the hindfeet rostral to the center of mass, and fused metatarsals are thought to resist the increased bending forces associated with bipedal takeoff and landing. Here, we explore the developmental mechanisms that establish growth rate and proportion in the limb bones and that promote lateral fusion of the metatarsals. We have shown that the size of terminally differentiated hypertrophic chondrocytes, and thus endochondral growth rate, is influenced by the amount of cellular dry mass produced after a phase of cytoplasmic swelling. Current work is focused on identifying the genetic mechanism(s) that regulate mass production in growth plates that elongate at different rates. Together with metatarsal elongation, the most derived of the jerboas have co-evolved fusion of the three central metatarsals into a single element. We find this occurs gradually from the second to fourth week of postnatal development and involves precise pattern and activity of osteoblasts that deposit bone around the circumference of the three elements while osteoclasts metabolize bone at the interfaces. These phenotypes together provide an opportunity to identify the cellular and genetic mechanisms that shape the skeleton during evolution and that contribute to bone development.

BON1-5 10:45 am

Effects of growth rate and flight on wing bone laminarity in bats and birds.

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Abstract: During flapping flight, vertebrate wing bones presumably experience high torsional loads. To resist these flight-induced loads, the wing bones of volant vertebrates have independently evolved similar anatomical form. Whether or not the histological form of wing bones is also constrained to resist torsion is less clear. Previous work suggests that laminar bone, which is a vascularized tissue with abundant circumferentially oriented vascular canals, may be a flight adaptation in adult birds. I have shown, however, that laminar bone is not necessary for flight; bats do not have any laminar bone in humeri despite them being as rigid to torsion as those in comparably-sized birds. Phylogenetically-informed scaling analyses reveal that birds simply grow faster than bats. These results suggest that laminar bone is partly influenced by growth rate. To test this hypothesis further, my lab has tracked the proportion of laminar bone in the humerus, ulna, and radius of developing pigeons. Contrary to biomechanical expectations, wing bone laminarity is lower in post-fledge individuals than in pre-fledge ones. Logistic regression reveals a direct and significant correlation between wing bone laminarity and growth rate. Put together, my work suggests that wing bone laminarity may be an expression of ontogenetic allometry. Evolutionary shifts in ontogenetic allometry may explain interspecific variation of wing bone laminarity across birds.

BON2-1 11:30 am

Functional cranial joint histology in reptiles and birds and its significance for avian cranial kinesis.

Bailleul AM*, *University of Missouri*; Horner JR, *Montana State University*; Witmer LM, *Ohio University*; Holliday CM, *University of Missouri* bailleula@missouri.edu

Abstract: Joint microstructure has been intensively studied in mammals in many biological contexts, but comparatively little is known about joint tissues in the skulls of birds, archosaurs, and other reptiles, which is surprising given the extraordinary diversity of kinetic capacity among the fibrous and synovial joints that connect their cranial bones. The evolutionary origins of major clades hinge on modifications of their articulations. Thus, new data on cranial joint tissue structure and function are necessary to understand reptilian cranial evolution. Here, we investigated the microstructural details of numerous cranial joints (e.g., jaw, otic, palatobasal joints, craniofacial sutures, and flexion zones) of adult and young emus, ducks, alligators, lizards and several non-avian dinosaurs. Histology was paired with microCT data to better visualize 3D morphology. These findings were used to investigate 1) if clade-specific characteristics exist among reptiles at the microscopic scale; 2) if specific tissues coincide with particular loading environments; and 3) how joint structure reflects its function. For example, are akinetic synovial joints built similarly to mobile ones? How do flexion zones and other complex joints facilitate cranial kinesis? Whereas birds and non-avian dinosaurs form articular cartilage on the membrane bone components of their synovial joints, crocodilians and lizards do not. Moreover, whereas adult birds possess a periosteum in their craniofacial sutures, adult crocodilians and non-avian dinosaurs lack this layer, and sutural growth is mediated mostly via metaplasia. New data also show that suture fusion does not necessarily imply akinesis, since the flexible craniofacial hinge of ducks is a synostosis made of chondroid bone. These results have significant implications for the origins of avian cranial kinesis within non-avian dinosaurs, the developmental underpinnings of joint homology, and the inference of kinetic capacity in extinct reptiles.

BON2-2 12:00 pm

Atmospheric oxygen conditions do not constrain growth or biomechanical performance of limb bones in Alligatoridae: *Alligator mississippiensis*.

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Abstract: Growth rates in extinct taxa are frequently based on comparisons with those of extant relatives; this assumes that prevalent environmental conditions influencing growth were similar to those of modern day. An often overlooked factor is atmospheric oxygen; today's levels are 21% (normoxia) but during the Phanerozoic levels may have ranged from 15% O₂ (hypoxia) to 35% O₂ (hyperoxia). To test the effects of available oxygen on growth and biomechanics in a non-traditional vertebrate model, eggs were incubated and hatchlings of the American alligator reared in five distinct oxygen environments (16-36%). Alligators were sacrificed at intervals, femora removed and cross-sectional geometry of the mid-diaphyses studied. A preliminary analysis with femur length growth modeled as either a determinant or indeterminate process found no significant difference among treatments, so traits were standardized to this feature to compare differently sized animals. Results of analysis of covariance with femur length as covariate reveal no significant differences in cross-sectional geometry between treatment groups. Subsequent analyses with all groups pooled showed that anteroposterior and mediolateral diameters scale with significant negative allometry, while cross sectional area scales with significant positive allometry. Inertial moments also scale with negative allometry, but section moduli scale isometrically. The alligator femora exhibit a narrower mid-diaphyseal diameter but significantly more cortical bone than expected by isometry. The combination of these two scaling patterns results in a bone as resistant to bending as predicted. Lack of an observed treatment effect in either skeletal growth or limb biomechanics suggests that extant alligators are not limited by available oxygen. We hypothesize that the unique cardiac morphology in alligators may allow the animals to regulate their internal oxygen milieu

independently of atmospheric conditions. Supported by NSF IOS- 0922756.

BON2-3 12:15 pm

Effect of embryonic calcium constraint on post-hatching growth and bone microstructure in the American alligator (*Alligator mississippiensis*).

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Abstract: Among oviparous reptiles, archosaurs lay eggs with the thickest and most rigid eggshells. During embryonic development, archosaurs mobilize eggshell calcium to the yolk sac, and upon hatching rely on this calcium reservoir to supplement their dietary calcium intake. This additional source of calcium may have allowed archosaurs to achieve high post-hatching growth rates. We tested this hypothesis by incubating eggs of the American alligator, and following post-hatching growth for over two months. The calcareous eggshells were either experimentally peeled or sham-handled with the fibrous shell membrane left intact in both treatment groups. At hatching, experimental animals were significantly smaller than the clutch-matched controls. There was considerable variation in growth rates within both groups, but overall control animals grew significantly faster than experimental ones. Standardized to bone length, femora and lower jaws of three month-old experimental animals had smaller cross-sectional area, second moment of area, and polar moment of inertia. Cortical thickness was decreased, as was lacunar density. Incomplete osteone formation resulted in prominent vascular spaces in the lower jaws of experimental alligators. Considering a lower bone mineral content in the experimental group, these results suggest that insufficient calcium supply exerts negative feedback on bone tissue growth, and archosaurs cannot compensate for decreased material stiffness by augmenting the geometric properties of skeletal elements, even those critical to locomotion or feeding. We propose that selective forces on post-hatching survival drove the evolution of ever-thicker and mineralized eggshell of archosaur eggs. Eggshell and bone microstructure of extinct archosaurs may contain clues to their calcium-handling strategies.

BON2-4 12:30 pm

How's your apatite? Structure and mechanics of elasmobranch skeletal tissues.

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Abstract: Elasmobranchs are singular among vertebrate clades in having cartilaginous skeletons. An understanding of the functional properties of elasmobranch skeletal tissues, and their phylogenetic relationships to other vertebrate tissues, is only possible through investigations of their growth, structure, and mechanical behavior. Despite meticulous early work on elasmobranch skeletal anatomy, the study of fine-scale skeletal structure and its relationship to skeletal mechanics is still in its infancy. Previous efforts have been limited by difficulties in visualizing and mechanically testing biological tissues with complex ultrastructures and comprised of materials with dissimilar mechanical properties. However, advances in imaging resolution and techniques, and the increased application of engineering tools to biological questions have brought rich insight into the form and function of elasmobranch tissues. We synthesize available data on the anatomy of the known types of elasmobranch cartilage (areolar cartilage, tessellated cartilage), discussing the mechanics and ultrastructure of these tissues, while also highlighting less studied natural variations on tessellated cartilage (e.g., structural reinforcements in the jaws of durophagous species, "woody" cartilage in lamnid rostra) and types of pathologic mineralization (e.g., vertebral calluses, mineralized endophytic masses), which have been linked to developmental, nutritional, and behavioral factors. Furthermore, we integrate our knowledge of skeletal structure and tissue mechanics, by presenting data from physical and FEA models that speak to the functional advantages and disadvantages of a purely cartilaginous skeleton and selective pressures associated with its evolution. In particular, we highlight recent modeling data showing that stress distribution and mechanical efficiency appear to be improved in more derived morphologies, where mineralized cartilage is more homogeneously distributed.

BON2-5 12:45 pm

Evolution read in tooth and jaw: synchrotron tomography reconstructs a comparative model for dental evolution in Osteichthyes.

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Abstract: Teeth are a key vertebrate innovation, underlying the diversification of jawed vertebrates and their dominance in vertebrate diversity. Moreover, teeth are an important model system in evolutionary and developmental biology, to understand development of organ systems in vertebrates. However, our understanding of the evolution of teeth could not be more confused, with competing hypotheses seeking to explain the evolutionary origins of teeth. Previous studies focused mainly on sharks, which were considered to reflect ancestral conditions. However, sharks

are derived and have lost many skeletal elements present in primitive jawed vertebrates and, therefore, are not an effective ancestral model. To better constrain ancestral patterns of tooth evolution, we characterised tooth development in *Polypterus senegalus*. This non-teleost actinopterygian occupies a unique phylogenetic position at the base of the clade of extant actinopterygians and shows many primitive features. It can be considered as a useful model for phylogenetic comparisons of oral and pharyngeal tooth development, and thus yield insights into the evolution of teeth. We employed Synchrotron Radiation X-ray Tomographic Microscopy (SRXTM) at the Swiss Light Source; as well as molecular biology techniques to characterise tooth initiation and development in *Polypterus senegalus*, and to compare these to dental development in *Danio rerio*, a derived, teleost actinopterygian, and to a tetrapod sarcopterygian such as *Mus*. Our results show tooth initiation and development in *Polypterus senegalus*, which possesses both pharyngeal and oral dentition, and in *Danio rerio*, which has pharyngeal dentition only. Moreover, our high resolution, three-dimensional analysis gives insight into spatial relations of developing dentitions, thus contributing complementary information to previous studies; while application of molecular biological techniques elucidates the earliest onset of tooth formation in *Polypterus senegalus*.

BON3-1 2:30 pm

3D virtual bone histology reveals the life history of the early tetrapod *Acanthostega*.

Sanchez S.*, Uppsala University and SciLife Lab; Tafforeau P., European Synchrotron Radiation Facility; Clack J. A., University of Cambridge; Ahlberg P. E., Uppsala University sophie.sanchez@ebc.uu.se

Abstract: How did tetrapod adapt to a life on land? This question has been a focus of interest for geologists, palaeontologists and evolutionary biologists for more than a century. Although various hypotheses have been put forward about the selective pressures of terrestrialisation, we actually know almost nothing about the life histories and reproductive strategies of the earliest tetrapods. Here we show 3D virtual histological data based on the long-bone microstructure of the Devonian (360 million-year-old) tetrapod *Acanthostega* to elucidate its development and life history. We discovered that the Greenland mass-death locality, which yielded the specimens of *Acanthostega*, was dominated by, and might in fact consist exclusively of, juveniles. This predominance suggests that the juveniles gathered in schools and were separated from the adults at least at certain times. The late onset of limb ossification indicates that the juvenile *Acanthostega* were exclusively aquatic. The palaeoecology of adults however would remain unknown. The juveniles grew almost to full observed size before their humeri began to ossify. This developmental trait is primitive for tetrapods as it aligns with the lobe-fin development of the Devonian fish *Eusthenopteron*. As well, *Acanthostega* proved to have a long pre-reproductive growth period (spanning much more than 6 years, probably at least a decade) as in lobe-finned fishes and Palaeozoic tetrapods (*Discosaurus*). Such a prolonged juvenile stage in this early tetrapod is considerably longer than in most extant amphibians. This study highlights the utility of synchrotron microtomography as a non-destructive tool to shed new light on the palaeobiology and life history of key fossils. Even a single limb bone can, in principle, provide crucial information. Not only useful for its non-destructive aspect, virtual bone histology also permits 3D modelling, thereby yielding a more complete overview of fossil bone evolution.

BON3-2 2:45 pm

Adaptive patterns in aquatic amniote bone microanatomy: was it more complex than previously thought?

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Abstract: Numerous amniote groups are secondarily adapted to aquatic life. This change of habitat naturally leads to numerous convergences (e.g., streamlined body, limb transformation into paddles, modification of sense organs, reproductive mode, diving adaptations, inner bone structure specializations). The various adaptive traits vary pending on the degree of adaptation to aquatic life, between shallow water taxa still able to occasionally locomote on land and open-marine forms totally independent from the terrestrial environment, but also between surface swimmers and deep divers, freshwater and marine forms. As a consequence, despite convergences, there is a high diversity within aquatic amniotes in shape, size, physiology, swimming mode. Bone microanatomy is considered to be strongly associated with bone functional requirements, thus is a powerful tool to understand bone adaptation to functional constraints and to make functional inferences on fossil taxa. Two major microanatomical specializations have been described in aquatic amniotes, referred to as bone mass increase and a spongy "osteoporotic-like" organization respectively. However, between extremes in these specializations, numerous intermediary (and some contradictory) patterns occur. Moreover aquatic taxa display various distributions of these specializations in their skeleton. Here we propose, based on the analysis of the various microanatomical patterns observed in long bones, vertebrae and ribs of a large sample of aquatic amniotes, to illustrate and discuss this variability and the distinct types of microanatomical adaptations to various aquatic ecologies.

BON3-3 3:00 pm

Bone histology of osteoderms of archosauriform diapsid reptiles (Sauropsida: Archosauriformes).

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Abstract: The presence of osteoderms (dermal armor) within the integument is widespread in many vertebrate lineages, hence the integumentary skeletogenic potential has been proposed to represent a case of deep homology of vertebrates. The presence of osteoderms can be seen as a plesiomorphic trait in archosauriforms, constituting a very important skeletal component, besides the endoskeleton, which is useful for taxonomy and systematics and is known to serve multiple functional aspects. Among archosauriforms, some stem group members (Doswelliidae, Proterochampsia, Phytosauria) and many crown group archosaurs (Pseudosuchia, Avemetatarsalia) show stunning examples of osteoderm formation, such as bucket-sized osteoderms of titanosaurian sauropods, stegosaur plates and spikes, ankylosaur tail clubs, or hand-sized paravertebral shield osteoderms of giant crocodylians. It is surprising that until recently, only few studies (mostly focusing on Avemetatarsalia) on the development, microanatomy, and histology of osteoderms were available, especially when compared to histological studies focusing on long bones. Here we compare and review the osteoderm histology of several Archosauriformes, including doswelliids and proterochampsians, as well as crown group members (aetosaurs, rauisuchians, and few crocodylians). Results reveal a diversity of histological structures, but the mode of growth of all osteoderms is intramembraneous or metaplastic ossification. Besides crocodylian osteoderms, at least some members of the each group presents woven or fibrolamellar bone tissue, indicating faster bone deposition rates, whereas lamellar-zonal tissue in crocodylian osteoderms indicates a reversal to lower growth rates. Further, doswelliid osteoderm histology bears closer resemblance to phytosaurs and pseudosuchians than to proterochampsians and osteoderm histology in fossil archosauriforms has become an important tool for age determination of individuals, and even for growth curve reconstruction.

BON3-4 3:15 pm

In search of the basal amniote condition of Lines of Arrested Growth (or something along those lines...).

Sumida S.S.*, California State University of San Bernardino; Segovia B., Western University of Health Sciences; Mathew N., Western University of Health Sciences; Rega E.A., Western University of Health Sciences

Abstract: Lines of arrested growth ("LAGs") are normally interpreted as cessation or slowing of growth between more favorable growing seasons. In fossil specimens this is confounded by animals that lived in environments with little seasonal variation, experienced little resource variation, or in endothermic animals whose physiology may have buffered formation of clearly visible LAGs. Prolific recent advances have been seen in dinosaurian archosaurs, and within the varying grades of Synapsida, but little has been done to determine whether patterns seen in these two groups are homologous or convergent. The Late Paleozoic Diadectomorpha have been suggested as basal-most amniotes, or as the sister group to Amniota as traditionally defined. Regardless, definitive LAGs in the group could provide a clearer understanding of the basal condition for LAGs for all Amniota. Diadectomorphs present significant potential, as concentric bony ridges mark the zygapophyseal surfaces in a pattern that radiate from their innermost aspect to the distal edges. These ridges have been proposed as indicators of annual or seasonal growth. Universally considered as ectotherms, diadectomorphs have been recovered from deposits reflective of seasonally variable environments. If the ridges could be shown to correspond to internal LAGs, a basal amniote condition for LAGs might be developed. Virtually all such assertions that LAGs are equivalent to annual growth lines for derived members of Synapsida and Dinosauria have been made in the absence of a testable models tying LAGs to documented age. Studies involving crocodylians could bear on such assertions in dinosaurian archosauromorphs, but may be less reliable for the more distantly related Synapsida. Understanding the condition in diadectomorphs could set a baseline standard for LAG characteristics and/or polarity of LAG features for all Amniota, and whether the formation of LAGs in Synapsida and Reptilia should be considered as independently acquired.

BON3-5 3:30 pm

Novel insight into the growth dynamics of sauropodomorph dinosaurs.

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Abstract: The Sauropodomorpha comprise of the more basal members, the non-sauropod sauropodomorphs, and the more derived members of the clade, the sauropod dinosaurs. The basal sauropodomorph dinosaurs are reported to have cyclical growth dynamics (evidenced by the cyclical deposition of growth marks), while the sauropods, are considered to have uninterrupted rapid rates of growth (inferred from the lacks of growth marks). These deductions pertaining to the growth dynamics of the Sauropodomorpha have largely been derived from histological studies of only a few basal taxa, and several more derived sauropod taxa (Neosauropoda). The current study examines a comprehensive sample of the bone microstructure of thirteen sauropodomorph dinosaur taxa, which includes seven basal non-sauropod sauropodomorphs. Our findings revealed that except for *Mussaurus*, growth marks occur throughout the cortex in all basal sauropodomorphs, but were also found to occur in the sauropod, *Lessemsaurus*. Additionally, a single growth mark was recorded in *Volkheimeria*, while several poorly defined annuli were observed in the outer cortex of *Patagosaurus*. Our results agree with the current consensus that the plesiomorphic condition for the sauropodomorpha is cyclical growth dynamics. However, our findings show that the uninterrupted and sustained

rapid growth (the so called "sauropod pattern"?) also occurred in the basal taxon, *Mussaurus*. Furthermore, we found that the basal sauropod, *Lessemsaurus* exhibited the cyclical growth strategy generally associated with basal sauropodomorphs. Thus, our study reveals that the "typical" sauropod growth pattern arose more than once during the evolution of Sauropodomorpha and that such a growth pattern was not exclusive to the Sauropoda.

BON3-6 3:45 pm

Intraskkeletal growth dynamics and functional maturation in the limb bones of "dinobirds".

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Abstract: Growth rate and functional maturity of a tissue are known to be inversely related because cells capable of fast proliferation and thereby ensuring fast growth are undifferentiated, while differentiated cells of mature tissues specialized to perform a certain task cannot proliferate at a high rate. Differing energy allocation into growth vs. maturation results in diverse ontogenetic strategies, such as the altricial – superprecocial spectrum in birds. To get insight into the degree of precociality in five extinct paravian dinosaurs (dinosaur-bird transitional forms), *Anchiornis*, *Aurornis*, *Eosinopteryx*, *Jeholornis* and a yet unnamed taxon, we inferred dynamics of postnatal development of their limb bones from intraskkeletal histovariability because many osteohistological traits (e.g. vascularity, osteonal development, secondary remodelling) are indicative of growth rate and functional maturity of the bone tissue. Differential growth rates as well as histological traits implying differences in functional maturity among limb elements of the same skeleton were detected in all specimens. Except in the fully grown *Aurornis* and the subadult specimen of the unnamed taxon, humeri appear to mature functionally the latest among all limb bones, whereas radii and ulnae exhibit histological signs of more extensive functional demands already in earlier stages of development. Hand bones generally show high functional maturity even in the juvenile *Eosinopteryx* specimen. Degree of maturity of femora appears to correspond with that of radii and ulnae, except in the unnamed taxon where it is the least mature element. Thus, in most taxa femora could have enabled precocial bipedal cursorial locomotion, while the apparent proximodistal gradient of increasing functional maturity in the forelimb elements may relate to different ontogenetic onset and extent of arm-assisted grasping, climbing, or in some taxa even gliding or flying. E.P. is funded by BOF (grant nr. 01P12815).

BON4-1 4:30 pm

Microstructure isn't enough: Additional diagnostic criteria to test among hypotheses of bone tissue identity.

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Abstract: Histologists describe skeletal tissues using many anatomical, compositional and developmental characters. Paleohistologists use these to infer the identity, function and evolution of fossil bone, but lack consensus on which characters are most useful, and often examine only a few microstructural features. This makes comparison difficult, leads to misidentification, and calls the resultant functional and evolutionary inferences into question. These problems worsen when fossil tissues share some but not all characters with extant bone, the range of extant variation is unknown, or etiologies cannot be linked unambiguously to bony features. We identify eight diagnostic criteria that test hypotheses of tissue identity: skeletal distribution, hormonal stimulus, development, duration, timing in context of life history, chemical composition, gross morphology and microstructure (using explicit aspects of fibrillar, vascular and osteocyte arrangement and morphology). All but stimulus can be evaluated in subfossil bone; most can be evaluated in fossils. We demonstrate the need for more comprehensive diagnoses using the examples of avian osteopetrosis (AOP; pathology) and medullary bone (MB; reproductive marker), common alternative hypotheses for endosteally-derived bone in bird-line archosaurs. Their correct identification informs questions of disease and life history evolution. We described the range of MB variation in extant birds, compared MB histology to that of genetically-diagnosed AOP, and re-evaluated every reported case of MB and AOP outside crown birds. Using the broader suite of characters, AOP can be rejected in most cases. Adopting common criteria and reporting more microstructural features provides greater diagnostic power and enables comparison among paleohistological studies. Additionally, clarifying definitions and diagnoses eliminates tautology by positing a test of an etiological hypothesis (definition) by independent lines of empirical evidence (diagnosis).

BON4-2 4:45 pm

Localized resorption spaces in femoral cortical bone of a mature *Tyrannosaurus rex* (Theropoda) are adaptive response to muscle traction.

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Abstract: Skeletochronology and growth curves have necessarily been the preoccupation of the majority of histological studies in Dinosauria. Because of specimen scale, rarity and the necessity of sampling areas most likely to produce lines of arrested growth (LAGS), research involving productive and expendable bones such as ribs and fibulae are over-represented in the literature. In this study, an unusual complete cross-section of the proximal femoral

bone of a mature *Tyrannosaurus rex* was created for exhibit in for the Los Angeles County Museum of Natural History. This complete cross section affords the opportunity to evaluate bone response to localized loading conditions. The cranial, lateral and medial surfaces of the femoral cortical bone are composed of the typical fibrolamellar bone normally observed in this location in other specimens. However, numerous large resorption spaces throughout the posterior cortical bone demonstrate a localized osteopenia which is initially difficult to reconcile with the stresses placed on this limb. Hypotheses including pathology and bone depletion to support egg development are considered. However, traction of the m. caudofemoralis could provide the best explanation. These resorption spaces are lined with 1-2 concentric lamellae of reactive bone after cavity formation. The circular nature of the lacunae and the shell of bone would serve to resist crack propagation and lamellar separation which would otherwise occur under conditions of tension produced by muscle inserting over the area.

BON4-3 5:00 pm

Preliminary results on the bone histology of hadrosaurs (Ornithopoda, Dinosauria) from the Latest Cretaceous of Far Eastern Russia.

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Abstract: Hadrosaurs such as *Olorotitan* and *Edmontosaurus*, were among the most abundant and successful Cretaceous dinosaurs. They spread to all continents and some reached body masses rivaling those of the giant sauropods. However, some hadrosaur groups disappeared from the North American continent 5 to 6 million years before the extinction event, whereas the same groups thrived in Asia until the event. The Maastrichtian hadrosaur communities from Far Eastern Russia are a prime example to study the biology of late surviving lambeosaurine hadrosaurs. The bonebeds from which these taxa were excavated show a high species diversity and a high abundance of various skeletal elements, most notably long bones. We sampled long bones from different size classes of the lambeosaurines *Olorotitan* and *Amurosaurus*. Both taxa show highly vascularized cortical bone consisting mainly of a woven-parallel fibered complex with plexiform to laminar vascularization, indicative of high growth rates. Only few lines of arrested growth (LAG) could be observed in even the biggest specimens (femur length ~1 m). It remains unclear if this indicates an uninterrupted juvenile growth phase, or if mass increase was extremely high in the first years, but the high average growth rate is in accordance with high growth rates reported for North American hadrosaurs (e.g. *Maiasaura*). We also sampled the tibia of a large tyrannosaurid theropod (corresponding femur length ~ 0.92 m) which was recovered from the same layers as *Olorotitan*, however, its growth is in sharp contrast with that of the hadrosaurs. The thin section taken from the shaft of the proximal tibia shows a woven-parallel fibered complex with plexiform to laminar vascularization, however, it also shows numerous (>15) LAGs, indicating a much slower average growth and higher chance of survivorship than for hadrosaurs. These data add to a more global perspective on diversity and ecology of Latest Cretaceous dinosaur faunas.

Symposium — Evolution, development, and integration of the vertebrate brain and skull (BSI)

Organizers: Gabe Bever, Bhart-Anjan Bhullar, Marcelo Sánchez-Villagra

BSI1-1 2:30 pm

Evolution, development, and integration of the vertebrate brain and skull: Frontiers in neuroscience and paleontology.

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Abstract: Comparative neuroscience faces many formidable, yet exciting, challenges. The chordate brain began its remarkable evolutionary history well over 500 million years ago when changes in an increasingly complex and genetically controlled developmental network produced an anterior expansion of the deuterostome dorsal hollow nerve cord. Considering the depth of this history, it is no surprise that we continue to struggle with the structural identity and transformational history of both the brain's component features and the molecular networks that regulate these features during development. The antiquity of the brain exceeds even that of the surrounding cranial skeleton, establishing a temporal relationship paralleled in chordate ontogeny. The brain emerges during late neurulation and then likely serves an under-appreciated developmental role as an early signaling center and organizer of head mesenchyme-directing cells that contribute to a wide diversity of adult cranial structures, including the skull. The developmental and evolutionary influence of the brain on other cranial modules is an area of research just getting underway but one that possesses considerable explanatory potential. I will establish a context for the symposium by using the major chordate crown clades as a framework for reviewing phylogenetic transformations in the morphology and development of the brain. I will also discuss the logical framework for integrating the large amounts of molecular, histological, and functional data flowing from more traditional neuroscience labs with the deep-time perspective afforded by fossil endocasts. Endocasts break up long evolutionary branches, serve as natural experiments for relationships in morphospace, and provide the only access to the early evolution of features along their stem of origin.

These early histories often differ markedly from those expressed in the nearest crown clade, thus supplying insight into the changing variability of regulatory networks.

BS11-2 2:45 pm

Deep deuterostome origins of vertebrate brain regulatory programs.

Lowe C.J., *Stanford University*; Minor P.J., *University of Pennsylvania*; Yao Y., *Stanford University*; Pani A.M., *University of Chicago*; Epstein D.J. *

Abstract: Much of what we understand about the origins of the vertebrate brain has come from comparative studies within chordates. Invertebrate chordates, particularly cephalochordates, have played pivotal roles in providing key insights. It has generally been assumed that few insights are to be gained from broader comparisons with the other deuterostome phyla; hemichordates and echinoderms, as their body plans contrast so markedly with that of chordates. However, we have demonstrated in hemichordates that despite the marked difference in the overt morphological organization of their nervous systems, they share exquisite conservation of gene regulatory networks, previously considered to be stem vertebrate innovations. We have focused on ectodermal signaling centers that are characterized by the localized secretion of morphogens, and are key in the early regionalization of the brain. The Zona Limitans Intrathalamica (ZLI) patterns the thalamus and prethalamus in vertebrate brains. We have demonstrated by transient transgenic experiments that the temporal and spatial activation of the ligand that defines the ZLI, *Shh*, is regulated in hemichordates and vertebrates by a conserved cis-regulatory module. Reciprocal enhancer swap experiments demonstrate the ability of the hemichordate enhancer to drive reporter expression in a pattern similar to the native vertebrate enhancer and vice versa. I discuss the implications of these findings for understanding the early origins of the vertebrate brain, and how morphological and gene regulatory network evolution can become uncoupled over macroevolutionary time frames.

BS11-3 3:15 pm

Geometric changes in brain and skull, and the integration and interdependence of cranial modules.

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Abstract: The skull is the most distinguishing feature of the vertebrate skeleton. Its building blocks are multiple bones with different embryonic origins, yet it is the particular 3D spatial arrangement of the latter what renders identity, functionality and evolvability to the entire system. Classically, the skull is divisible in two inclusive domains, the cranium and the face, the former cradling the brain, and the latter housing the sensory organs. While such parts must be integrated with one another, because they develop, function and evolve jointly, the fact that each skull part serves for different functions lends the rationale that they must evolve semi-independently, as modules. Multiple investigations are beginning to clarify the molecular genetics involved in facial organization, and on the epigenetic influence of the brain upon the organization of the craniofacial system. However, new comparative studies in birds using geometric morphometrics are bringing alternative ideas which add new lines of enquiry to this agenda. For instance, congruent with recent neuroscientists claims, studies have shown that avian brain evolution is modular, entailing that we don't know how does skull morphology respond to this complex source of variation. Whereas the avian beak is tacitly seen as an evolutionary module, recent shape data suggests that craniofacial integration among unrelated clades of birds is much higher than expected (i.e., the facial skeleton and the braincase are not modules). This not only substantiates previous theoretical claims that the correspondence between functional and morphological modules is not straightforward, but also that patterns of skull modularity might be case-specific. Although comparative studies are limited approaches to determine the developmental processes underlying these patterns, they remain a unique heuristic tool to gain key insights and hypothesize which aspects of integration could be examined at the developmental level.

BS11-4 3:30 pm

Evolution and development of the head in agnathans and fishes.

Kuratani S*, *RIKEN*; Sugahara F, *RIKEN*; Ota K, *Academia Sinica*, *Yilan Marine Station*; Oisi Y, *Max Planck Florida Institute for Neuroscience* saizo@cdb.riken.jp

Abstract: Living cyclostomes consist of hagfish and lamprey, and the monophyly of this group is established by molecular analyses. Comparative morphology of these two cyclostomes, however, has contradicted the monophyly, especially for the embryonic craniofacial pattern of hagfishes: the hagfish adenohipophysis and related structures were suggested to arise from endoderm, unlike that of other vertebrates derived from the ectoderm. Thus, reexamination of hagfish embryology is critical to evaluate the anatomical traits of cyclostomes. By observing staged hagfish embryos, we show that the hagfish adenohipophysis arises ectodermally, as a posterior part of the medial placode, the hypophyseal plate, as in the lamprey larva. This finding allowed us to identify a craniofacial developmental pattern common to cyclostomes, but not to crown gnathostomes. From this cyclostome-specific developmental stage, lamprey and hagfish develop into distinct developmental trajectories, making it difficult to establish morphological homologies in adult anatomy of these animals. We also show that the comparison with gnathostomes, the out group of cyclostomes, implies that many of the hagfish peculiarities can be recognized as hagfish-specific derived traits (autoapomorphies). Thus the lamprey is likely to represent more ancestral state of cyclostomes, possibly reflecting the morphological and developmental pattern of the latest common ancestor of entire

vertebrates. Based on the above developmental scheme, we first showed homologies of skeletal elements between lamprey and hagfish chondrocrania.

BSI2-1 4:30 pm

Stability and flux in relationships between cranial bones and endocranial structures – paleontology and molecular development.

Bhullar B.-A.S*, Yale University bhart-anjan.bhullar@yale.edu

Abstract: There is a general conception that the architecture of the vertebrate cranial roof relates closely to, and perhaps is patterned by, the underlying brain. However, the degree to which there are consistent relationships between brain components and skull components throughout ontogeny, and the nature of the developmental association between the brain and calvarium, have seldom been rigorously explored. Current work in my lab suggests that early ontogenetic relationships between brain and cranial elements are remarkably conserved. This is the case, for instance, throughout the evolution of Reptilia. To a certain extent, relations hold true even in the adult, but there is a considerable amount of decoupling between brain regions and the skull during ontogeny, even as the growing skull compensates for the underlying brain. This suggests coordinated early patterning but an eventual loss of region-specific molecular feedback. Previous work on the development of the brain and calvarium was made difficult by the fact that mouse mutants with very small or very large brains tend to have an unossified cranial roof; but some preliminary data of ours indicate that the skull roof does indeed compensate for changes in brain proportions depending on timing and degree.

BSI2-2 4:45 pm

The heads of the earliest fossil vertebrates: evolution, development and diversity.

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Abstract: Early fossil vertebrates from the Ordovician to Devonian periods illuminate the evolution not only of the jawed vertebrate morphotype, but also of the developmental processes that underlie it. Numerous aspects of head anatomy and early development, conserved between extant cyclostomes and gnathostomes (notably the spatial relationship between pharyngeal slits, cranial nerves and neural crest streams), create a comparative framework for interpreting the anatomical landmarks of fossils. At the same time some early vertebrate morphologies lie well outside the range of extant gnathostomes and cyclostomes, providing invaluable information about evolution and diversity within the gnathostome stem group. All jawless stem gnathostomes ("ostracoderms") lack a discrete shoulder girdle; scapulocoracoids, if present, attach directly to the cranial endoskeleton. Unlike jawed vertebrates, the dermal bone pattern of ostracoderms does not reflect pharyngeal arch architecture. Head-shoulder separation and pharyngeal patterning of the dermal skeleton seem to have evolved simultaneously and may have a shared developmental basis. Different ostracoderm groups show three distinct relationships between pharynx and brain. In heterostracans and galeaspidids it is similar to the gnathostome condition, with two pharyngeal pouches anterior to the inner ear; in osteostracans the adult pharynx is strongly displaced anteriorly, a unique condition that contradicts the traditional view of osteostracans as fundamentally lamprey-like; in anaspids the adult pharynx is displaced posteriorly, like in extant cyclostomes, and a rasping tongue may have been present. The most primitive jawed vertebrates such as *Brindabellaspis* and *Romundina* are not similar to osteostracans, as has been claimed, but do resemble galeaspidids such as *Shuyu*. Shared specializations of anaspids and cyclostomes suggest that anaspids may be stem cyclostomes, not stem gnathostomes as generally believed.

BSI2-3 5:15 pm

The dinosaur and bird brain: evolution, ontogeny, and function.

Balanoff Amy M.*, Stony Brook University amy.balanoff@stonybrook.edu

Abstract: With almost 10,000 extant species, birds are one of the most diverse groups of modern vertebrates. Much of their success can be traced to the evolution of a hyper-inflated brain, which is larger than that of any other living reptiles and on par with that of most mammals. The expansion of the bird brain, especially the pallial regions of the cerebrum, has long been considered necessary for their increased cognitive faculties as well as their ability to coordinate the visual, vestibular, somatosensory, and motor components of powered flight. The relationship between the origin of avian flight within non-avian dinosaurs and encephalization, however, has proved to be more complex than previously appreciated, with at least one, and possibly numerous, volumetric increases in brain size occurring well before the evolution of powered flight. It would follow that this region of the avian stem lineage is witness not only to complex volumetric patterns but also to major structural rearrangements of the brain. Such changes, however, can be difficult to assess in the fossil record because the endocasts, on which we must rely for these data, have not traditionally been used explicitly to infer internal morphological structure. In order to more effectively integrate neuroanatomical and fossil endocast data, we need a better understanding of the relationship between the three-dimensional nature of various brain components and the two-dimensional surficial expression of those components as found on an endocast. I will explore these relationships for birds and demonstrate how, once established, these data can serve as a bridge between *in vivo* functional data and the deep history of character transformation along the avian stem that will afford us a better understanding of the avian brain, skull, and overall body plan.

BSI2-4 5:30 pm

On the interparietal and supraoccipital: the development of the mammalian skull roof and its coevolution with the brain.

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Abstract: It is known that the brain was expanded during the rise of mammals. Here I highlight the developmental changes which occurred in the skull roof concomitantly with such mammalian encephalization, i.e. changes in ossification and suture closure timing. Sequence of cranial skeletogenesis of 102 mammalian species was investigated and compared to those of non-mammalian amniotes. The developmental timing of the supraoccipital was found to be earlier on an average in mammals than in other amniotes. Squared-change parsimony analysis detected that the timing of the supraoccipital development became considerably accelerated in ancestral mammals and was further accelerated in multiple lineages as primatomorphans, cetaceans, talpids, and dipodid rodents, all of which are known as encephalized. Its relative ossification timing was confirmed to be negatively correlated with encephalization quotient. It was further found that the interparietal, which lays rostral to the supraoccipital, is present in all extant mammalian orders, although it was previously regarded as being lost in various taxa. The fact is that the interparietal is visible during fetal period but later often fuses to the supraoccipital and becomes indistinguishable. The tabulars, which have been thought to be lost in mammals, were also found during fetal period. They constitute the lateral parts of the interparietal, indicating that the so called mammalian "interparietal" is a complex of tabulars and postparietals of other amniotes. The timing of the fusion between the supraoccipital and "interparietal" occurs earlier in larger-brained species. Given this, we infer that the earlier fusion of the tabular and postparietal found in mammals could also be linked to brain size. I suggest that encephalization occurred in concert with earlier ossification and more fusion of the postparietal, tabular, and supraoccipital and point out the possible role of pleiotropic effects of *Lmx1b* and *Dlx5* behind this coevolution.

BSI2-5 5:45 pm

Developing humanized mouse models to study human evolution.

Dutrow EV*, Kavli Institute for Neuroscience, Yale School of Medicine; Reilly SK, Broad Institute of MIT and Harvard; Noonan JP, Kavli Institute for Neuroscience, Yale School of Medicine emily.dutrow@yale.edu

Abstract: We hypothesize that changes in morphology during human evolution required genetic changes in key developmental regulatory functions. Here, we focus on developmental enhancers marked both by human-specific histone modification gains and an accumulation of sequence changes that may account for these acquired epigenetic signatures. The aim of this study is to functionalize candidate human-gained enhancers involved in the development of major human-specific morphological features: an elaborate cerebral cortex and highly specialized limbs. In this study, we systematically target and edit up to 5.5kb regions of the mouse genome using CRISPR/cas9-mediated replacement in order to successfully produce two humanized mouse models. We are carrying out both molecular and tissue-level functional analysis of brain and limb development in these humanized mouse lines to identify phenotypic correlates of human biological traits. This work was supported by NIH GM094780 and T32 GM007499.

Symposium — Major challenges for vertebrate morphology, evolution and development (CHA)

Organizers: Julio Mario Hoyos, Rui Diogo

CHA1-1 2:30 pm

An historical introduction to the major challenges in vertebrate morphology.

Hoyos JM *, Departamento de Biología, Pontificia Universidad Javeriana jmhoyos@javeriana.edu.co

Abstract: "The best way to claim the value of the morphology is based on its history, where you can view its objectives, its applications and its projections" (Nyhart, 1994). This phrase is the basis of the presentation of the great challenges of the morphology for the coming years, taking into account, above all, the courage to recognize the morphology as a research program (or orientation, according Nyhart) from its "foundation" as such by J W Goethe. My inspiration to propose these challenges was David Gilbert (1862-1943), a German mathematician who proposed a list of 23 unsolved problems in the International Congress of Mathematicians in Paris in 1900, many of which have yet to be fully resolved or remain without any response. From the discussion of concepts such as the Platonic archetype by Kant and Owen in the eighteenth and nineteenth centuries, there have been throughout the history different challenges from the moment that the morphology became independent of physiology, back at the beginning of the 19th century in Germany. We should focus on some of those who have been appearing and have demonstrated that require our attention, without neglecting, of course, other related activities to feed these challenges. Some that have identified are: 1. General challenges: studies of structures and processes; developmental biology and evolution of vertebrates; how to use ontogenetic characters in systematic; multiple appearances or just synapomorphies. 2. Specific Challenges: sequential heterochronies of the development based on organs and systems; limb development in vertebrates; the evolution of the jaw in vertebrates; ultrastructures. 3. Languages: building ontologies. 4. Techniques: 4D morphology; clearing viscera (CLARITY); anatomical networks. These different challenges show that we should consider the study of vertebrates from the point of view of an Integrative Morphology.

CHA1-2 3:00 pm

Major challenges in vertebrate morphology, macroevolution, variation and human birth defects.

Esteve-Altava B*, Royal Veterinary College & Howard University; Molnar J, Howard University; Diogo R, Howard University boresal@gmail.com

Abstract: Together with other colleagues, we are creating a new field of science: Evolutionary Developmental Pathological Anthropology. The main goal of this new field is to bring together anatomy, human evolution, development, genetics, birth defects and medicine, by using both non-human model organisms and studies of humans with birth defects or anatomical variations to address these issues. The combination of these fields and, importantly, the inclusion of both hard- and soft-tissue-based information and of new, state-of-the-art methods such as anatomical network analyses, allow us to address evolutionary and developmental questions that are not tractable using other types of studies and methodologies. Here we provide a few examples to illustrate the main aims and potential of this new field, focusing on: 1) notions of purpose and progress in macroevolution and the parallelism between ontogeny and phylogeny; 2) the relationship between trisomies, 'atavisms', evolutionary reversions, developmental constraints and internalism vs externalism; 3) the variations and anomalies in the musculoskeletal system of modern humans and their evolutionary, developmental and medical implications; and 4) discussions on the relationships between modularity, integration, complexity and evolvability using data recently obtained from anatomical networks studies.

CHA1-3 3:30 pm

Major challenges in vertebrate morphology and developmental biology: links with human evolution and pathology, including relations between heart and head muscle development.

Kelly R. G., Aix Marseille University; Diogo R. *, Howard University ru.i.diogo@Howard.edu

Abstract: Here we introduce a new field of biology: Evolutionary Developmental Pathology and Anthropology (Evo-Devo-P'Anth), which combines experimental and developmental studies of non-human model organisms, biological anthropology, chordate comparative anatomy and evolution, and the study of normal and pathological development in humans. As a key case study, we refer to recent studies revealing a strong link between vertebrate heart and head muscle development in the early embryo. Evolutionarily conserved cardiopharyngeal mesoderm (CPM), associated with the developing foregut or pharynx, has recently been shown to contain common heart and head muscle progenitor cells. Addition of CPM drives elongation of the embryonic heart tube, giving rise to myocardium at the cardiac poles. CPM also gives rise to branchiomic craniofacial skeletal muscles that activate myogenesis through different upstream regulatory programs to somite-derived muscles. Within CPM, clonally distinct subpopulations have been shown to contribute to specific parts of the heart and subsets of branchiomic muscles, such as right ventricular myocardium and first arch-derived muscles of mastication or outflow tract myocardium and second arch-derived muscles of facial expression. Perturbation of the cardiopharyngeal developmental field results in a spectrum of cardiac and craniofacial congenital anomalies, typified by DiGeorge or 22q11.2 deletion syndrome. Esophageal, trapezius and sternocleidomastoid muscles have been identified as TBX1-dependent branchiomic muscles.

CHA1-4 3:45 pm

Major challenges in vertebrate morphology and theoretical biology: networks, macroevolution, and human birth defects.

Rasskin-Gutman D*, University of Valencia; Sánchez García JM, University of Valencia; Esteve-Altava B, The Royal Veterinary College; Navarro Díaz A, University of Valencia; Rasskin I, University of Montpellier; Diogo R, Howard University diego.rasskin@uv.es

Abstract: Looking at macroevolutionary challenges with a Theoretical Biology lens offers different perspectives that can reveal unexpected ideas about old morphological problems. In our recent work using Anatomical Network Analysis, we have found that three seemingly unrelated observations might provide clues for a theory of morphological change at large scales: (1) the relation between connectivity among bones in the skull and bone shape; (2) the net reduction of number of bones in all evolutionary lineages; and (3) the craniofacial consequences of early bone fusion in humans. The number of elements composing the skull has been declining in each of the major lineages of tetrapods. This macroevolutionary trend (Williston's Law) involves two morphogenetic mechanisms: the disappearance and the fusion of skull bones. The fusion of bones is critical during development and, if carried out at the wrong time, can cause morphological alterations called synostosis. These synostoses of the skull (craniosynostosis) occur in all vertebrate groups, and have been thoroughly studied in humans, since, while most do not cause major changes, some types can cause severe morphological alterations. While the medical literature has extensively studied the relationship between synostosis and craniofacial shape alterations, there is still a knowledge gap about the evolutionary significance of adjacent bone fusion and form change. This concurrence of processes and patterns provides a unique opportunity to analyze a dynamical evolutionary phenomenon in relation to a clear morphogenetic mechanism: the formation, maintenance and closure of the cranial sutures. If the relationship between synostoses and morphological change proves to be sound, we expect to be able to render an evolutionary model able to predict bone shape change as caused by the fusion of adjacent bones. Such a model should be able to reconstruct as well as to predict form changes associated with bone fusion.

CHA2-1 4:30 pm

Major challenges in vertebrate morphology, ecology and biophysics: Hummingbirds as a case study.

Rico-Guevara A*, University of Connecticut a.rico@uconn.edu

Abstract: A central challenge of biology is to describe the links among structures (e.g. organismal morphology), underlying biophysical mechanisms, and emergent phenomena (e.g. performance, ecological and evolutionary patterns) in live organisms. Because morphology varies among individuals, performance and the adaptive value of behaviors vary accordingly. Hence, a complete understanding of the evolutionary and ecological implications of phenotypical variability, the fuel of natural selection, requires us to quantify the causal link between variation in traits and the performance capabilities of their possessors. A major challenge in the study of vertebrate morphology is to explicitly link biomechanics to ecological determinants of species interactions at several levels. To tackle this challenge, I will show how I use hummingbirds as a study model to bridge the gap between our knowledge of coevolutionary and pollination patterns, and underlying foraging behavior and feeding apparatus morphology. I employ the induction-deduction method to gain a complete understanding of how the physics of nectar feeding mechanisms in hummingbirds shape their ecology and evolution. The last challenge I will address corresponds to the necessity to take advantage of multidisciplinary approaches and cutting-edge technology in the study of functional morphology. I propose mechanistic explanations based on electron microscopy, microCT scans, high-speed videos, and experiments under controlled conditions, that we use to develop biophysical models of each step of the feeding process. Then, we test the model predictions using data from birds feeding at wild flowers collected through customized camera traps. I will present how we can establish the way in which the biophysics of the tongue-nectar interaction, and thus the mechanics of the entire drinking process, creates boundary conditions for the energetics of feeding on flowers, and thereby the ecological and co-evolutionary patterns in hummingbirds.

CHA2-2 4:45 pm

Major challenges in vertebrate morphology: 2D, 3D, and 4D visualization and network tools applied to study the origin and evolution of tetrapod limbs.

Molnar JL*, Howard University; Esteve-Altava B, Royal Veterinary College & Howard University; Johnston PS, University of Auckland; Diogo R, Howard University julia.molnar@howard.edu

Abstract: Innovations in imaging and computing are making great contributions to vertebrate morphology. Complex virtual models allow us to estimate physiological properties that are difficult to measure experimentally and compare vast amounts of data among species. Meanwhile, technologies such as micro-computed tomography, magnetic resonance imaging (MRI), iodine staining, and 3D printing give us new and more detailed anatomical information about both extant and extinct animals, and they make it possible for researchers to share rare specimens with colleagues across the globe. In our lab, we are applying some of these techniques, in combination with traditional anatomical methods and molecular data, to make progress on the puzzle of how musculoskeletal anatomy and function changed over the transition from fish fins to tetrapod limbs. The origin of tetrapods has been the subject of intense debate for more than a century, but little is known about the soft tissue anatomy or locomotion of the first terrestrial vertebrates. We used MRI scans of lungfish and coelacanths, the closest living relatives of tetrapods, to identify homologous appendicular muscles among the two lobe-finned fish and salamanders. Then, we used anatomical networks to quantify topological organization within the appendages of each animal. Finally, we built 3D biomechanical models to compare the leverage of various muscle groups over the step cycle. These methods allow us for the first time to compare functionally important parameters across morphologically disparate species. In the future, we plan to use similar methods in conjunction with fossil specimens to reconstruct and analyze changes in limb muscle anatomy and function in early tetrapods and their close relatives. This case study illustrates how 2D, 3D, and 4D visualization and network tools can provide new ways to approach old problems in vertebrate morphology.

CHA2-3 5:00 pm

Major challenges in vertebrate morphology, muscle evolution and evolutionary change via heterochrony.

Ziermann Janine*, Howard University College of Medicine; Diogo Rui, Howard University College of Medicine jziermann@yahoo.de

Abstract: Evolutionary developmental biology (Evo-Devo) aims to unravel changes in development or developmental mechanism that led to evolutionary change. In other words, which developmental modifications and processes led to morphological changes and/or to novel features of species? By comparing developmental processes between different organisms the developmental basis of homoplasy and homology, as well as changes in developmental timing, i.e. heterochrony, might be revealed. In recent years Evo-Devo studies tended to address the more developmental part of Evo-Devo focusing mainly on genetic/molecular analysis. This led to a shift of attention towards the genomic basis for developmental processes instead of addressing older and/or broader evolutionary concepts and theories. One striking example for the application of Evo-Devo studies to analyze evolutionary theories comes from our myological studies of muscle development and morphology in the head, neck, heart, and pectoral and pelvic appendages in vertebrates. The comparison of developmental patterns of cephalic muscles revealed general developmental gradients that seem to be conserved throughout vertebrates (e.g. an anterior to posterior gradient during the differentiation). Furthermore, amphibians and bony fishes, show a parallel in phylogeny and ontogeny of cephalic muscles. However, those large scale comparative studies reveal also heterochronies that might be

responsible for species specific morphologies. Including the analysis of development in species without a cranium, e.g. the Cephalochordate *Amphioxus*, and with only cartilaginous craniums, e.g. sharks, unravels the early evolution and origin of cephalic muscles in vertebrates. Finally, we can include ourselves, *Homo sapiens*, a species seen by many as highly neotenic for some features, in Evo-Devo studies in order to understand the importance of heterochrony, the links between phylogeny and ontogeny, birth defects, and other broader evolutionary topics.

CHA2-4 5:15 pm

Major challenges in vertebrate morphology: bridging the gap between genotypes and musculo-skeletal phenotypes in primates using functional genomics and developmental genetics.

Capellini TD*, Harvard University; Dingwall H, Harvard University; Willen J, Harvard University; Wohls A, Harvard University tcapellini@fas.harvard.edu

Abstract: Primates exhibit remarkable diversity in musculo-skeletal morphology, much of which is apparent in skeletal appendages that interact with substrates during locomotion and positional behavior. Differences in the lengths, shapes, and proportions of the major long bones of the forelimb (scapula/humerus/radius/ulna) and hindlimb (pelvis/femur/tibia/fibula) reflect the myriad of skeletal adaptations primates have evolved to occupy diverse ecological niches. This diversity is not only observable at the level of the entire appendage or individual limb segment, but at specific functional zones, such as growth plates, joints, and muscle-attachment sites. From an evolutionary perspective, this striking morphological diversity reflects the actions of natural selection on variation in pre- and postnatal developmental processes. Yet despite many decades of research relatively little is known about the molecular mechanisms that control the specific shapes of bones, let alone how modifications to pre- and postnatal developmental programs influence the morphological variation within and between species. We use a modern synthetic approach, one that integrates experimental findings from developmental biology, genetics, functional genomics, and bioinformatics to improve the connections between genotype to phenotype and reveal the causative mutations that underlie adaptive morphological evolution. Given the complex relationship between genotypes and phenotypes, we explore how to identify functionally important loci and gauge how much variation they control, how to sift through the numerous genetic variants within an identified locus to find the variants responsible for species-specific phenotypes, and how to functionally test these sequences to reveal molecular mechanism and their impacts on development. We address these challenges in the context of comparative appendage skeletal development, genetics, and evolution in primates.

CHA2-5 5:30 pm

Biomechanics as part of the evo-devo-morphology synthesis, and the challenges of including fossil taxa.

Hutchinson John*, The Royal Veterinary College, Univ. London jrhutch@rvc.ac.uk

Abstract: A relatively complete characterization of a major evolutionary transformation would integrate data from microscopic and macroscopic morphological levels across ontogeny (including genetic and environmental influences) with biomechanical analyses of function, performance and behaviour across phylogeny, and thence on to evaluations of potential links to fitness and thereby adaptation. This of course is no simple task, but here I explain, using examples from my team's research, how biomechanical data in particular can add value to the "evo-devo synthesis" by making function part of that synthesis, moving closer to inferences about natural selection and other evolutionary processes by demonstrating rather than assuming how form, function and behaviour are linked. A principal challenge in such a synthesis is to reconstruct how intermediate (or uniquely derived) morphologies in extinct taxa functioned. In this challenge, science needs to escape from constraints on identifying function, such as relying solely on studies of extant descendants of those major evolutionary transformations, crude analogues of ancestral form and function, or 'functional traits' (e.g. body mass, limb lengths) that may be correlated with actual function but often simply are reiterations of morphology. Computer modelling and simulation offer one solution to this challenge, but themselves recursively depend on studies of living animals to refine and test them in order to maximize confidence in their application to extinct taxa. However, I paint an optimistic picture of how these multi-pronged avenues of research could be advanced, by finding and exploiting synergy and common ground between them, to gradually build a more robust synthesis of the evolution of the morphological and developmental bases underlying the greatest transitions in organismal history. I focus on examples from our research on dinosaurs, early tetrapods and sesamoid bones but the concepts are transferrable to any clade of life.

Symposium — Diffusible iodine-based contrast-enhanced computed tomography (diceCT) and related imaging techniques for evolutionary morphology (DCT)

Organizers: Paul Gignac, Nele Herdina, Nathan Kley, Ashley Morhardt, Julia Clarke, Matthew Colbert

DCT1-1 9:30 am

DiceCTing the future: new horizons for 3-D visualization of vertebrate morphology.

Gignac PM*, Oklahoma State University Center for Health Sciences; Herdina AN, Karolinska Institutet; Kley NJ, Stony Brook University; Morhardt AC, Ohio University; Colbert MW, The University of Texas at Austin; Clarke JA, The University of Texas at Austin paul.gignac@okstate.edu

Abstract: The ability to rapidly discriminate soft tissues in three dimensions using X-ray computed tomography (CT)

has been difficult to realize fully, because of similarities in X-ray attenuation properties among non-mineralized structures. However, recent pioneering work in this area has demonstrated that radiodense contrast agents, such as Lugol's iodine (I₂KI), can be highly effective for differentiating many types of soft tissues using CT. Over the last several years, a handful of morphologists the world over have become a driving force in advancing such diffusible iodine-based contrast-enhanced CT (diceCT) imaging and utilizing the remarkable data it generates to reconstruct soft-tissue phenotypes and functional anatomy in three and four dimensions. For the 11th International Congress of Vertebrate Morphology, we have assembled a cadre of well-established researchers and emerging early-career scientists to: (1) highlight recent advances in diceCT imaging, (2) discuss the integration of soft-tissue visualization into existing research toolkits, and (3) lay out the future directions for contrast enhancement in the study of vertebrate soft tissues. In the introduction to our symposium, we provide a critical review of recent contributions to this emerging field and help make sense of its now complex landscape of methodologies. We also report on new initiatives aimed at formally convening the diceCT community for regular exchanges of ideas, methodological advances, and novel research applications. These include published recommendations for best practices, a techniques workshop to help beginners overcome methodological hurdles, and a digital hub to connect researchers (www.diceCT.com). We aim to grow our community further by spurring the more widespread adoption of these methods and facilitating conversations and collaborations among labs already exploring this powerful new tool with those considering how to apply it to their own research questions for the first time.

DCT1-2 10:00 am

Using the STABILITY protocol prior to IKI staining to provide the first accurate, in situ quantification of mammalian brain proportion scaling using marsupials.

Weisbecker V*, School of Biological Sciences, University of Queensland; Carlisle A, School of Biological Sciences, University of Queensland; Hinds L, CSIRO Health and Biosecurity Flagship; Selwood L, University of Melbourne; Whish Sophie, University of Melbourne v.weisbecker@uq.edu.au

Abstract: Iodine-based staining of soft tissue is rapidly gaining popularity in a wide range of applications such as biomedicine, comparative anatomy, and palaeontology. One major downside of this technique is the fact that iodine solution (IKI) stained soft-tissue shrinks substantially and differentially, so that accurate volumetric measurements are not possible. Here we present data on our work on marsupial brain tissue using the STABILITY technique, in which the specimen is hybridized with a hydrogel before IKI staining. The technique worked easily, particularly after we replaced the pre-incubation step of replacing air with nitrogen through a vacuum pump with the simpler protocol of pouring a layer of oil over the hydrogel mixture prior to incubation. Shrinkage in untreated brain tissue stained with 1.75% IKI averaged 35%, whereas in hydrogel-treated specimens shrinkage averaged 11%. Staining took longer in hydrogel-treated specimens, but the contrast was the same. Using STABILITY, we were able to provide the first developmental series of in-situ brain growth in three marsupial species (*Macropus eugenii*, *Trichosurus vulpecula*, and *Monodelphis domestica*), using Mimics as our segmentation software. The volumetric growth of different brain parts (neocortex, hippocampus, cerebellum, and medulla) contradict several hypotheses of brain partition evolution, including that brain partition development in mammals has a uniform slope and intercept, displays the same allometry of adult mammalian brain partition scaling, and contains no phylogenetic signal. We conclude that the STABILITY protocol currently represents a powerful avenue of gaining volumetrically accurate soft-tissue reconstruction, while preserving a near-histological level of resolution on soft-tissue anatomy. This research was supported by Australian Research Council DECRA DE120102034

DCT1-3 10:15 am

Mind the gap: ontogenetic shape differences between brains and endocasts in archosaurs.

Watanabe A*, American Museum of Natural History; Gignac PM, Oklahoma State University Center for Health Sciences; Norell MA, American Museum of Natural History awatanabe@amnh.org

Abstract: The braincase is a crucial osteological correlate for neuroanatomy and an indispensable resource for inferring the brain morphology of extinct vertebrates. As an internal mold of this space, endocasts provide size and shape approximations, allowing the exploration of neurological structures, capacities, and evolution. Nevertheless, the validity of such investigations pivots on the accuracy of these estimations. In mammals and birds, volumetric studies have shown that endocasts closely reflect the size of actual brains, which occupy nearly the entire braincase. Although size is an important metric, volumetric measurements are limited in their characterization of morphology and may obscure localized morphological biases. Here we test shape differences between endocasts and brains reconstructed from computed-tomography imaging of model archosaurs—the American alligator and the chicken. Using a dense ontogenetic sampling of each taxon, we evaluated whether endocast-brain shape discrepancies (1) exist, (2) change through ontogeny, and (3) are greater than intra- and interspecific variation in brain shape. Alarmingly, the results show that endocasts are significantly distinct from brains in shape due to lack of furrows, relative mediolateral reduction in the cerebrum, and less dorsoventral flexion in both the cerebellum and medulla. In both taxa, these discrepancies generally decrease through ontogeny. However, the endocast-brain difference is still greater than shape differences charted across all of ontogeny. Moreover, even with a broad taxonomic sampling, we find that endocranial shapes are collectively shifted to a more "juvenilized" morphology relative to brain shape. Researchers should be aware, therefore, that endocasts contain critical systematic biases in their characterization of

brain morphology and that these artifacts may substantially impact the results of comparative neuroanatomical study.

DCT1-4 10:30 am

Incorporating diceCT into multi-scale structural studies of the brain for highly divergent lineages of acrodont lizards: validation of preservation methods conducted in the field.

Hughes DF*, University of Texas at El Paso; Walker EM, University of Texas at El Paso; Gignac PM, Oklahoma State University Center for Health Sciences; Khan AM, University of Texas at El Paso dfhughes@miners.utep.edu

Abstract: Biodiversity hotspots, which harbor more endemic species than elsewhere on Earth, are increasingly threatened. There is a need to accelerate collection efforts in these regions before poorly understood or undocumented species become extinct. However, traditional specimen preparations do not permit researchers to retrieve neuroanatomical data at high resolution. We field-tested two traditional laboratory-based techniques for brain preservation (transcardial perfusion and immersion fixation) while collecting specimens of Agamidae and Chamaeleonidae in the Eastern Afromontane biodiversity hotspot of Central Africa. Field- and laboratory-perfused brain samples were compared for tissue cytoarchitecture and chemoarchitecture using Nissl-based staining and fluorescence immunocytochemistry, respectively. We found that transcardial perfusion fixation and long-term storage, conducted under remote field conditions without access to cold storage, had no observable impact on cytoarchitectural integrity or stain evenness. Further, immunostaining for small neurotransmitter and neuropeptide biomarkers was similar between our comparisons. With respect to immersion-fixation methods, field-preserved chameleon brains were readily compatible with subsequent diffusible iodine-based contrast-enhanced computed tomography (diceCT) imaging, which facilitated the non-destructive imaging of the intact brain within the skull. In particular, diceCT images revealed excellent contrast of brain tissue structures, including myelinated and unmyelinated portions of the brain. When paired with cytoarchitectural and immunocytochemical techniques, the use of diceCT allows for the neuroanatomical study of poorly known and often inaccessible species across micro- to macroscopic scales of analysis. Our protocol serves as a malleable framework intended for future researchers attempting to rescue irreplaceable neuroanatomical information from disappearing regions.

DCT1-5 10:45 am

Applying diceCT to PET: new tools for correlating morphology to function in living animals.

Gold MEL*, Stony Brook University; Schulz D, Yeditepe University; Budassi M, Stony Brook University; Gignac PM, Oklahoma State University Center for Health Sciences; Vaska P, Stony Brook University; Norell MA, American Museum of Natural History mariaeugenia.gold@stonybrook.edu

Abstract: The evolution of flight-related features in theropod dinosaurs is iconic and well documented in the fossil record. Although much of the morphological adaptations for flight precedes crown-group birds in non-avian dinosaurs, the precise origin of powered flight has eluded paleontologists because of the difficulty in directly linking morphology to flight capacity. Recently, endocranial data have demonstrated that a highly encephalized brain evolved in non-avian theropods, but whether these neuroanatomical changes reflect behavioral transformations is untested. To explore brain function during locomotion we used positron emission tomography (PET) scanning to record brain activity in flying starlings. Diffusible iodine-based contrast-enhanced computed tomography (diceCT) scans of an intact starling head provided the pivotal neuroanatomical detail used to identify which nuclei of the brain were activated during flight. By overlaying PET data onto diceCT scans, we identified the active brain regions as the entopallium and anterior Wulst, which are involved in visual processing and somatosensory integration. These results imply that the visual and somatosensory processing systems mainly used for flight are completely separate from the optic tectum—a structure thought to be in control of all visual processing in avians. The entopallia and anterior Wulst may work together to create a short-term conflict avoidance system to bridge fast approaching visual input to locomotor controls, allowing for rapid interpretation of the flightscape. Expansion of the Wulst through increased use during volancy may have driven the dorsal expansion of this structure along theropod evolution. Combined with fossil data, these findings point towards the evolution of volant behaviors at Avialae, with the appearance of the Wulst. Brain activation maps in starlings represent a first step in a new aspect of paleontology, bridging the gap between fossil morphology and living behaviors.

DCT2-1 11:30 am

Musculoskeletal modelling and simulations of the mouse hindlimb during locomotion: the role of high-resolution scanning and contrast imaging.

Charles JP*, Royal Veterinary College; Cappellari O, Royal Veterinary College; Spence AJ, Temple University; Wells DJ, Royal Veterinary College; Hutchinson JR, Royal Veterinary College jcharles@rvc.ac.uk

Abstract: Terrestrial animals are able to move over various terrains in a stable and controlled way. This occurs through interactions between nerves, muscles and the environment, however their inherent complexity means they are not yet understood. Here we describe the creation of a biomechanical model of the hindlimb of the mouse, an animal commonly used in studies related to treatments for neuromuscular disorders and movement control. With this model, it will be possible to explore the intricacies of vertebrate locomotion in new detail, and as mice are thought to be close to the morphology of early mammals, it may give insights into the evolution of this lineage. To develop the model, 39 muscles of the hindlimb were identified through I2KI enhanced microCT scanning, which allowed muscle

attachment points to be determined. These were then dissected to determine their architecture, which was used to estimate their force-generating and length-change potential. A sensitivity analysis supported its validity. To simulate mouse locomotion, the hindlimb kinematics and ground reaction forces throughout a single representative stride were measured experimentally and added to the model. It was then possible to calculate individual muscle moments around each joint as well as predict patterns of muscle activation during running. Using a forward dynamics approach, we can predict the responses within the hindlimb to sensory or motor perturbations. These responses will be compared to experimental data, where optogenetics will be used to apply perturbations during movement. This systems approach may give valuable and novel insights into neuromuscular movement control, both within small rodents and potentially more generally within terrestrial vertebrates. Importantly, all of this potential for biomechanical simulation and insight into neuromotor control within animals such as the mouse depends on the high-fidelity imaging of musculoskeletal anatomy enabled by I2KI enhanced microCT scanning.

DCT2-2 11:45 am

The evolution of the mammalian jaw adductor musculature—inferences from soft-tissue imaging of extant taxa.

Lautenschlager S*, University of Bristol, School of Earth Sciences; Gill P, University of Bristol, School of Earth Sciences; Fagan M, University of Hull, School of Engineering; Rayfield E J, University of Bristol, School of Earth Sciences glzsl@bristol.ac.uk

Abstract: The evolution of the mammalian jaw is characterised by the gradual reduction of its individual bones into a single element and the concomitant transformation of the jaw joint and incorporation of the post-dentary bones into the middle ear complex. This osteological transformation is accompanied by a rearrangement and modification of the jaw adductor musculature, which is thought to have allowed the evolution of a more efficient masticatory system in comparison to the plesiomorphic reptilian condition. While osteological characters relating to this transition are well documented in the fossil record, little is known about the exact arrangement of the individual adductor muscles and reconstructions have often been unclear or conjectural. Here, we use comparative data derived from contrast-enhanced CT scanning of an extant taxon (e.g. *Monodelphis*) and digital restoration techniques to reconstruct the jaw adductor musculature of a number of representative non-mammalian cynodonts and mammaliaforms (including *Thrinaxodon*, *Diademodon*, *Probainognathus*, *Morganucodon*). Three-dimensional digital models of the adductor muscles were created on the basis of osteological correlates, homological criteria and spatial constraints. Different hypothesized arrangements were tested taking into account maximum muscle stretch factors and differences in muscle architecture. Results of this study show that the mammalian muscle division, including a loss of the pseudotemporalis musculature and the separation of the masseter, was already present in Eucynodontia. Furthermore, the mammalian muscle arrangement, with a shift of the pterygoideus musculature to the dentary, was completed in early mammaliaforms. Consequently, both events appear to have preceded the formation of the temporomandibular jaw joint and the appearance of true mammals.

DCT2-3 12:00 pm

Masticatory muscle anatomy of African mole-rats revealed by diceCT.

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Abstract: African mole-rats (Bathyergidae) are a family of rodents united by a subterranean lifestyle. Of the six extant genera of mole-rats, five are known to construct their burrows using chisel-tooth digging i.e. they dig with their incisors. The remaining genus, *Bathyergus*, is a scratch digger, tunnelling using its forelimbs only. Previous research has shown that the chisel-tooth digging bathyergids all show cranial and mandibular morphologies that facilitate high bite force and wide gape. However, much less is known about the morphology of the masticatory musculature in mole-rats, and whether differences exist between the scratch and chisel-tooth diggers in the size or configuration of the muscles. Diffusible iodine-based contrast enhanced CT (diceCT) provides a method to visualise soft tissues, such as muscles, with CT scanning. Six specimens of mole-rat heads, one representing each extant genus, were fixed in formaldehyde and stained with a 3.75% solution of iodine-potassium iodide for several months, before being scanned with microCT. Voxel dimensions of the resulting image stacks ranged from 0.04-0.08 mm. The scans revealed a highly complex set of jaw-closing muscles in the Bathyergidae. The masseter complex is the largest component of the adductor musculature, forming 50-60% of the total muscle mass. Unlike other families in the Ctenohystrica, mole-rats also have a large temporalis muscle, comprising 25-30% of muscle mass. Differences between the chisel-tooth and scratch diggers are largely seen in the size of the pterygoid muscles, which are highly reduced in *Bathyergus* compared to the other mole-rats. However, despite minor variations, the relative sizes of the jaw-closing muscles in the Bathyergidae are remarkably consistent across species. Overall, it appears that differences in bite-force abilities between mole-rat genera are attributable to variations in the orientation of muscle pull rather than muscle mass.

DCT2-4 12:15 pm

Integration of diceCT with XROMM and fluoromicrometry enhances functional morphology and biomechanics research: a case study of the macaque (Mammalia: Primates) feeding apparatus.

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Abstract: X-ray Reconstruction of Moving Morphology (XROMM) and fluoromicrometry permit unprecedented opportunities to study functional morphology and biomechanics with high precision and in three-dimensions. Adaptation of these techniques to study muscle function often requires time-intensive dissection and measurement that destroy the specimen in order to confirm marker location and muscular attachment sites on bone. This research bypasses such destruction and presents the integration of diffusible iodine-based contrast-enhanced computed tomography (DiceCT) into our model system for the neuromechanics of primate feeding, which uses the rhesus macaque (*Macaca mulatta*) and employs XROMM, fluoromicrometry, electromyography, and nerve stimulation experiments. Specifically, we visualize soft tissue structures using DiceCT to reconstruct in vivo muscle length changes, confirm marker and electrode placement, and plan surgical approaches. A known drawback to staining involves loss of contrast between bone and other structures; therefore, specimens used for XROMM should have a prestaining scan in order to obtain bone models. Alternative stains, such as phosphomolybdic acid (PMA), produce greater contrast between muscle and bone; however, PMA's slow diffusion rate, high cost, and permanent discoloration may be undesirable for those studying larger organisms. We register post-staining scans with pre-staining scans to superimpose soft tissue structures of interest, such as muscle and tendon attachments, onto the bones for reconstruction of soft tissue dynamics. We also use DiceCT to visualize regions with significant morphological complexity, such as the infratemporal fossa, where surgical targets for nerve stimulation experiments are imbedded in vascular structures. DiceCT gives researchers unprecedented insight into morphology, and its integration with XROMM and fluoromicrometry will enhance the impact of these methods on the fields of functional morphology and biomechanics.

DCT2-5 12:30 pm

Contrast-enhanced CT provides insight into amphibian lingual morphology.

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Abstract: The tongue plays an important role in amphibian prey capture, and several lingual projection modes are known. Some amphibians utilize hydrostatic (frogs: *Hemisus*, Microhylidae) or ballistic (salamanders: *Bolitoglossa*, *Hydromantes*) tongue projection, though the most common method involves contracting the protractor muscles to cause the sticky tongue pad to flip forward and secure the prey. Newly developed imaging methodologies allow the structures of the tongue to be visualized and analyzed at high resolutions in three dimensions, expanding on the data available from traditional methods (histology, dissection) and allowing for larger-scale comparative surveys of tongue anatomy across amphibian diversity. Here we present processed data from diffusible iodine-based contrast-enhanced (dice) CT scans of ranoid frogs, reconstructing serial 2D tomograms and 3D volumes to visualize and quantify anuran lingual anatomy. We compare our findings with those of previous studies for the same taxa using histology and scanning electron microscopy, and provide insights into the relationship between the morphology of the tongue and other anatomical systems.

DCT2-6 12:45 pm

Studying metamorphosis of the cranial musculoskeletal system in the axolotl using contrast-enhanced μ CT.

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Abstract: In amphibians, metamorphosis is understood as rapid attainment of somatic maturity associated with the transition from water to land, but how developmental processes reorganize musculoskeletal morphology is only beginning to be understood. We used contrast-enhanced μ CT to study changes in the cranial musculoskeletal system of the axolotl (*Ambystoma mexicanum*) across experimentally-induced metamorphosis. We identify significant changes in cranial osteology by 28 days post-injection, including reorganization of the palate and lower jaw, and expansion of some ossification centers in the palate, braincase, and cranial vault. Changes in the cranial skeleton are matched by changes in cranial musculature, including an increase in the size of the optic retractor, jaw depressor, and opercularis musculature. We identify a number of morphological systems to target for future studies of metamorphosis, and note differences in the impact of metamorphosis on neurocranial and dermatocranial ossifications. We identify a number of osteological features that, although previously conceptualized as evidence of paedomorphosis or miniaturization in lissamphibians, are instead indicative of exaggeration of late-ontogeny remodeling processes, with implications for lissamphibian phylogeny.

DCT3-1 2:30 pm

Contrast-enhanced micro-CT imaging of fish and frogs: digital dissections and biomechanical applications.

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Abstract: Traditional dissection is destructive and may be unsuitable for very small specimens or anatomical structures. Micro-computed tomography (μ CT) is excellent for visualizing three-dimensional, hard-tissue anatomy in

high-resolution; however, it cannot differentiate between low-density soft tissues. Methodological advancements in the use of various contrast-enhancing agents has resulted in detailed, three-dimensional digital dissections of an increasingly wide range of vertebrates. Contrast-enhanced μ CT was used to differentiate between soft tissues in the heads of two extant teleost fishes—the northern pike (*Esox lucius*) and European eel (*Anguilla anguilla*)—and throughout the entire body of an African clawed frog (*Xenopus laevis*). Specimens were stained using either iodine potassium iodide (pike and *Xenopus*) or phosphomolybdic acid (eel), with concentrations and staining times varying with staining agent and specimen size. Visualization of pike and eel data resulted in detailed models of cranial musculature, with different relative muscle sizes being correlated to different feeding modes (suction versus biting). Digital dissection of *Xenopus* provides the first comprehensive guide to the anatomy of this model organism in over 90 years, including visualization of the skeleton, muscles, organs and nervous system in phenomenal detail. In addition to digital dissections for understanding and quantifying morphology, information from these contrast-enhanced CT data sets were used in biomechanical analyses. Muscle information from the fish were used to load finite element models of the skulls simulating biting while data from frog hind limbs will be applied to dynamic models of jumping.

DCT3-2 2:45 pm

The curious case of the vomeronasal organ in bats: genetics asks questions only anatomy can answer.

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Abstract: In mammals, pheromone communication signals are detected and processed in the vomeronasal system in the nose. Nearly every terrestrial mammal uses vomerolfaction, although variation is present among Old World primates and bats. The neurons of the vomeronasal organ (VNO) are packed with receptors that bind directly to pheromone compounds and relay the signal to the accessory olfactory bulb (AOB) for interpretation. The ion channel protein *Trpc2* is indispensable for vomeronasal function, as it depolarizes the cell to transduce the signal to the brain. Histological evidence suggests that most bats lack a VNO or AOB, and the *Trpc2* gene is pseudogenized in many lineages. New World leaf-nosed bats (Phyllostomidae) are one dramatic exception, showing well-developed vomeronasal system morphology and a functional *Trpc2* gene. Recent genetic evidence, however, shows *Trpc2* pseudogenization of some nectarivorous lineages. Do these species truly lack a vomeronasal system while all other phyllostomids retain it? We investigated if phyllostomid species with a nonfunctional *Trpc2* also reflected this degraded vomeronasal system pattern at the morphological level. Using diffusible iodine-based contrast-enhanced computed tomography (diceCT), we characterized and measured vomeronasal structures in a diversity of phyllostomids. Many species with a disrupted *Trpc2* gene show non-detectable vomeronasal organ structures. We emphasize that scanning parameters, such as peak X-ray tube voltage and amperage are critical to obtaining clear resolution of vomeronasal organ structures. This powerful method allowed us to bridge a connection between genes and morphology.

DCT3-3 3:00 pm

Comparative morphology of bat cranial muscles using contrast-enhanced micro-CT imaging.

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Abstract: By harnessing the power of micro-CT imaging, functional morphologists have been able to describe, quantify and compare many aspects of the diverse skeletal anatomy of bats, and to relate this diversity to functional, ecological, and lineage diversity. However, similar progress has not been achieved for soft tissues, and many aspects of the morphological and functional diversity of bats remain unknown. Here we describe, for the first time, how soft-tissue components of the cranial anatomy of bats can be fully visualized in adult individuals using diffusible iodine-based contrast-enhanced computed tomography (diceCT) protocols. DiceCT methods have proven successful in the study of soft-tissue morphology in invertebrates, vertebrate embryos, archosaurs, rodents, lagomorphs and carnivorans. This research capitalizes on these previous studies and compares tissue contrast levels resulting from treatments of Lugol's iodine on intact bat heads. Using a taxonomically and ecologically diverse sample of bat species, we are able to visualize the precise anatomy of jaw adductor muscle groups that are difficult to access via traditional dissection. We further demonstrate the value of diceCT methods for generating realistic computer renditions of the three-dimensional anatomy of structures, including the brain and cranial musculature, allowing for accurate documentation, quantification and modeling of their function.

DCT3-4 3:15 pm

Advantages and difficulties of alcoholic iodine staining for correlative 2D and 3D microCT imaging and histomorphology in bat developmental studies.

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Abstract: Iodine contrast staining has successfully been used in a number of studies on fetal and adult vertebrates, because soft tissues can thus be differentiated in microCT images. In this ongoing study, we use 1% (w/v) elemental iodine in 100% ethanol (I2E) to study the development of reproductive organs in a sample of 14 *Cynopterus brachyotis* (Chiroptera: Pteropodidae) from the collection of the Museum Zoologicum Bogoriense (Indonesia) and compare it to the postnatal development of three other bat species. Bats occupy a large variety of different ecological niches and have evolved diverse morphological specializations. The prenatal development of different bat organ systems has mainly been studied using histological methods, dissection, or clearing and staining. The skeletal system has also been studied with x-ray techniques including microCT (X-ray microtomography). In a previous study on the postnatal development of the baculum (os penis) in the bat species *Pipistrellus pipistrellus* we found that the distal part of the baculum reaches its adult shape before the proximal part. The different states of medullary cavity development we found suggest the medullary cavity first forms from the ventral side of the baculum, where the branches of the base meet the shaft and that it is later replaced by a secondary medullary cavity. In the long term, we will compare the pre- and postnatal development of the reproductive organs of different bat species, to test if different baculum shapes develop similarly or if they start to calcify at different ossification centers. Correlating 3D microCT imaging with serial, surface-stained, undecalcified ground sections of the material enables us to get a precise histomorphological evaluation of a larger number of samples and even of other species.

DCT3-5 3:30 pm

DiceCT and the staining of old museum specimens, exemplified by the analysis of venom glands in viperid snakes.

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Abstract: Thanks to advances in computed tomography and histological staining methods, the comparative study of soft-tissue anatomy across wider taxonomic scales is becoming increasingly popular, and by now also involves non-freshly sampled specimens from natural history collections. However, staining is an invasive approach and in many cases it is not allowed to alter valuable collection specimens, either in structure or in color. In addition, the specimens have often been preserved using diverse fixations, some of which prevent the tissues from being successfully stained. Here we report on our experiences with the most common fixations like formalin and ethanol, as well as with specialized cases such as gasoline, and compare their effect on the staining of soft tissues by considering also body mass and the individual and historical age of the specimens. Furthermore, we present a case study on the comparative morphology of venom glands and associated muscles in viperid snakes, which represent a great challenge for staining due to the often old and large-sized material characterized by high muscle density, strong fixation with formalin and/or gasoline, and the additional storage in ethanol. Careful development of protocols and comparative tests of different approaches has now made it possible to even visualize the thin fibers of the pit organ of crotalid vipers. Also, we were able to calculate approximate staining periods based on the estimated fixation and storage times, the body mass of the specimen, and the fixation chemicals. To destain the material we discovered it is best to use watery solutions for staining, which results in a slow dissolving of the stain after return into storage ethanol, as more traditional destaining solutions such as sodium-thiosulfate are not appropriate for most museums specimens because of their chemical reactions with the inorganic components of the bone tissue.

DCT3-6 3:45 pm

Diffusible iodine-based contrast enhancement of large, post-embryonic, intact vertebrates for CT scanning: staining, destaining, and long-term storage.

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Abstract: Diffusible, iodine-based contrast enhancement of computed tomography (diceCT) is a successful technique for studying in situ soft tissues in fixed specimens, but studies have identified soft-tissue shrinkage as an artifact of staining with physiologically hypertonic solutions of Lugol's iodine (aqueous iodine potassium iodide; I2KI). Shrinkage introduces error into analyses of quantitative data collected from stained tissues. Our study seeks to clarify the effects of physiologically hypertonic I2KI on large, post-embryonic, intact vertebrate specimens. In our study, results from post-mortem, fixed lab mouse (*Mus musculus*) specimens show a significant difference in mass loss between specimens stained with hypertonic I2KI and those pretreated with 20% sucrose and stained with isotonic I2KI. Additionally, an age-matched set of seven Virginia opossum (*Didelphis virginiana*) pouch young was used to test the effects of different physiological pretreatment solutions and concentrations of I2KI. Of protocols tested, results indicate that, when combined, PBS pre-treatment and hypertonic (15%) I2KI staining resulted in 41.6% mass loss

and equivalent volume loss. Pretreating with a 20% sucrose solution and staining with physiologically-isotonic (1.25%) I2KI greatly reduced mass and volume losses. Results are supported by data from a wide range of vertebrate taxa (i.e., African-clawed frogs, alligators, several mammals and birds). Therefore, to mitigate the shrinkage effects of hypertonic I2KI, we recommend pretreatment with sucrose and staining with isotonic I2KI, although this protocol comes at the cost of added time for staining and the need to refresh the I2KI solution. Finally, destaining using sodium thiosulfate allows stained specimens to regain pre-stain coloration and remain stable for future re-staining and/or gross dissection. Together, these practices limit shrinkage and make diceCT more of a reversible, non-destructive technique.

DCT4-1 4:30 pm

An evaluation of the efficacy and mechanism of contrast-enhanced X-ray Computed Tomography for avian cranial material utilizing iodine through experimental and simulation approaches.

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Abstract: Diffusible iodine-based contrast-enhanced X-ray computed tomography (diceCT) is a comparatively new tool kit for imaging fine scale 3-D phenotypes. Although it is rapidly becoming standard anatomical practice, relatively few studies have attempted to gain insights into staining mechanisms by looking at subtle differences in staining protocol or model tissue interactions. There also has been only limited data available to inform detailed protocols for optimizing staining duration and concentration of solution when staining large adult specimens. A low concentration of iodine-based buffered formalin solution with a long staining period was used to visualize soft-tissue structures in avian crania. The staining effect was analyzed by serially measuring micro-CT-number profiles across coronal sections at intervals spanning the staining period. Regular replacement of the staining solution combined with a longer staining period significantly improved contrast within tissues. A simplified one-dimensional Diffusion-Sorption model with multiple-tissue domains was used to simulate transport process by calculating the concentration profile of iodine across the cranial regions. This model fits well with our experiment data and better explains previously reported difficulties in staining large samples comprised of tissues with high partition coefficients. Differences in partition coefficient, bulk density, and porosity could further explain the observed variation in staining rate and maximal staining effect between different tissues. By adjusting the parameters obtained in our experiments and simulations, it will be possible to calculate the optimal staining duration using a similar solution for different sized specimens. Additional follow-on experiments further support tailoring the staining solution concentration and staining regime by specimen type (e.g., whole body, single tissue) based on Diffusion-Reaction modeling.

DCT4-2 4:45 pm

Microscopic anatomy of the animals—a project in integrative publishing.

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Abstract: This talk introduces the *Microscopic Anatomy of the Animals* (MAA) as a project in integrative publishing. The project builds-up on the background that structures carry functions and knowledge of the structures is the fundament for functional studies, be it physiological, biochemical or molecular. New methods (e.g., confocal laser scanning, correlative microscopy, μ CT-imaging), new data, and new approaches spawned modern concepts of organismal morphology. The dynamic interaction of structures, their functions and the environment have now moved into the center of knowledge making morphology a truly integrative field in biology. With the widely accessible imaging tools, large data set become available that invite data-miners to fully utilize the available information. However, all this exciting new information is scattered in the major journals of cell biology and morphology, or some public data depositories, but it has never been integrated properly. MAA proposes a comprehensive and concise database of microscopic anatomy of the animals as the main access portal to microscopic anatomy, histology, and cell biology of animals. The database is built upon correlative imaging, i.e., image information always refers to all levels of the animal, from the general Bauplan through organs, tissues and cells. The intensive crosslinking of data facilitates comparative searches and data mining, so that morphological information, even from enigmatic species, becomes accessible also to scientists in other fields of biology than morphology. It includes all available technical features of digital publishing like interactive graphics, 3D-images, and virtual microscopy. It is addressed to the broad community of biologists, biochemists, molecular biologists, veterinarians, students and teachers.

Symposium — Mechanisms of whole dentition patterning in extant and extinct amniotes (DEN)

Organizers: Joy Richman, Leslea Hlusko, Theresa Grieco1

DEN1-1 9:30 am

Asymmetry and developmental integration in the replacing leopard gecko dentition (*Squamata: Eublepharis macularius*) provide evidence for *in ovo* jaw patterning maintained throughout life.

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Abstract: Jaw-wide control over tooth shedding may be necessary in many animals to preserve the integrity of the functional tooth row. Reptilian teeth are initiated *de novo* throughout life, but it is unclear whether tooth replacement patterns are dependent on conditions established *in ovo*. We used the leopard gecko as a model to study the

patterns and synchrony of dental replacement over space and time. We first determined the characteristics of the dentition present at hatching, prior to function. Micro-CT scans revealed a high degree of symmetry in erupted and unerupted teeth between the right and left jaw halves. To test the subsequent degree of independence between tooth positions, we studied the ontogeny of shedding asymmetry during two periods in 10 post-hatching geckos: an early period where the dentition was entirely comprised of teeth initiated in ovo, and a much later time where teeth were initiated after hatching. We analyzed data from wax bite impressions by tooth position, scoring the teeth that were shed either unilaterally (asymmetric) or bilaterally (symmetric). Two distinct motifs of asymmetric shedding were also observed. The majority of animals displayed a time lag of 3-4 days between right and left tooth shedding. The other group of animals had a position difference such that teeth at consecutive positions on right and left sides were lost. These motifs were strongly propagated in the early and late periods, and the percentage asymmetry remained constant between time periods for all animals. Large regions of the posterior maxilla are coordinated in the right-left polarity of their asymmetry, refuting the null hypothesis of shedding event independence along the jaw. This polarity bias is antisymmetric at the cohort level, and is never observed to flip polarity over time. Taken together, these patterns favor the hypothesis of a tooth cycling process patterned during embryonic development and extremely robust to environmental and developmental perturbation.

DEN1-2 10:00 am

Early dental development and the origins of toothlessness in amniotes.

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Abstract: A key question at the intersection of evolutionary and developmental biology is how complex structures such as teeth arise; identifying developmental discrepancies between taxa with and without these structures can help address this. Although BMP4 and FGF8 antagonistically initiate tooth development in mice, it is largely unknown whether odontogenesis is initiated the same way in other amniotes. Moreover, changes in BMP4-signaling have previously been implicated in evolutionary tooth loss in Aves. Here we demonstrate that *Bmp4*, *Msx1*, and *Msx2* expression is limited proximally in the red-eared slider turtle (*Trachemys scripta*) mandible at stages equivalent to those at which odontogenesis is initiated in mice, similarly to previously reported results in chicks. To address whether the limited domains in the turtle and the chicken indicate an evolutionary molecular parallelism or simply an ancestral phenotype, we assessed gene expression in a toothed reptile (the American alligator, *Alligator mississippiensis*) and a toothed non-placental mammal (the gray short-tailed opossum, *Monodelphis domestica*). We demonstrate that the *Bmp4* domain is limited proximally in *M. domestica* and that the *Fgf8* domain is limited distally in *A. mississippiensis* just preceding odontogenesis. Further, we show that *Msx1* and *Msx2* expression patterns in these species differ from those found in mice. Our data suggest that a limited *Bmp4* domain does not necessarily correlate with edentulism, and reveal that the initiation of odontogenesis in non-murine amniotes is more complex than previously imagined. Our data also suggest a partially conserved odontogenic program in *T. scripta*, as indicated by *Pitx2*, *Pax9*, and *Barx1* expression and the presence of a *Shh*-expressing palatal epithelium, which we hypothesize may represent potential dental rudiments based on the fossil record.

DEN1-3 10:15 am

Crocodiles as perfect models to investigate the mechanisms of continuous dental replacement as it functioned in mammalian ancestors.

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Abstract: As evidenced by the fossil record, toothed vertebrates originally were polyphyodont, which means that their dentition was continuously replaced throughout life. Although polyphyodonty still prevails in most extant non-mammalian toothed vertebrates, various reductive types emerged convergently a high number of times over evolution. The most emblematic trend in the reduction of dental generation number can be traced along the transition from pre-mammalian to mammalian synapsids, during which the continuous dental replacement slowed down into a maximum of two dental generations throughout life (diphyodonty). Since pre-mammalian synapsids do not have any present descendants, we selected crocodiles as the best living proxy to evaluate the situation of the dentition in pre-mammalian synapsids. Crocodiles have three characteristics that make them suitable for experimental studies: (1) Crocodiles are polyphyodont; (2) embryos can be procured on a seasonal basis from captive colonies; and (3) crocodiles are the only living non-mammalian tetrapods with thecodont dentitions. Thus tooth attachment in crocodiles is similar to mammals in that their teeth are anchored into bony sockets by a periodontal ligament. Using various techniques (histology, 3D X-ray microtomography and in situ hybridization) we characterized the pattern of dental replacement in Nile Crocodiles from La Ferme aux Crocodiles de Pierrelatte (France). Especially, Synchrotron tomography allowed us to 3D reconstruct spatial relationships of different dental generations, even at cellular level and revealed left-right symmetric tooth replacement pattern. These results suggest a spatio-temporal dynamic control. We discovered temporally and spatially restricted expression of Notch-Delta signaling molecules and target

genes. These patterns suggest that a subset of Notch ligands is active during tooth development and replacement.

DEN1-4 10:30 am

Stem cells and molecular circuits in alligator tooth renewal.

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Abstract: Alligators have robust regenerative powers for tooth renewal. In contrast, extant mammals can either renew their teeth once (diphyodont dentition, such as in humans) or not at all (monophyodont dentition, such as in mice). Previously, we used multiple mitotic labeling to map putative stem cells in alligator dental laminae which contain quiescent odontogenic progenitors (Wu et al., 2013. Proc Natl Acad Sci U S A. 110:E2009-18). We demonstrated that tooth cycle initiation is related to β -catenin/Wnt pathway activity in the dental lamina bulge. Here we use transcriptome analysis to examine the molecular pathway related to the tooth renewal process. We collected juvenile alligator dental lamina at different cycling stages and performed RNA-sequencing. Our data shows that several pathways, such as Wnt, BMP, FGF and ECM/MMP pathways are activated at the transition from the pre-initiation stage to the initiation stage. In addition, we identified the molecular circuitry among different stages of tooth cycling. The Wnt pathway may play the most important role in the tooth cycling, accompanied by other molecular pathways. We conclude that multiple pathways are involved in the molecular circuitry regulating tooth cycling. This result opens a possibility to apply this knowledge to mammalian tooth renewal.

DEN2-1 11:30 am

Osr2 patterns the mammalian dentition through modulation of Wnt signaling.

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Abstract: We previously reported that the transcription factor Osr2 is expressed in a buccolingual gradient across the molar tooth developmental field and restricts mouse molar tooth formation in a single row through suppression of propagation of the mesenchymal odontogenic activity by the Msx1-Bmp4 signaling pathway. Recently, we found that supernumerary tooth initiation in the Osr2^{-/-} mice could occur in the absence of mesenchymal Bmp4. To elucidate further the molecular mechanism patterning the molar tooth field, we isolated developing tooth mesenchyme from the Osr2^{-/-} and Msx1^{-/-} mutant mouse embryos, respectively, and from their control littermates and carried out RNA-seq analyses. We found that expression of several genes encoding secreted Wnt antagonists, including Dkk2, Sfrp1, and Sfrp2, was significantly upregulated in the Msx1^{-/-} tooth mesenchyme and significantly down-regulated in the Osr2^{-/-} tooth mesenchyme. Remarkably, in situ hybridization analysis revealed that Dkk2 and Sfrp2 are preferentially expressed in the oral mesenchyme lingual to the developing molar tooth germs, in a pattern similar to that of Osr2 mRNA expression. Expression of both Dkk2 and Sfrp2 mRNAs was dramatically reduced in the oral mesenchyme immediately lingual to the molar tooth germs in Osr2^{-/-} embryos but significantly expanded into the molar tooth mesenchyme in the Msx1^{-/-} and Bmp4-deficient embryos. We found that in utero treatment with the Dkk inhibitor IIC3 was sufficient to rescue mandibular molar morphogenesis in Bmp4-deficient mice but not in Msx1^{-/-} mice. Whereas inactivation of Sfrp2 was also insufficient to rescue molar tooth morphogenesis in Msx1^{-/-} mice, treatment of Msx1^{-/-}Sfrp2^{-/-}Sfrp3^{-/-} compound mutant mice in utero with IIC3 rescued maxillary molar morphogenesis. Together, these data indicate Osr2 and Msx1 interact to pattern the mouse molar tooth morphogenetic field through regulation of both Bmp4 and Wnt signaling. This work was supported by NIDCR grant DE018401.

DEN2-2 12:00 pm

Development of the diphyodont dentition in minipigs.

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Abstract: Minipigs have a normodont diphyodont dentition without a diastema and exhibit numerous morphological similarities compared with the human dental pattern. They are therefore an excellent model for studying the mechanisms of replacement and patterning of heterodont teeth. All tooth germs in the minipig are initiated at the tip of the dental lamina. The dental lamina grows into the mesenchyme in a lingual direction, and its inclined growth is underlined by asymmetrical cell proliferation and expression of SOX2 and PCP proteins. Moreover, there are

differences in growth intensity between dental and interdental areas of the lamina, with the interdental area lagging behind in development from an early stage. Loss of growth potential is characterised by a reduction in cell proliferation and down-regulation of the progenitor marker SOX2. Interestingly, the tip of the successional lamina is SOX2-negative in the dental area while its expression is expanded to the tip of the interdental lamina, indicating that the level of SOX2 expression may be linked to odontogenic potential. The successional dental lamina, which is necessary for permanent dentition formation, is apparent at the late bell stage with formation of a bud lingual to the deciduous tooth. At this stage, the superficial part of the dental lamina begins to fragment. Disintegration is initiated on the side facing the tooth anlagen while the opposite side is still proliferating and SOX2-positive. This pattern of fragmentation suggests that loss of the lamina may be triggered by signals from the deciduous tooth. Interestingly, only a few TUNEL positive cells were evident in the dental lamina during disintegration. In conclusion, minipigs provide an important experimental model to uncover developmental mechanisms contributing to the formation of replacement dentitions as well as providing a detailed analysis of the processes important in limiting the number of tooth generations in mammals. The research was supported by Grant Agency of Czech Republic (14-37368G to MB lab, 14-29273P to JS).

DEN2-3 12:15 pm

Genetic and phenotypic modularity in the mammalian dental arcade.

Hlusko LJ*, University of California Berkeley; Brasil MF, University of California Berkeley; Clay S, University of California Berkeley; Hoehna S, University of California Berkeley; Huelsenbeck J, University of California Berkeley; Huffman M, University of California Berkeley; Monson TA, University of California Berkeley; Takenaka R, University of California Berkeley; Schmitt CA, Boston University; Yoo S, University of California Berkeley; Mahaney MC, University of Texas Rio Grande Valley hlusko@berkeley.edu

Abstract: The dental arcade is essentially one organ system, but because it is comprised of individual teeth that develop and erupt over an extended period of ontogenetic time, we tend to conceptualize teeth as separate biological entities. For example, in cladistics analyses, biologists often include multiple dental traits, assuming them to be developmentally and genetically independent. Here, we describe over 15 years of research that explores variation across the mammalian dental arcade using a phenotype-back approach. In contrast to developmental genetics, which provides a gene-forward view of how genes influence and determine teeth, we employ analytical methods related to evolutionary quantitative genetics. These analyses yield results that enable us to redefine dental phenotypes that more accurately reflect the underlying genetic mechanisms that influence their variation. We will present results from our quantitative genetic analyses of dental variation in two pedigreed populations: mice and baboons. From these analyses, we developed hypotheses about genetic modularity in the mammalian dentition. We then tested these hypotheses using large phenotypic datasets of dental variation within and across primates, artiodactyls, and carnivores. By adding fossil data to these analyses, we then show how patterns of evolutionary change further strengthen support for our new phenotype definitions, and in so doing, yield insight to major taxonomic shifts in evolution. Funding was provided by NSF (BCS 0130277, 0500179, and 0616308). NIH provided support for the pedigreed baboon colony at the Southwest National Primate Research Center.

DEN2-4 12:45 pm

Discerning genetic architecture from phenotypic covariance in human dentitions.

Huffman M*, University of California, Berkeley; Brasil M, University of California, Berkeley; Monson T, University of California, Berkeley; Hlusko LJ, University of California, Berkeley michaela.huffman@berkeley.edu

Abstract: Quantitative genetic analyses of dental variation in mice and baboons provide a set of hypotheses as to how human phenotypic variation will be patterned if underlain by the same genetic architecture. Phenotypic correlation matrices were calculated for humans (n=300), Old World monkeys (n=752), and apes (n=180) to test the hypothesis that these phenotypic correlation matrices will reflect the published genetic correlation matrices for baboons. We find that humans return lower phenotypic correlations on average compared to baboons and other Old World Monkeys, and consequently do not clearly reflect the same pattern of correlation. One possible explanation is that the genetic architecture of humans was disrupted (and therefore differs) because our dentitions are dwarfed compared to our fossil ancestors. For comparison, we estimated phenotypic correlations matrices for a sample of cervids (n=30) that included pudu, a dwarfed South American deer. The dwarfism hypothesis was not supported, as the results yielded high correlations (0.76-0.95) similar to baboons, and unlike what we found for humans. Phenotypic correlations are influenced by genetic and non-genetic factors. If the non-genetic influences are high, the underlying genetic architecture may be obscured. When Principal Component Analysis (PCA) was applied to all samples included in this study, results show that the latent structure of human dental variation clusters near our closest living relatives, and as such, appears to be influenced by the same genetic architecture. Correlation matrices may be too blunt of an instrument for discerning genetic architecture from phenotypic covariance in human dentitions.

DEN3-1 2:30 pm

Embryonic tooth development in an Early Jurassic dinosaur.

Reisz RR*, University of Toronto Mississauga; LeBlanc ARH, University of Toronto Mississauga; Maddin H, Carleton University robert.reisz@utoronto.ca

Abstract: The rare occurrences of dinosaurian embryos are punctuated by even rarer preservation of their teeth. Some aspects of dinosaur embryonic development have been studied recently, but no such opportunities have presented themselves for the study of embryonic dental development. Here we report on the discovery of the oldest known embryonic jaw materials with teeth in a terrestrial vertebrate, the Early Jurassic sauropodomorph dinosaur *Lufengosaurus* from China. The preservation of maxillary and dentary teeth at various developmental stages permits the first detailed investigation of dental embryology in a dinosaur. Our results show that tooth development occurred early in sauropodomorph embryogenesis, resulting in several tooth replacement events prior to hatching with none of the teeth erupting. High-resolution micro-computed tomography and histology show that none of the embryonic teeth attach to the jaw, and successive generations were located within a common, large crypt. We propose that this pattern of tooth development and early replacement permitted the evolution of complex dental batteries in the giant herbivorous diplodocoid sauropods through paedomorphosis, the retention of early ontogenetic features in the adult. Similarly, ontogenetic changes in the morphology of successive generations of embryonic teeth of *Lufengosaurus* indicate that the pencil-like teeth within a single large crypt seen in large sauropods also evolved via paedomorphosis, suggesting that these were essential events leading to the success of the largest land dwelling animals of all time.

DEN3-2 3:00 pm

The simplification of sauropod teeth as an adaptation to herbivory.

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Abstract: In the vast majority of vertebrates, a simple correlation can be drawn between tooth complexity, either in terms of overall shape or in terms of cusp number, and diet. As reliance on carnivory increases, tooth complexity diminishes: consider the carnassial teeth of felids and canids relative to the complex, multicusped molars of ungulates. The drivers behind this pattern of morphological evolution are perhaps obvious—animal tissue requires less oral processing due to its ease of digestion, and so teeth are largely used as prey capture devices and as tools to slice off boli of flesh small enough to be swallowed, whereas plant tissue typically locks its nutrients behind a tough-to-digest cellulose wall which must be mechanically broken down before digestion can occur. However, in the largest herbivorous animals to ever walk the earth, sauropodomorph dinosaurs, we see a refutation of this trend through evolutionary time. The earliest sauropodomorphs were small and likely omnivorous with teeth of a general archosaur shape—leaf shaped, with many marginal cusps—good for slicing both plant and animal tissue as needed. Through time, these organisms became larger and more reliant on herbivory, and the initial trend in tooth morphology appears to reflect the expected patterns. Sauropod teeth became more massive, with larger slicing and (potentially) grinding surfaces and distinct wear patterns consistent with direct occlusion. Starting in the Mid- to Late Jurassic, however, multiple clades of sauropod dinosaurs began to sharply reduce tooth size and complexity, resulting in small, peg-like teeth without evidence of direct occlusion. Although this appears to have little adaptive value for an animal requiring massive quantities of difficult to digest forage daily, studies indicate that this may have been an adaptation to increase the replacement rate of teeth in an effort to combat extreme tooth wear caused by equally extreme rates of plant ingestion.

DEN3-3 3:30 pm

The evolution of dental batteries: new insights from extinct reptiles.

LeBlanc A/RH*, University of Toronto Mississauga; Reisz R/R, University of Toronto

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Abstract: Most non-mammalian amniotes exhibit very limited oral processing and have simple conical teeth. Some groups have, however, evolved dentitions that allowed them to access new food resources. The most dramatic dentition-level changes are seen in taxa possessing dental batteries, which incorporate multiple generations of teeth at a single position into a larger grinding or shearing surface. The developmental processes that underlie such dramatic changes in dental organization are poorly understood. Here we present comparative histological studies of the teeth and jaws of the Permo-Carboniferous captorhinid reptiles and Late Cretaceous hadrosaurid dinosaurs to highlight the development of two types of dental batteries. Many captorhinid taxa possess multiple rows of teeth on the dentaries and maxillae. Studying single and multiple-rowed taxa reveals that an asymmetrical pattern of jaw growth and a delay in tooth replacement are responsible for the observed diversity of dentitions in Captorhinidae. In hadrosaurids, teeth are stacked and interlocked vertically and mesiodistally into a mass of up to 300 teeth. Thin sections of complete dental batteries reveal accelerated development in the formation of tooth attachment tissues and extensive deposition of dentine. The former prevented each tooth from being replaced by its successor, and the latter allowed each tooth to contribute to the integrity of the battery and continuously erupt. These results show that in order to develop a dental battery, tooth replacement must be delayed so that older teeth can be retained. Studying these unique dentitions shows that tooth development and the replacement are actually two independent events that can be spatially separated by jaw growth or by heterochronic acceleration in tooth development. The lack of modern amniotes with dental batteries highlights the importance of studying fossils to gain insight into conserved and plastic processes of dental development and evolution.

DEN4-1 4:30 pm

Tissue-level analysis of ziphodont teeth in terrestrial animals.

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Abstract: Tooth morphology and development can provide valuable insights into the feeding behaviour and evolution of extinct organisms. A predominant tooth morphology in terrestrial carnivorous animals over the past 290 million years is ziphodont. These teeth are labio-lingually compressed, distally recurved, and have mesial and distal carinae bearing denticles. Known today only in varanid lizards, ziphodonty is much more pervasive in the fossil record. The first occurrence of ziphodonty is in the Early Permian non-mammalian synapsid *Dimetrodon* and several groups of therapsids, and convergently became widespread in archosaurs, especially theropod dinosaurs. This study aims to document the structural differences in tooth tissues of ziphodont teeth of different terrestrial carnivores through time. The teeth of synapsids, phytosaurs, crocodylians, dinosaurs, and modern varanid lizards were examined histologically. Results show that some teeth considered as ziphodont based on the external morphology of the denticles are in fact ornamented with serrations composed of enamel only, as in some species of *Dimetrodon* and the canines of *Smilodon*. True denticles possess a dentine core with an enamel cap, thereby increasing the surface area available for enamel and strengthening the tooth. Among those taxa with teeth bearing true denticles, the internal structure of the teeth differs. Theropod dinosaurs have specialized structures composed of globular and sclerotic dentine between each denticle, which are absent in synapsids, phytosaurs, and varanid lizards. These structures, previously hypothesized to prevent tooth breakage, are now suggested to have first evolved to shape and maintain the characteristic denticles through the life of the tooth. The convergent evolution of the ziphodont tooth morphology in several taxonomic groups reveals the efficiency of ziphodont teeth in facilitating a carnivorous lifestyle.

DEN4-2 5:00 pm

Morphological integration of deciduous and permanent dentitions in carnivorans.

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Abstract: In many mammals, the milk teeth are transient yet crucial structures for processing food during their early stages of life. Selection on the morphology of milk teeth may have important influence on the evolution of replacement teeth through shared developmental pathways. We investigated the patterns of morphological integration of deciduous and permanent dentitions at macroevolutionary scales, focusing on the order Carnivora. We collected ecomorphological data (based on linear measurements) for the milk (DP3-4/dp3-4) and replacement teeth (P4-M1/p4-m1) of 49 extant species representing eight families. Analyses of this data set have led to four key observations: (1) the morphology of carnivoran milk teeth, while diverse, is significantly less disparate than that of replacement teeth, supporting earlier, qualitative observations by Leche (1909, 1915); (2) nevertheless, the sizes and, to lesser extent, shapes of milk teeth are significantly correlated with those of their functional counterparts in the permanent dentition among all the species in the data set; (3) milk-tooth morphology preserves relatively deep (tribe- to family-level) phylogenetic relationships more faithfully than replacement-tooth morphology; (4) different families tend to show characteristic deciduous-to-permanent transitions in the morphospace. We interpret these results to suggest that milk teeth evolve in similar directions to replacement teeth but at slower rates. Overall, our findings are consistent with the hypothesis that morphological evolution of deciduous dentition is an important catalyst for that of permanent dentition at relatively fine phylogenetic scales. Dramatic evolutionary transformation of replacement teeth, however, appears to require additional modification of the shared developmental pathway between deciduous and permanent dentition.

DEN4-3 5:30 pm

Voies, molars, and molecules: integrating quantitative morphology, genetics, and evo-devo to study evolutionary processes.

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Abstract: The innate biases of the fossil record dictate that certain anatomical systems offer unique insight into the process of evolution. Dentition is one such anatomical system. Teeth are complex anatomical structures displaying a wide-range of ecomorphologies, they are relatively abundant in the fossil record, and they have a long history of detailed study. The intersection of the genetic and developmental mechanisms underlying tooth development, and the evolutionary history of those mechanisms, provide opportunities to explore mechanistic and philosophical/conceptual questions within evolutionary biology. For example, dissecting the conceptual framework of how we integrate mechanisms of dental patterning and their evolutionary history with material data from the fossil record highlights areas where modern evolutionary constructs conflict or resolve one another. I describe an empirical system focused on a proposed anagenetic change in the dental morphology of the Sagebrush Vole, *Lemmyscus curtatus*. This study integrates quantitative morphology, phylogeography, quantitative genetics, and evo-devo to understand how dental patterning within *L. curtatus* evolved over time. Beyond reconstructing the evolution of dentition in *L. curtatus*, I also explore how the paradigms of emergent morphology (developmental biology) and transformational morphology (paleontology) may inform and/or conflict with one another. For example, can developmental mechanisms cause true convergent evolution, i.e., the origination of the same morphological feature, from the same genetic architecture, in separate populations or species? Because a detailed understanding of the evolutionary history and genetic

architecture for dental patterning is available for *Lemmiscus*, the system offers the opportunity to synthesize these micro- and macroevolutionary phenomena.

Symposium — Show me your ear - The inner and middle ear in vertebrates (EAR)

Organizers: Cathrin Pfaff, Julia Schultz, Rico Schellhorn

EAR1-1 9:30 am

The utility of the shark inner ear as a 'landmark' for hyoid arch position.

Bronson A. *, American Museum of Natural History; Hutchins R., University of Montana; Denton J., American Museum of Natural History; Maisey J., American Museum of Natural History abronson@amnh.org

Abstract: The inner ear of sharks (a group whose skeletal anatomy is generally poorly sampled) has been studied using CT scanning technology. Apart from its obvious functional interest, the skeletal labyrinth of the inner ear can provide 'landmark' points of reference that help describe the position of other anatomical structures, such as the location and extent of the craniohyoid attachment connecting the hyoid arch to the neurocranium. Few external features of the braincase otic region are available to define the extent of this articulation. However, by isolating the labyrinth endocast via tomographic segmentation, we were able to utilize morphological features of the skeletal labyrinth to qualitatively describe hyomandibular attachment in 25 modern elasmobranch species. After constructing a preliminary phylogeny based on hyoid attachment characters, potential synapomorphies were identified for some groups. The supposed anterior location of the craniohyoid articulation in galeomorphs is critically evaluated. In the *Orectolobiformes* the articulation extends farther anteriorly than in many other modern elasmobranchs, and is so far forward in *Eridacnis* that it extends beneath the utriculus. Our preliminary findings suggest that further investigations (including morphometric analyses) will clarify anatomical descriptions and character definitions, while also providing novel phylogenetic characters.

EAR1-2 9:45 am

Inner ear morphology in early neopterygian fishes (Actinopterygii: Neopterygii).

Giles Sam *, University of Oxford; Rogers Molly, University of Oxford; Friedman Matt, University of Oxford sam.giles@earth.ox.ac.uk

Abstract: Endocasts of the osseous labyrinth have the potential to yield information about both phylogenetic relationships and ecology. Although inner ear morphology is well documented in many groups of fossil vertebrates, little is known for early Neopterygii, the major fish radiation containing living teleosts, gars and the bowfin. Here we reconstruct endocasts of the inner ear for a sample of Mesozoic neopterygian fishes using high-resolution computed tomography. Our sample includes taxa unambiguously assigned to either the teleost (*Dorsetichthys*, "*Pholidophorus*", *Elopoides*) and holostean ("*Aspidorynchus*", "*Caturus*", *Heterolepidotus*) total-groups, as well as examples of less certain phylogenetic position (an unnamed parasemionotid and *Dapedium*). Our models provide a test of anatomical interpretations for forms where inner ears were reconstructed based on destructive tomography ("*Caturus*") or inspection of the lateral wall of the cranial chamber (*Dorsetichthys*), and deliver the first detailed insights on inner ear morphology in the remaining taxa. With respect to relationships, traits apparent in the inner ear broadly support past phylogenetic hypotheses concerning taxa agreed to have reasonably secure systematic placements. Inner ear morphology supports placement of *Dapedium* with holosteans rather than teleosts, while preserved structure in the unnamed parasemionotid is generalized to the degree that it provides no evidence of close affinity with either of the crown neopterygian lineages. This study provides proof-of-concept for the systematic utility of the inner ear in neopterygians that, in combination with similar findings for earlier-diverging actinopterygian lineages, points to the substantial potential of this anatomical system for addressing the longstanding questions in the relationships of fossil ray-finned fishes to one another and living groups.

EAR1-3 10:00 am

Mesosuchus browni (Rhynchosauria: Archosauromorpha) and the early evolution of the archosaur ear.

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Abstract: Rhynchosauria is a clade of herbivorous stem-archosaurs that were abundant in many Triassic terrestrial ecosystems. *Mesosuchus browni* represents the basalmost rhynchosaur taxon and its morphology has been important to understand the phylogenetic relationships and early evolution of the clade. However, the braincase anatomy remained largely unknown. To shed more light on its morphology, we scanned the braincase of *Mesosuchus* for the first time using high-resolution micro-computed tomography. In comparison to the stem-diapsid *Youngina*, the semicircular canals of *Mesosuchus* are more slender and more rounded, with a substantial elongation of the posterior canal. Together with the enlargement of the floccular lobe, this is indicative of a more active lifestyle and a more upright posture, since these structures are responsible for ensuring balance control during locomotion. The borders of the small fenestra ovalis and metotic foramen are also more well-defined. The thickening of the ventral ramus of the opisthotic more effectively separates these structures, resulting in an enhanced sense of hearing. It avoids sound transmission along non-sound-detecting routes and increases the pressure-relief function of the metotic foramen. However, the inner ear of the more derived archosauriform taxon *Euparkeria* shows further

improvements of these mechanisms such as a larger metotic foramen and more elongate cochlea and semicircular canals. This places the morphology of *Mesosuchus* as intermediate between stem-diapsids and stem-archosaurs and points to a gradual acquisition of derived hearing characters. In contrast, the stapes of *Mesosuchus* resembles more that of *Youngina* than of other closely-related taxa. The anatomy of the stapes seems to be at odds with these general trends, possibly indicating a unique evolutionary history of hearing within rhynchosaurs.

EAR1-4 10:15 am

Ear ossicle morphology of the Jurassic euharamiyidan *Arboroharamiya* and evolution of mammalian middle ear.

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Abstract: Here we report the stapes and incus from the early Middle Jurassic (~160 Ma) euharamiyidan, *Arboroharamiya*, from northern China, which represent the earliest known mammalian middle ear ossicles. Both bones are greatly reduced in size in relation to those of non-mammalian cynodonts, and the stapes-skull length ratio falls in the range of extant mammals. The stapes is "rod-like" and has a large stapedia foramen and a distinct posterior process. The process is unique in shape and size among known mammals and interpreted as for insertion of a sizable stapedius muscle. The incus differs from the quadrate of non-mammalian cynodonts, such as morganucodontids, in having a small size and a slim short process. Coupled with lack of the postdentary trough/Meckelian groove on the medial surface of the dentary, these ossicles indicate that the postdentary unit (articular, prearticular, and angular) must have been completely detached from the dentary and the definitive mammalian middle ear (DMME) had developed in euharamiyidans. Among various higher-level phylogenetic hypotheses of mammaliaforms, the one we prefer shows that allotherians (containing "haramiyidans" and multituberculates) form a clade that is nested within Mammalia. This hypothesis implies that detachment of the middle ear ossicles from the dentary bone took place once in allotherians, from an ancestral condition represented by *Haramiyavia* to the common ancestor of euharamiyidans and multituberculates and that acquisition of the DMME in allotherians was independent to those of monotremes and therians; thus, the DMME evolved at least three times independently in mammals. Other hypotheses that place "haramiyidans" outside of Mammalia but leave multituberculates within mammals would require independent acquisition of the DMME as well as parallel evolution of numerous dental, cranial and postcranial similarities in euharamiyidans and multituberculates, respectively.

EAR1-5 10:30 am

Inner ear morphology in gondwanatherian mammals and implications for ear evolution in mammaliaforms.

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Abstract: Therians are exceptional among vertebrates in detecting high-frequency sounds. This ability has been associated with the evolution of an ossified cribriform plate, ossified primary and secondary laminae, and elongation of the cochlear canal following the loss of a lagena. The temporal sequence of acquisition of these features remains largely unknown. A lagena is present in most extant non-mammalian vertebrates and monotremes, but absent in therians. Based on this distribution it is assumed that a lagena was present in basal mammaliaforms and lost in stem therians. Fossil evidence supporting this hypothesis is ambiguous. In fossils a lagena is assumed to have been present if the apex of the cochlear canal is expanded and a separate canal for the lagena nerve is present, as in monotremes. As such, a lagena is assumed to be present in *Haldanodon* and absent in cladotherians. Osseous laminae are equally ambiguous, being present in cladotherians and possibly in some multituberculates. Here I present the inner ear of two gondwanatherian mammals, *Vintana* and an undescribed genus, from the Cretaceous of Madagascar. Both taxa have a cochlear canal that is short and slightly curved at the apex, and preserve a modern innervation of the cochlea (primary and secondary osseous laminae, cribriform plate, cochlear ganglion canal). Whereas a lagena is absent in *Vintana*, a separate canal to the apex of the cochlea is present in the new Malagasy taxon. The new taxon is unique among extinct and extant mammaliaforms in preserving a lagena and osseous laminae. These taxa demonstrate the plasticity within gondwanatherian ear evolution and, if future analyses support placement of Gondwanatheria within Allotheria, within Mesozoic mammals. A lagena may have been lost independently in some multituberculates, *Vintana* and cladotherians. Osseous laminae seem to have evolved either at the base of Gondwanatheria and Cladotheria or independently within these two clades.

EAR1-6 10:45 am

New study of the membranous labyrinth of monotremes and comparative morphology of mammalian inner ears.

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Abstract: Extant monotremes are distinctive from therians (i.e., marsupials and placentals) in many structures of the membranous inner ear labyrinth. We re-examined the membranous labyrinth and innervation in the platypus (*Ornithorhynchus anatinus*) and short beaked echidna (*Tachyglossus aculeatus*), using histological sections and 3D reconstruction. Our investigations revealed inner ear features that were not described previously, or poorly

understood in monotremes. For instance, the membranous scalae (scala vestibuli, scala media and scala tympani) holding the organ of Corti and macula lagena have different lengths. Scala tympani is shorter than scala media and scala vestibuli, and is not involved in the apical coil of the bony labyrinth. The helicotrema, a conduit between scala vestibuli and scala tympani, is in sub-apical position near the isthmus of the apically coiled scala media. In contrast, the therian cochlea shows all three scalae in equal lengths, coiling to the same degree, and the helicotrema in apical position. In monotremes, scala tympani bridges over scala media to connect to scala vestibuli where the organ of Corti ends. Scala vestibuli and scala media extend beyond the helicotrema forming coiled blind sacs holding the macula lagena. Bridging of scala tympani and scala vestibuli proximally to the blind ending of scalae media and vestibuli is common in some extant non-mammalian amniotes. Thus monotremes retain an ancestral condition of the helicotrema. However, in monotremes the cochlear apex that contains the lagena is enlarged and coiled. Histosections of subadult ear regions show a thin bony wall separating lagenar nerve fibers from cochlear nerve fibers. In CT scans this separation seems less prominent and fibers of cochlear and lagenar nerve are interwoven. Overall, the membranous labyrinth is more coiled than the external bony cochlear canal. The newly documented features have broad implications for the evolutionary morphology of inner ears of early mammals.

EAR2-1 11:30 am

Functional morphological adaptations of the bony labyrinth in marsupials (Mammalia: Theria) .

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Abstract: Diprotodontia represents the largest and ecologically most distinct order of marsupials occurring in Australasian with almost 125 extant species. They are highly divers in size, locomotion (gliding, hopping, subterranean), habitat preferences (rain forests, arid areas), feeding (omnivorous, carnivorous, insectivorous), but also activity pattern (nocturnal, diurnal). The spatial orientation in the habitat and therefore the three-dimensional space is detected by the vestibular system of the inner ear, more precisely by the three semicircular canals (anterior, posterior, lateral), which are enclosed by the bony labyrinth. Previous studies of mammals were focusing on the functional morphological adaptations and the corresponding link between the morphology of the semicircular canals and the locomotion mode of the investigated taxa. In this study, we are investigating the bony labyrinth of 26 diprotodontian marsupial mammals of almost all genera with non-invasive micro-CT scanning and 3D reconstructions with an additional standardization of the measurements prior to statistical analyses, successfully applied in squirrels, to elucidate the functional morphological signal of the bony labyrinth. For reconstructing the ancestral state in Theria, three species of marsupials of South America were additionally included. In the principal component analyses, we found a clear distinction of arboreal and hopping species with an overlapping space of gliding and fossorial taxa. The highest loadings of this functional distinction are clearly found in the diameter of the semicircular canals, whereas the overall shape (height, width, length) of the semicircular canals is less important. Additionally, the investigated arboreal and fossorial species of South America are nested in the morphospace of the Australasian taxa. In future, by including fossil specimens of marsupials in this database, the locomotion mode of extinct taxa can be postulated without any evidence of postcranial material.

EAR2-2 11:45 am

Head posture and orientation of the lateral semicircular canal in xenarthrans (Mammalia).

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Abstract: The semicircular canal system of the inner ear is specialized for the detection of rotational accelerations and decelerations of the head. The orientation of the semicircular canals is one of the determinants of the capacity of this system to detect a given rotational movement. As a result, their position in the basicranium is highly constrained. Due to its potential link to the head posture, past studies on the orientation of the semicircular canals essentially focused on the lateral canal, which is supposedly held close to horizontal during rest and/or alert behaviors. Until now, functional studies on the orientation of the lateral semicircular canal (LSC) mainly focused on a limited number of taxa, often distantly related. Based on 3D models reconstructed from μ CT-scans of skulls, we investigated the diversity of orientations of the LSC within one of the four major clades of placental mammals, i.e. the superorder Xenarthra, with a dataset that includes almost all extant genera and two fossil taxa (*Megatherium*, *Pelecyodon*). We observed a wide range of LSC orientations relative to the basicranium at both intra- and inter-specific scales. The estimated phylogenetic imprint on the orientation of the LSC was moderate within the superorder, though some phylogenetic conservatism was detected for armadillos that were characterized by a strongly tilted LSC. A convergence between extant suspensory sloths was also detected, both genera showing a weakly tilted LSC compared to the basicranium. Our preliminary analysis of usual head posture in extant xenarthrans (based on photographs of living animals) further revealed that the LSC orientation in armadillos is congruent with a strongly tilted head, but portrayed a more complex situation for sloths and anteaters. Several aspects of the posterior part of the skull, such as its relative height, also appeared to covary with the LSC orientation in Xenarthra and are likely

related to functional and/or developmental constraints.

EAR2-3 12:00 pm

Bony labyrinth of Carnivora (Mammalia): the significance of phylogeny and the sensorial adaptation to aquatic environments.

Grohe C.*, American Museum of Natural History; Tseng Z.J., American Museum of Natural History; Lebrun R., Institut des Sciences de l'Evolution de Montpellier; Boistel R., Universite de Poitiers; Flynn J.J., American Museum of Natural History cgrohe@amnh.org

Abstract: The bony labyrinth is an osseous structure surrounding the inner ear, a primary sensorial organ involved in hearing, body perception in space, and balance in vertebrates. We investigated the influence of phylogenetic relationships and locomotor patterns on shape variation of the bony labyrinth in carnivoran mammals. We chose musteloids as a model group (skunks, red panda, coatis, raccoons, badgers, martens, otters, etc.) as it constitutes the most species-rich superfamily among Carnivora and it includes taxa with a wide array of locomotory styles (semi-fossorial, semi-aquatic, scansorial, arboreal, and generalized terrestrial forms). We reconstructed virtual bony labyrinths of 31 species based on X-ray microCT data of basicrania and we characterized their shape using 3D geometric morphometrics. PCA from shape data show distinct morphospaces between the four traditionally recognized families of musteloids (Mephitidae, Procyonidae, Ailuridae, Mustelidae). The phylogenetic variation of bony labyrinth shape in musteloids is associated with the size and curvature of the semicircular canals, angles between canals, presence or absence of a secondary common crus, degree of lateral compression of the vestibule, orientation of the cochlea relative to the semicircular canals, proportions of the cochlea, and degree of curvature of its turns. We also detected significant differences in the shape of the vestibular system between semi-aquatic and non-aquatic musteloids: otters and minks display an oval rather than circular anterior canal, sinuous rather than straight lateral canal, and acute rather than straight angle between the posterior and lateral semicircular canals compared to the remaining musteloid sample. Those modifications could be related to the sensorial adaptation of Carnivora for detecting head motion in aquatic environment and will be compared to the shape variation observed in Pinnipedia (seals, sea lions, walrus).

EAR2-4 12:15 pm

Morphological diversity among the inner ears of extinct and extant baleen whales (Cetacea: Mysticeti).

Ekdale E.G.*, San Diego State University eeekdale@mail.sdsu.edu

Abstract: The ears of cetaceans are of special interest given the polarity of auditory physiology between the two major extant clades—the high-frequency sensitive Odontoceti and low-frequency sensitive Mysticeti. Our knowledge of the evolution and phylogeny of mysticetes is at a point where we can investigate the diverse morphologies of the inner ear of baleen whales through time, as well as explore functional diversity among mysticete species. Landmark-based 3D geometric morphometric analyses were performed to investigate the morphologic diversity of the bony labyrinths of the inner ears of extinct and extant mysticetes in comparison with other cetaceans. Principal component analyses (PCAs) show that the cochlear morphospace of odontocetes is tangential to that of mysticetes but is completely separated from mysticetes when semicircular canal landmarks are included. The majority of cochlear variation, including number of coils and graded curvature among successive turns, is related to auditory threshold frequencies. The cochlea of the archaeocete *Zygorhiza kochii* plots within the morphospace of mysticetes, suggesting that mysticetes possess ancestral cochlear morphology, and likely ancestral cochlear physiology. PCAs indicate a large degree of variation among mysticete species, suggesting that there are multiple hearing regimes among mysticetes, as has been demonstrated for odontocetes and hypothesized for mysticetes based on behavioral observations. Most of the variation among the semicircular canals is related to shape and orientation of the lateral semicircular canal, which is sensitive to yaw rotations (around a vertical axis). Semicircular canal variation may correspond to differences in locomotor behaviors. However, cochlear shape is phylogenetically informative for Neoceti and Chaemysticeti (edentulous mysticetes), and the semicircular canals for multiple cetacean clades, which indicates that the form of the inner ear cannot be explained by function alone.

EAR2-5 12:30 pm

Hooves on the roof: the ear region of *Diplobune minor*, an arboreal artiodactyl from the Early Oligocene of France.

Orliac M.J.*, Institut des Sciences de l'Evolution; Brualla N., Institut des Sciences de l'Evolution; Assemat A., Institut des Sciences de l'Evolution; Guignard M., Institut des Sciences de l'Evolution; Lihoreau F., Institut des Sciences de l'Evolution maeva.orliac@univ-montp2.fr

Abstract: Apart from cetaceans, modern artiodactyls all walk the ground on their four feet. Among extinct taxa, Anoplotheriinae which lived during mid-Cenozoic times (40-30 million years ago) in Europe, show a unique postcranial morphology with an unusually large finger II and a lack of finger V on the hand and foot, a very mobile elbow articulation, and an uncommon orientation of the forelimbs and hind limbs. This peculiar morphology led to various hypotheses regarding their locomotion, from semi-aquatic to partly arboreal, or partly bipedal. Here we study the middle and inner ear morphology of *Diplobune minor*, a medium-sized anoplotheriid from the locality of Itardies (Early Oligocene, MP23, Quercy, France) through a case study of both in situ and isolated petrosals. This work allows

for describing the stapes, the petrosal, and the bony labyrinth of this extinct taxon. The characteristics of the cast of the bony labyrinth indicate that *D. minor* had hearing capabilities similar to these of the extant goat (neither high nor low frequency specialist). The vestibular apparatus shows an unexpected variation of the shape and length of the semicircular canals that would support the hypothesis that *D. minor* was a slow tree-dwelling animal.

EAR2-6 12:45 pm

3D geometric morphometrics and cladistics analyses of the tragulid bony labyrinth: morphological variability and implications for ruminant phylogeny.

Costeur L*, Natural History Museum Basel, Switzerland; Mennecart B, Natural History Museum Basel, Switzerland loic.costeur@bs.ch

Abstract: The bony labyrinth is known for its phylogenetic relevance. However, it has been vastly understudied in ruminants. We analyse sets of bony labyrinths of the three living tragulid genera (traguline ruminants) including *Tragulus kanchil* (juvenile and a late foetus stage), *T. napu*, *Hyemoschus aquaticus*, and *Moschiola meminna*. We use 3D geometric morphometrics to capture most of the bony-labyrinth shape. Through a PCA of the 3D data we show that intergenera disparity is higher than intragenera variability. Intraspecific variability is also observed (e.g. shape and extent of the lateral semi-circular canal, size and shape of the common crus). The late foetal stage plots slightly apart from the other *T. kanchil* specimens, but it remains identifiable at the species level. Issues related to timing of ossification of some parts (mostly canals) may partly account for this. However, early ontogenetic stages (foetus and post-natal) are not significantly different from adult stages (shape and size). The bony labyrinth in ruminants is fully formed before birth and its size and volume does not significantly change from this point on. Incorporating juvenile specimens in palaeontological studies is thus not problematic since they fall within the morphological range observed in adults. We run a cladistics analysis comparing all living tragulid genera and the fossil tragulid *Dorcatherium crassum* (ca. 15 Ma) to Pecora. Our study identifies new synapomorphies of the family Tragulidae based only on petrosal bone and bony labyrinth. This phylogenetic analysis confirms previous morphological and molecular analyses (e.g. sister-taxa relationship of *Tragulus* and *Moschiola*). This study shows the potential of the ruminant ear region and more specifically of the bony labyrinth in phylogenetic studies. Both shape analysis and discrete morphological characters are useful to decipher phylogenetic relationships. Study supported by the SNF project 200021-159854.

Symposium — Past, Present and Future of Ecological Morphology (ECO)

Organizers: Lance McBrayer, Eric McElroy, Robbie Wilson

ECO1-1 9:30 am

Introduction to the symposium.

McElroy EJ*, College of Charleston; McBrayer LD, Georgia Southern University; Wilson R, University of Queensland McelroyE@cofc.edu

ECO1-2 9:45 am

Ecomorphology: Insights into adaptation from the analysis of form-function complexes to the dynamics of species diversification.

Miles DB*, Ohio University urosaurus@gmail.com

Abstract: The discipline of ecological morphology has its origins in quantifying the adaptive significance of variation in form-function relationships. Delineating how morphological form affected function within the context of a species' environment provided evidence for the adaptive role of a trait. A key modification of ecomorphological analyses was the application of microevolutionary theory to derive an explicit statistical linkage between morphological variation, performance and fitness. The rise of new methods for estimating performance spurred the additional investigations in ecomorphology. Subsequent extensions include using an historical approach by incorporating phylogenetic information when the conducting comparisons in among-species patterns in the covariation between trait and performance. The integration of phylogenetic information into ecomorphological analyses refined our ability to recognize examples of convergence, community organization and adaptive radiations. There are a surfeit of studies illustrating the link between morphology and performance and performance with ecology, yet we have far fewer examples linking performance with fitness. Recent analyses have shifted to understanding the evolution of performance and determining how trade-off with other key traits, e.g., immunocompetence, mating behavior (courtship and territoriality) can affect physiological performance and alter patterns in ecomorphological associations. These represent promising approaches for linking performance to key components of fitness. Recent approaches in ecomorphological analyses also seek to link species diversification with morphological and functional diversification. However, new challenges are emerging in ecomorphological analyses as a result of the quest to predict how species may cope with rising temperatures and avoid extinction. The ability of species to persist in novel environments may be determined by plasticity in both morphology and physiological performance.

ECO1-3 10:00 am

Adaptations, innovations, and diversification.

Wainwright P.C. *, University of California, Davis pcwainwright@ucdavis.edu

Abstract: Innovations in functional morphology, physiology and biochemistry are thought to be a major force in shaping evolutionary patterns, with the potential to drive adaptive radiation and influence the evolutionary prospects for lineages. But the evolutionary consequences of innovation are diverse and usually do not result in adaptive radiation. What factors shape the macroevolutionary impact of innovations and can we predict what kinds of innovation will lead to diversity as opposed to those that result only in greater specialization? I discuss a framework for studying biological innovations in an evolutionary context. Innovations are discrete changes in functional mechanisms that involve novelties and enhance organismal performance. The ubiquity of trade-offs in functional systems means that enhanced performance on one axis often occurs at the expense of performance on another axis, such that many innovations result in more of an exchange of performance capabilities, rather than an expansion. Innovations may open up new resources for exploitation but their consequences on diversification depend heavily on the adaptive landscape around these novel resources. I survey innovations in labrid fishes, an exceptionally successful and ecologically diverse group of reef fishes, and explore their consequences for performance, patterns of resource use, and macroevolution. All of the innovations provide performance enhancements and result in changes in patterns of resource use. But the majority is associated with ecological specialization and only one has promoted further ecological diversification. Because selection acts on the specific performance enhancement and not on the evolutionary potential of an innovation, the enhancement of diversity may be highly serendipitous. The macroevolutionary potential of innovations depends critically on the interaction between the performance enhancement and the ecological opportunity that is exposed.

ECO1-4 10:15 am

Life-history of the multivariate performance phenotype.

Lailvaux SP*, University of New Orleans slailvaux@gmail.com

Abstract: Whole-organism performance traits are key intermediaries between the organism and the environment, as exemplified by the status of performance as the median link in the ecomorphological paradigm. This status means performance evolution is influenced by dynamic organismal factors that shape performance expression in addition to external selection pressures. Because performance traits are energetically costly to both build and maintain, performance will compete with other life-history traits over a limited pool of acquired energetic resources at any given time, potentially leading to trade-offs in performance expression. However, differential resource allocation itself is a function of the genetic architecture underlying the integrated, multivariate organismal phenotype. A proper grasp of the phenotypic relationships among performance and other fitness-related traits therefore requires understanding of the underlying genetic relationships as well. I highlight recent studies that have attempted to uncover these relationships in several animal species using methods ranging from traditional quantitative genetic breeding designs to pedigree analyses and genomics/transcriptomics. I also consider the utility of such methods for predicting performance evolution based on an explicitly multivariate, genetically-informed ecomorphological paradigm.

ECO1-5 10:30 am

Trajectories of insight in ecological morphology: phenotypic integration, speciation, and the

Anthropocene. Langerhans RB*, North Carolina State University langenhans@ncsu.edu

Abstract: The study of ecological morphology is currently at a critical stage for uncovering insights in several major areas of research. This current status emerges from technological advances and recent work laying a strong foundation for current pressing questions. Focusing on ecomorphology of locomotion and feeding in animals, I review three core research areas where studies of ecological morphology seem particularly poised for breakthroughs, highlighting promising directions of current and future research in each case. First, understanding the evolution of the whole-organism phenotype is obviously a complex problem, but ecomorphological approaches offer useful means of testing hypotheses about the evolution of phenotypic integration. Recent work has uncovered complex genetic associations among disparate traits, and ecomorphological studies can provide powerful tests for whether genetic architecture largely reflects inherent constraints that bias the direction of evolution, or adaptive trait correlations shaped by correlational selection. Second, ecomorphological studies can help uncover the role of ecology in speciation, specifically by testing how both similar selection and divergent selection can lead to enhanced reproductive isolation through ecomorphological change. This work will help integrate natural and sexual selection, and unite the two contrasting patterns in ecomorphological data of parallel and nonparallel evolution across similar environmental gradients. Finally, ecomorphological studies can serve as a key tool in predicting organismal responses to a rapidly changing, human-dominated world. Ecomorphology could prove critically important for understanding and predicting trait changes in the Anthropocene, helping forge a new conservation science that uses evolutionary biology to help forecast and mitigate biodiversity change, as well as uses prescriptive evolution to guide future biodiversity in desired manners.

ECO1-6 10:45 am

Ecomorphological adaptations to an invasive predator: insights from lizards and fire ants.

Langkilde T*, Pennsylvania State University; Thawley C, Pennsylvania State University tl130@psu.edu

Abstract: Invasive species are notorious for wreaking ecological havoc, but provide an (almost unique) opportunity to

study ecomorphological adaptations of organisms to novel environmental change. My research utilizes the invasion of one of the world's worst ant pests to study behavioral, morphological and physiological adaptations of a native lizard. The red imported fire ant (*Solenopsis invicta*) acts as a novel predator of the eastern fence lizard (*Sceloporus undulatus*). Our research reveals that lizards within fire ant invaded sites have longer hind limbs than do lizards from fire ant free areas. This heritable morphological change supports behavioral adaptations that allow lizards to avoid and escape fire ant attack, as do elevated levels of stress hormones. While the benefits of these adaptations are obvious, fire ants have reversed natural latitudinal gradients in these traits, potentially mismatching animals to the natural environment. Controlled manipulations of individuals' lifetime exposure to the invader, comparisons of populations with different invasion histories, and the use of museum specimens collected from a single population over time have provided insight into the mechanisms driving the responses to fire ants, revealing that evolutionary and lifetime exposure to a threat can interact across ontogeny in complex ways to shape adaptive responses. Our ever-changing world calls for a multi-disciplinary approach to understanding how morphological adaptations interact with changes in other traits to allow population persistence.

ECO2-1 11:30 am

Ecometric patterning in hind limb morphology of North American carnivorans (Carnivora, Mammalia): community-level functional morphology and evolutionary ecology.

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Abstract: Ecometrics is the quantitative study of the distributions of functional traits within local communities and the environmental sorting of those traits at regional and continental scales. Functional traits are properties of organisms that have a direct physical or physiological relationship to an underlying quality of the environment, which in turn has indirect links to broader environmental factors such as temperature, precipitation, elevation, atmospheric composition, or sea level. Ecometric patterns across space and through time arise through a combination of biogeographic sorting, evolution, and extinction driven by changes in environments. Hind limb locomotor morphology in living carnivorans (Mammalia, Carnivora) has an ecometric distribution that is associated with terrain and vegetation cover. Measured as a gear ratio from the calcaneum, I show that the mean value in North American carnivoran communities is strongly linked to biome types. Interestingly, within-species variation is not correlated with environment in the same way, or at least not strongly so. Phylogenetic community analysis combined with phylogenetic history of carnivorans shows that ecometric patterning in this trait arises from clade-based sorting of digitigrade, semidigitigrade, and plantigrade family-level groups. The association between hind limb gear ratio and vegetation is strong enough that the vegetation cover of North America can be reconstructed from carnivoran limb morphology with a similar degree of accuracy as vegetation models based on temperature and precipitation. Anthropogenic changes to the North American landscape and its carnivoran fauna have had large but erratic effects on ecometric patterns compared to the environmental and faunal changes associated with the last deglaciation.

ECO2-2 11:45 am

500 million years of form and function in fishes: perspectives from Deep Time.

Friedman M*, University of Oxford; Close R, University of Oxford; Delbarre D, University of Oxford; Dobson C, University College London; Giles S, University of Oxford; Johanson Z, Natural History Museum, London matt.friedman@earth.ox.ac.uk

Abstract: The long fossil record of fishes spans roughly half a billion years of geological history. A variety of depositional setting yield fish remains over this interval, and these specimens are often characterized by a higher degree of completeness and articulation than fossil tetrapods. This extensive archive of extinct phenotypes provides a rich substrate for analyses targeting questions of convergence, morphological innovation, and ecological diversification over long evolutionary timescales. However, the fish record presents challenges. From a geological standpoint, horizons characterized by excellent preservation are idiosyncratically distributed both spatially and temporally, and the specimens they yield are often—but not always—highly compressed. From a research standpoint, extinct fishes receive far less scrutiny than their terrestrial relatives, meaning that many basic aspects of their structure, taxonomy, and relationships are less clear than for tetrapods. From a biological standpoint, the numerical dominance of teleosts in the living fauna means that many extinct taxa lack obvious modern analogues in which hypotheses of ancient ecologies and functions might be firmly grounded. This talk reviews the progress that has been made in the ecomorphology of fossil fishes in recent years, drawing on examples from throughout the Phanerozoic. Quantification of jaw mechanics and overall body geometry remain the easiest and most widely used approaches to flattened fossil material. However, the application of tomographic approaches to three-dimensionally preserved material yields considerable information that can augment existing work. This reveals information that is usually (e.g., gill-arch structure and elaboration of associated dentition and rakers) or always (e.g., geometry of the buccal cavity, morphology of the inner ear) obliterated in compression fossils, providing tests of previous ecological hypotheses and the empirical data to formulate new ones.

ECO2-3 12:00 pm

Reciprocal illumination of body shape on predator-prey interactions and trophic morphology.

Mehta RS*, University of California, Santa Cruz; Baliga VB, University of California, Santa Cruz; Diluzio A, University of California, Santa Cruz; Higgins BA, University of California, Santa Cruz; Harrison JS, University of California, Santa Cruz rmehta2@ucsc.edu

Abstract: Body shapes in fishes vary on a continuum from nearly spherical to highly elongate or eel-like. In these extreme morphologies, we tend to find gratifying relationships between form and function. Moray eels (Anguilliformes: Muraenidae) comprise a large radiation of highly snake-like marine predators that attain relatively large standard lengths. Many species of morays are known to use a diversity of prey subjection strategies to assist in feeding, such as shaking, body rotation, knotting, and ramming prey against other objects. There is little diet data informing us of the maximum prey size of morays and exactly when manipulation strategies are employed. Here, we supplement feeding performance trials in a controlled laboratory environment with field dietary data for the California moray (*Gymnothorax mordax*). In feeding trials, both ingestion ratio and relative prey mass were calculated from various sizes of cephalopod and fish prey. We discovered that morays had greater success tearing apart fish prey with behaviors such as knotting, while cephalopods were either swallowed whole or only their tentacles were consumed. When we examine the relationship between prey size, measured in standard length, and predator size, measured as oral gape width, from field stomach contents, we find that morays consume a wide size range of fish prey. Larger morays do not omit small prey from their diet. To better understand the prey accessible to morays, we explore the scaling relationships between California morays and prey available in their environment. Not surprisingly, we find that prey species vary in body shape and how they scale in relation to moray gape width. We show that studying shape of both the predator and prey can be a reciprocally illuminating process: we gain insight into the different size classes of prey that are readily available to morays and how prey shape affects the maximum size morays may consume.

ECO2-4 12:15 pm

Ecological morphology in neotropical lizards: is Tropiduridae a key biological system?

Kohlsdorf T*, University of São Paulo; Barros FC, University of São Paulo; Lofeu L, University of São Paulo; Rothier PS, University of São Paulo; Brandt R, University of São Paulo tiana_kohlsdorf@ffclrp.usp.br

Abstract: Ecological morphology is a very active research field extensively applied to several animal groups. As other disciplines, some major conceptual advances in ecomorphology are achieved through subsequent studies focusing on lineages that have specific characteristics endorsing them as ideal systems for that given research program. In this talk I will summarize 15 years of ecomorphological studies using neotropical lizards from the family Tropiduridae, and will also present new data incorporating additional dimensions to the field. Data on limb and head proportions provide evidence for ecomorphological associations in Tropiduridae: head shape evolved in association with inclusion of hard prey in the diet, limb and tail proportions differ with the use of arboreal environments, and species are characterized by long feet. Some of these morphological specializations have been recovered at the population level in Tropiduridae. Ecomorphological associations in this lizard family have functional implications, as we identify morpho-physiological components associated to locomotor performance among species ecologically divergent. Some associations between morphology and locomotion also respond to sexual selection: *Tropidurus* males perform better than females in four types of performance, and sexes are different not only in size but also in body shape and muscle morphometrics. An additional dimension recently incorporated to this complex equation resides on effects of ontogenetic changes on ecomorphological associations. To conclude, data for Tropiduridae show solutions to equivalent selective pressures that differ from those generalized for lizards based on studies with *Anolis*. The possibility of obtaining embryos and raising eggs and juveniles under controlled conditions ascends this lizard family as a key biological system for inferring associations under a modern framework that combines ecological morphology with ecological evolutionary development.

ECO2-5 12:30 pm

Success in nature and sport: exploring the biological basis of excellence in physical activities?

Wilson R S*, University of Queensland r.wilson@uq.edu.au

Abstract: All physical activities rely on a complex assortment of anatomical, physiological, motor and behavioural traits. Discovering the determinants of individual success in physical activities has become central to the study of functional morphology because it allows one to understand the coevolution of organismal form and function. In a similar way, determining the combination of traits most responsible for success in human functional tasks is of enormous interest to the sports industry for discovering and developing athletes and the health sciences for facilitating improved pathways of recovery following injury. But despite the parallels in research programs between the natural and health sciences, each discipline has operated in relative isolation. I will explore the parallel lines of research that explore the determinants of success in physical activities in two very different but complimentary systems: (i) natural populations of the small marsupial, the northern quoll (*Dasyurus hallucatus*) from Australia, and (ii) semi-professional soccer players. The northern quoll is the world's largest semelparous mammal, which means mating is highly synchronous, males live for only one year, and all males undergo die-offs soon after reproduction. Given the importance of procuring mates in such a short period (approx. 2 weeks), the ability for males to win fights and cover long distances to find reproductively mature females is presumably of critical importance. Female quolls live for two to three years and their die-off occurs after the young are weaned - which is around four months after the mating season. Soccer is also ideal for integrative studies of success because we can readily identify, isolate and

quantify many of the possible underlying determinants of success among large numbers of individual players. Using these two very different study systems, I will discuss the implications of my work for understanding the evolution and ecology of physical performance in nature.

ECO2-6 12:45 pm

Symposium roundtable discussion.

McElroy EJ*, College of Charleston; McBrayer LD, Georgia Southern University; Wilson R, University of Queensland
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Contributed Session — Evo-Devo - Evolution of Developmental Processes (EVD)

EVD1-1 2:30 pm

The evolution of collagen and SPARC secretion during tooth development in vertebrates.

Debiais-Thibaud M*, Montpellier University, France; Enault S, Montpellier University, France; Munoz D, University of Concepción, Chile; Ventéo S, INSERM U1051, Montpellier, France; Sire JY, CNRS UMR7138, Paris, France; Marcellini S, University of Concepción, Chile Melanie.Debiais-Thibaud@umontpellier.fr

Abstract: Vertebrate skeletal tissues develop from the activity of specific cells, all able to secrete a collagenous extra-cellular matrix which may or may not calcify. In this work, we describe the expression patterns of the major fibrillary collagen genes and genes of the Secreted Protein, Acidic, Cysteine-Rich (SPARC) family in two chondrichthyan species and one tetrapod where the SPARC family has not (chondrichthyans) or poorly (*Xenopus*) expanded into Secretory Calcium-binding PhosphoProtein (SCPP) duplicates. We show expression of all these genes in the mesenchymal compartment (odontoblasts) of teeth and the placoid scales of the catshark, except for the expression of SPARCL1 in the inner epithelium of chondrichthyan teeth and transient faint expression of SPARC in the *Xenopus* inner dental epithelium. Our results involve a restrained SPARCL1 expression in the epithelial layer of calcifying teeth (maturation stage) in chondrichthyans and no expression of collagen genes by ameloblasts. This result questions the cellular origin of chondrichthyan enameloid and its homology to enamel/enameloid found in osteichthyans. In contrast, a strongly conserved feature of odontoblasts in jawed vertebrate is therefore the co-expression of major fibrillar collagen genes and the SPARC gene. This observation calls for a putative gene regulatory network involved in extracellular matrix calcification that could also be shared between odontoblasts and osteoblasts of osteichthyans. These results therefore lead to various scenarios for the evolution of SPARC/SCPP genes in the gene regulatory networks involved in ameloblast and odontoblast function.

EVD1-2 2:45 pm

Reduction in tooth site regeneration underlies morphological novelty during pufferfish dental regeneration.

Thiery AP, University of Sheffield; Fraser GJ*, University of Sheffield g.fraser@sheffield.ac.uk

Abstract: Consisting of approximately 25,000 species, morphological diversity within teleosts is rife. However, few morphological adaptations can rival the unique pufferfish 'beak', composed of multiple generations of parasymphyseal replacement teeth. In pufferfish, the transition between the first and second dental generation coincides with the emergence of this novel beaked morphology. As Sox2 has been identified as an important factor in maintaining dental regenerative competency in oral epithelium, we localised its expression in pufferfish. SOX2 is abundant throughout the oral epithelium but in conjunction with Dil cell labelling we highlight the labial oral epithelium as a putative dental stem cell site. We implicate canonical Wnt signalling in the activation of these dental progenitor cells and localise an odontogenic activation site to the base of the oral epithelium, labial to the first generation teeth. Despite the unusual morphology, we identified high levels of developmental conservation between pufferfish dental replacement and other vertebrate models studied. This study identifies a loss of dental replacement at all but four tooth sites as a fundamental driver of this morphological change. This elucidates how highly derived yet closely related teleosts have evolved extreme morphological novelty through modifications in dental number during rounds of dental regeneration.

EVD1-3 3:00 pm

Tammar wallaby *Macropus eugenii* (Macropodidae) as a model for tooth evolution, development, and replacement in mammals.

Nasrullah Q*, Monash University; Renfree M, The University of Melbourne; Evans AR, Monash University gamariya.nasrullah@monash.edu

Abstract: Unlike their reptile-like ancestors, modern mammals replace their teeth only once (diphyodonty) or never (monophyodonty). Within mammals, eutherians and metatherians differ in the number of teeth in several of the tooth classes (incisor, canine, premolar and molar) and the mode of replacement. This study aims to resolve dental homology between eutherian and metatherian mammals using the Tammar wallaby *Macropus eugenii* as an opportune model for studying mammalian odontogenesis. *Macropus eugenii* has tooth replacement, four tooth classes, and – unusually among mammals – molar progression, but only preliminary investigations in the 1960s and 1980s have been carried out on its dental development. To provide a more comprehensive documentation of the spatio-temporal pattern of tooth development, we stained heads of pouch young aged between 0-135 days in 10%

Lugol's Iodine (I2KI), then microCT scanned using a Zeiss Xradia 520Versa and the micro-CT Imaging and Medical Beamline at the Australian Synchrotron. These were reconstructed and segmented in Avizo, generating 3D models. Our results reveal the position and orientation of developing tooth structures including: primary and secondary dental lamina; initiating tooth germs; major stages of tooth development (bud, bell and cap); and mineralised tissues. We tracked the overlapping development of two generations of teeth when present, and observed that deciduous incisors and canines were vestigial and cease development before eruption. The 'stain and scan' technique proved both time and cost effective in producing complex 3D models of the entire dentition at each stage with tissue-level resolution. Using these new models, we characterise tooth replacement in this marsupial by pinpointing the developmental origins of primary and secondary tooth generations, allowing us to clarify metatherian-eutherian dental homologies.

EVD1-4 3:15 pm

Developmental mechanism and genetic basis of the unique morphological characters of non-model organisms: investigation in bear molars as an example.

Asahara M*, Mie University; Kishida T, Kyoto University asahara@ars.mie-u.ac.jp

Abstract: The developmental mechanism and genetic basis of the unique morphology of non-model organisms and fossil taxa are interesting topics in biology; however, their investigation is difficult. Recently, a developmental model, the inhibitory cascade model, was proposed in a developmental study. The model explains the relative size of lower molars in mammals by a proportion of inhibition and activation molecules affecting the molar germ. According to the model, molar size decreases, is uniform, or increases along the molar row ($M1 > M2 > M3$, $M1 = M2 = M3$, or $M1 < M2 < M3$). Most mammals morphologically fit this model; accordingly, the model explains the variation in molar size in mammals. However, in bears, the second molar is the largest ($M1 < M2 > M3$); bears were considered an exception to the model, and the cause is unclear. Here, we used a combination of genetically modified mice, and morphological and molecular evolutionary analyses to reveal the cause of the unique molar in bears. We found a unique pattern of variation in relative molar sizes in the order Carnivora, i.e., lower slope of the regression of $M3/M1$ on $M2/M1$ than that in the original model. The molar pattern of bears appears to be an extension of this line. We also examined mice hetero-deficient for BMP7, a gene encoding an antagonist of a molecule involved in the model. Their molar morphology resembles the trend of variation in the Carnivora. Molecular evolutionary analysis revealed natural selection of the gene, especially of the domain binding its antagonist, in the ancestral lineage of bears. We conclude that variation in expression or affinity of low diffusible signaling molecules such as BMP7 can affect mesial molars more than distal molars, and it explains the variation in the Carnivora, including the unique phenotype of bears. Our method of combined analysis can be an example of investigating the unique phenotypes of non-model organisms.

EVD1-5 3:30 pm

Morphology and function of the tooththrow in a rodent knockout model and implications for mammalian tooth evolution.

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Abstract: Tooth morphology is the result of many complex tissue interactions within the developing tooth. Differences in cusp shape, size and orientation provide evidence of phylogeny, as well as alterations in feeding strategy and amount of intraoral processing. Many families of regulatory genes play key roles in the resultant morphology of the tooth. Determining and quantifying the effect of these regulatory genes on the morphology and function of mammalian dentition has implications for understanding the underlying mechanisms that drove the degree of dental diversity that we see in both extinct and extant mammals. We tested the hypothesis that changes in regulatory gene expression can lead to changes in morphology and function of the tooththrow using a neural crest specific knockout of the first coding region, exon 1, of bone morphogenetic protein 7 (BMP7). These BMP7 mutants have distinctive craniofacial morphology, which includes noticeably altered tooth morphology. Mutant molars have extra cusps, mostly on the first upper and lower molars, along with differences in cusp morphology. The cusps on mutant molars are shorter and blunter than the control cusps and the orientation of the cusps in relation to other cusps differs. To quantify differences in morphology, a landmark set was developed and geometric morphometric methods were applied to 3D models of the right upper and lower tooththrows. Significant morphological differences between the control and BMP7 mutant mice were found for both the upper and lower tooththrows. Additionally, mutant and control mice were found to have different wear facets, indicating that along with a change in morphology, there was also a change in function. This research shows that changes in the expression of BMP7 can lead to changes in the morphology and function of the tooththrow and suggests that BMP7 could have played a role in structuring the amount of dental diversity that we see in extinct and extant mammals.

EVD1-6 3:45 pm

The influence of mechanical loading on jaw joint morphology during development.

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Abstract: It is accepted that mechanical loading via muscle activity is required for normal skeletal development, particularly at joint contact surfaces. Despite this, little is known about the effect of disrupted mechanical loading on

craniofacial skeletal development. Using zebrafish as a model system, genetic and pharmacological studies have demonstrated that mechanical loading is required for accurate joint morphogenesis. Using anaesthetised and genetically manipulated fish, here we show that removal of muscle activity during zebrafish development results in a reorganisation of jaw joint (Meckel's cartilage and palatoquadrate) shape from a ball and socket articulation to a flattened and overgrown joint surface. We find that control fish begin to voluntarily open and close their mouths at days 4 to 5 and that muscle activity at this time is crucial for normal joint formation. Removal of muscle loads at days 4 to 5 results in abnormal joint formation, whereas removal of loads earlier during development has little effect on joint formation and most fish develop normally once muscle activity is renewed. After recording the number of adductor muscle fibres, fibre area and estimated muscle force, we use finite element modelling to reconstruct strains within the developing cartilages. Abnormal joint morphology modifies strains within the developing jaw cartilages, and, when muscle-induced strain is removed, cells on the medial side of the joint change their orientation. Our results suggest that muscle-induced strain regulates cell orientation at the developing joint and that biomechanical loading via adductor muscle contraction plays a key role in normal zebrafish jaw joint formation.

EVD2-1 9:30 am

The development and evolution of cranial nerves and head muscles in two actinopterygian taxa, the longnose gar (*Lepisosteus osseus*) and the turquoise killifish (*Nothobranchius furzeri*).

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Abstract: The vertebrate head has been modified largely during the course of evolution, resulting in enormous craniofacial diversity. These changes did not only include the skull, but also associated structures such as muscles and nerves. Data on the developmental patterning and morphogenesis of these structures are essential for understanding the mechanisms underlying these changes. Recent studies on vertebrate development have mainly focused on axis formation. Ontogenetic data on the head are mostly focused on skeletal elements. Soft tissues of the head are still understudied. Where research on cranial myo- and neurogenesis was performed, mostly tetrapod model organisms like *Xenopus*, axolotl, chicken and mouse were used. With about 30000 species, the Actinopterygii comprises around half of all extant vertebrates and is the sister group to the Sarcopterygii, including the tetrapods. Understanding the morphological changes of the vertebrate head during evolutionary history therefore inevitably calls for the study of actinopterygians. Insights into head morphogenesis from non-tetrapod vertebrates are mainly based on studies of the zebrafish. The zebrafish belongs to the Teleostei, a derived taxon within the Actinopterygii. To provide an evolutionary view, further representatives of the Actinopterygii, need to be studied and put in comparison. We have examined the development of cranial muscles and nerves in two actinopterygian taxa [the longnose gar (*Lepisosteus osseus*) and the turquoise killifish (*Nothobranchius furzeri*)], using μ CT scans and whole-mount antibody stainings. The early formation of the head musculature in these taxa is relatively conserved whereas later morphogenetic events, such as the partitioning of the adductor mandibulae complex and the differentiation of the branchial muscles are much more variable. However, the development of the cranial nerves seems to be the most conservative pattern of head morphogenesis within the Actinopterygii.

EVD2-2 9:45 am

Embryonic derivation of the bony skull and cranial musculature in the axolotl (*Ambystoma mexicanum*).

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Abstract: The vertebrate skull is a complex structure that arises from three embryonic sources—cranial mesoderm, somitic mesoderm and neural crest. Head muscles are also derived from cranial mesoderm and as such are distinct from somite-derived trunk muscles. The contribution of cranial mesoderm to the bony skull and head musculature is well documented in two amniote models, the mouse and chicken. Additional data from anamniotes would facilitate comparisons in a wider phylogenetic context and provide fundamental data regarding features that have been lost in amniotes, including gill musculature. To delineate the fate of cranial mesoderm, we utilize GFP-transgenic axolotls, which permit long-term fate mapping. Several elements in the skull exhibit a dual embryonic origin from both mesoderm and cranial neural crest, including the parasphenoid (the dominant component of the amphibian palate), the squamosal and the stapes. Myogenic unsegmented mesoderm extends posteriorly to the axial level of somite 3 and contributes to both the posterior gill-levator muscles and the cucullaris muscle. These results constitute the first long-term fate map of cranial mesoderm in an amniote vertebrate.

EVD2-3 10:00 am

Correlation between *Hox* code and vertebral morphology in archosaurs.

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Abstract: The vital importance of the axial column for vertebrate life is clear, because its key functions, the protection of the neural chord and providing a balance between stability and mobility, have remained the same in a huge variety of taxa. However, vertebrae show considerable variation in number and shape across the axial column, resulting in varying degrees of axial regionalization. Nevertheless, functionally equivalent master control genes mediate the embryonic development of the axial column in animals as different as mouse and chicken. The combined expression of *Hox* genes is a requirement to establish specific vertebral morphologies, indicating that the morphological variation

across taxa is likely due to modifications in the pattern of gene expression. In archosaurs, *Hox* codes have been established for birds, but not yet fully for the crocodilian lineage. First, we analyzed the *Hox* gene expression in the axial column of the Nile crocodile. Second, by using geometric morphometrics, the present study shows a correlation between *Hox* code and quantifiable vertebral morphology in living archosaurs, in which the boundaries between morphological subgroups of vertebrae can be linked to *Hox* gene expression limits. Our results reveal homologous units of vertebrae in modern archosaurs, each with their specific *Hox* gene pattern. Based on these results, we used the morphological pattern as a proxy to reconstruct the underlying *Hox* code in fossil taxa where the genetic information is not available. This allows us for the first time to rigorously hypothesize the genetic complexity of an extinct archosaur, the sauropodomorph dinosaur *Plateosaurus*. By connecting the morphological patterns to developmental processes, inference of the genetic changes that underlie the evolutionary modifications of the axial column appears feasible. This is not only an important case study, but will lead to a better understanding of the origin of morphological disparity in archosaur vertebral columns.

EVD2-4 10:15 am

Comparative anatomy of the nasolacrimal duct: different origins but same end point.

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Abstract: The nasolacrimal duct (NLD) connects the orbital and nasal region in many tetrapods. Caudally, this duct opens into the anterior/ medial orbital region, often in close association with the nictitating membrane or an anterior orbital gland (e.g.: Harderian gland). Rostrally, this duct opens into the nasal cavity, though variation exists: it opens into the nostril region (some mammals), near the vomeronasal Organ (VNO: squamates and amphibians) or onto the lateral nasal wall (other mammals and archosaurs). A similar level of variation is evident in the ontogeny of the nasolacrimal apparatus. There are three different published origins of the NLD in vertebrates: 1) originates from the orbit and grows into the nasal capsule (Mongolian gerbils, rabbits and the common quail), 2) originates from the VNO and grows towards the orbit (squamates) and 3) a groove that sinks into the facial mesenchyme and becomes an enclosed epithelial tube (humans). In most developing vertebrates the rostral part of the NLD becomes longer as the nasal cavity grows. There are at least two major variants. In some archosaurs (Laysan albatross and alligator): 4) The NLD originates as a solid point on the lateral nasal wall, which sinks into the mesoderm, dissociating from the lateral wall and growing to connect the orbital and nasal region. However, the NLD does not elongate, rather the nasal region continues to grow rostral to the NLD. As a result, the NLD remains truncated, and opens in the posterior end of the nasal cavity. Other variants may emerge later in development; for example, in anthropoid primates and tarsiers, the rostral part of the NLD disappears during fetal development. Though the origin of the NLD is variable, its initial connections are evolutionarily conserved. The final structure of this duct is largely determined by the growth of the nasal region.

EVD2-5 10:30 am

An earful of jaw, then and now: using marsupial evo-devo to understand a major evolutionary transition in the paleontological record.

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Abstract: During synapsid evolution, postdentary elements in the reptilian jaw transitioned into the middle ear of mammals. Though this astounding change is well documented in the fossil record, questions regarding the developmental sequence that drove the ossicular transition still remain. At birth, modern marsupials possess a very reptilian jaw joint with functional articulation between the articular and quadrate. These elements will later become the malleus and incus, respectively, of the middle ear. This entire transition occurs postnatally, and represents a natural system for comparison with the fossil record. We utilized *Monodelphis domestica* as a model organism, and traced the development of ossicular structures as they separate from the jaw and fully incorporate into the middle ear. Micro-CT scans throughout development and three-dimensional reconstructions show decreasing size and rearward movement of ossicles are illusions created by continued growth and expansion of the surrounding skull elements. Cryosections and immunohistochemistry (IHC) reveal separation of Meckel's cartilage from the malleus occurs at postnatal day 20 and is facilitated by apoptosis. Additionally, laser capture microscopy and RNA sequencing identify differential gene expression at the time of separation and breakdown of the connecting Meckel's cartilage. Key gene findings are then verified with fluorescent in situ hybridization (FISH). The morphological changes are facilitated by an upregulation of cartilage resorption genes paired with simultaneous downregulation of proliferative genes. Finally, marsupial developmental stages were compared with the known fossil record of early mammals exhibiting transitional forms of the definitive mammalian middle ear in order to resolve the question, in this instance, of whether ontogeny is truly recapitulating phylogeny.

EVD2-6 10:45 am

Revisiting the homologues hypotheses: are we really testing it?

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Abstract: For Owen the features that are the same under any variety of form and function in different specimens were designated as homologues. The causal explanation of a homologue is sharing the same Archetype, what he called as Homologies. Nowadays, both of these terms are synonymous and its definitions and functions are directly associated to phylogenetic inferences (e.g., Patterson's tests). However, this procedure eliminated the causal explanation for the shared similarities proposed. Moreover, as a consequence, congruence became the main way to test a homologues hypothesis. The zenith of the congruence test is observed in de Pina propositions, where primary homology is the character propositions being tested on a cladogram, and when (and if) is corroborated it became a secondary homology. When primary homology was falsified it is referred as homoplasy. Here, I identify all these assumptions are based on circular reasoning, both homologue and homology definitions as well the congruence tests. In both cases, the data used to construct the cladogram is also used to test them. Popper proposes that a test must be performed based on an independent data set inferred from the data being explained. Homoplasy is an ad hoc hypothesis and there is no empirical reason to treat it as an error. The homologue must be proposed between the same features on different individuals based on arguments, for example the femur bone articulate proximally with pelvic bones. To test this homologue proposition, studies based on ontogeny, molecular, and others anatomical studies must be performed, in this way, if all referred specimens which a homologue is proposed between the bones called femur share the same ontogenetic origin this homologue hypothesis is corroborated. Therefore I conclude that hypotheses and tests must be looked at with care. Also characters as homologues must be more deeply studied and not only seen as "numerical data" for phylogenetic inferences.

EVD3-1 11:30 am

Sample size artifacts in analyses of ontogenetic sequences.

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Abstract: The resolution of hypothesized ontogenetic sequences within a taxon or population depends on the number of specimens and the number of included events. Simplistically, complete sequence resolution (i.e., every event's position resolved relative to every other event) requires at least as many sampled individuals as ontogenetic events. In practical terms, one needs to include many more individuals than events because multiple individuals can represent the same transformation state. Furthermore, event-order can be variable, requiring large samples to establish the frequency of variant sequences. The negative effects of inadequate sampling are predictable, and include poor resolution and underestimation of sequence variation. Unfortunately, many studies assume that unresolved order between events indicates synchronicity, leading to a false equivalence of sequence position in comparative analyses. Underestimating sequence variation results in a false assertion of fixed sequence order for events, which also affects comparative analysis. While sample size artifacts are generally unavoidable, they need to be acknowledged. The Ontogenetic Sequence Analysis (OSA) method can identify the adequacy of sequence resolution - pinpointing under-sampled regions of 'sequence-space' (which generally correspond to particular maturity levels). Knowledge of under-sampled regions of sequence-space not only informs the suitability of sequence comparison between taxa, but presents a rationale for targeted sampling to address sampling biases. Accordingly, while attempts to establish ontogenetic sequences are encouraged, even with limited samples, it is imperative to consider and evaluate sampling effects – particularly with comparative analyses. Analysis of topological differences in ontogenetic sequence-space is considered the most promising avenue for development of a method that can interpret ontogenetic sequence evolution while accounting for sequence sampling artifacts.

EVD3-2 11:45 am

Variation in onset of ossification and conserved regions of bone contact in the bony skull development of marsupial mammals.

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Abstract: Among mammals, different life strategies can be observed ranging from altricial to precocial forms at birth. Development in marsupials is specialized towards an extremely short gestation resulting in highly altricial neonates. As a result, marsupial neonates display a number of morphological adaptations at birth related to functional constraints such as the crawling behavior to reach the mother's teat directly after birth. The early fixation of marsupial neonates to the teats results in further constraints including the uniform construction of the skull in the pouch young. Little is known about the variability of marsupial skull development and how this relates to the variation observed in adult skull anatomy. We studied bony skull development in five marsupial species by μ CT-scanning specimens of various ontogenetic stages. The relative timing of the very first onset of ossification was compared to literature data and the cranial ossification sequence of the marsupial ancestor was reconstructed using squared-change parsimony. The first appearance of ossification centers shows a high range of intra- and interspecific variation with little biological implications. However, for the first time, this study presents observations on the timing of the initial developmental contacts of cranial bones in later stages of development and their evolutionary and ecological implications. Although certain bone contacts display similar levels of variation compared to the initial onset of ossification, other connections are quite conserved. Bones that surround the oral cavity are generally the first to connect and the bones of the occipital region are among the last. The sequence of bone connections can be related to a size of the respective

bones in adulthood. Overall, bone contact was shown to be more suitable for studying cranial bone diversity among species when compared to the onset of ossification.

EVD3-3 12:00 pm

Description and comparison of ossification sequences in Colombian species of frogs.

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Abstract: Colombia is one of the richest countries of the world in amphibian species, but there are very few studies about ossification sequences in Colombian species of frogs. Owing to skeleton transformations during metamorphosis in most anuran species involve ossification of structures, these data can contribute to carry on heterochrony analysis and to expand anuran phylogeny studies based on skeleton development. We describe and compare ossification sequences of chondrocranial and postcranial structures, from tadpoles to adults, of Neotropical frogs. Variability ossification ranges (ossification timing of different structures) in five hylid species and three leptodactylid ones were analyzed. Hylid species examined were *Hypsiboas crepitans*, *Dendropsophus labialis*, *Dendropsophus minutus*, *Scinax ruber* and *Trachycephalus typhonius*, and leptodactylid species examined were *Leptodactylus colombiensis*, *Leptodactylus insularum* and *Engystomops pustulosus*. Our results show that there are differences in the timing of appearance of the first ossified elements among these species, such as the transverse processes of the vertebrae. It is remarkably that the early ossification of the chondrocranial elements (*exoccipital*, *parasphenoid* and *frontoparietale*) was common in Hylidae, while in leptodactylid species the ossification timing of these elements was in later stages. Ranges and number of ossified elements presented variability in all species: In leptodactylid frogs, we found three ranges for 11 ossified elements; in hylids, more than 15 ossified elements reached into more than five ranges. We made the first phylogenetic tree of Colombian species of frogs based on cranial ossification sequences in using Parsimov and PGI. There are near 2% of ossification sequences published of almost 6500 species of frogs, showing that we are far from having a comprehensive perspective of both the ossification sequences and the heterochrony of the development in frogs.

EVD3-4 12:15 pm

Breeding with and without water: What are the consequences of terrestrialization for embryonic morphology in anuran development?

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Abstract: In all three orders of Lissamphibia (Urodela, Gymnophiona and Anura), a high number of different reproductive modes exist including terrestrial forms of development where reproduction is independent from direct access to bodies of water. The steps towards complete independence from water are not well understood in amphibian evolution, but the presence of different developmental modes, with different degrees of terrestrialization, has the potential to inform us on how a terrestrial way of development could have evolved. In anurans, alternative reproductive strategies, where the ancestral requirement for aquatic reproduction is removed, have evolved several times independently and include terrestrial larval development and direct development. Several African taxa including Afrobatrachia and Pyxicephalidae show such alternative trends towards terrestrial reproduction, ranging from complete aquatic development to complete non-aquatic, terrestrial development (terrestrial larva and direct development). In this study, embryonic and post-embryonic development of terrestrial larval developing forms (Afrobatrachia: Brevicipitidae: Breviceps and Pyxicephalidae: Arthroleptella) and direct developing forms (Afrobatrachia: Arthroleptidae: Arthroleptis) are investigated and compared with the biphasic, aquatic and semi-aquatic development of close relatives within these two groups. In general we know little about the effects of such highly modified reproductive strategies on embryonic development, especially how it differs from closely related species with a 'normal', aquatic tadpole larva. We particularly focus on the extent as to how the ancestral larval developmental pathways have been altered in terrestrially breeding frogs. The tadpole larva has been proposed to represent a distinct developmental and evolutionary module in anurans. This idea is controversial and studying species that independently evolved apparently similar modes of reproduction will help in a critical appraisal of the 'tadpole module hypothesis'.

EVD3-5 12:30 pm

Testis-ova and male gonad variability in the European blind cave salamander, *Proteus anguinus* (Amphibia: Urodela): consequence of sex-chromosome turnover?

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Abstract: The reproductive biology of the blind cave salamander, *Proteus anguinus*, endemic to underground waters in the Dinaric karst of Southern Europe, is unique in many ways. *Proteus* matures late (14 years), and has a very extended reproductive period lasting at least 30 years with a life span of more than 70 years, with females laying eggs at intervals of 6 - 12.5 years. Unlike most other salamanders, *Proteus* males and females are morphologically indistinguishable. Furthermore, the embryonic mortality rates are quite high (> 50%), and they have a sex ratio (nearly 2:1) in favor of females. The objective of this study was to describe the detailed morphology of the testes of

adult *Proteus** and determine the maturation state of the gonads with respect to body size and seasonality. We found that testis morphology is highly variable and is independent of the size of the specimen. At least three testes morphologies were found: 1) a simple narrow testis with germ cells in early stage of spermatogenesis, 2) multi-lobed testis with spermatogonia and early spermatocytes, and 3) a broad, non-lobed, elongated testis with all stages of spermatogenesis including spermatozoa. Remarkably, testis-ova were found regardless of the morphology or meiotic condition of the testes. The testis-ova were located randomly among groups of spermatogonia and spermatocytes and corresponded mainly to primary oocytes in diplotene stage with lampbrush chromosomes. Testis-ova in other species of amphibians are usually associated with hormonal dysfunction or possible exposure to endocrine disruptors. In the case of the *Proteus* we think they might be related to current evidence that *Proteus* has undergone a sex-chromosome turnover involving X-Y translocation. *The testes were removed from preserved archived specimens collected for other research purposes with permission of the Ministry of the Environment and Spatial Planning of the Republic of Slovenia. (35701-81/2004-9 and 35601-1/2010-6).

EVD3-6 12:45 pm

The phoenix rises: reversal of cave adaptations in the blind cave salamander, *Proteus anguinus* (Amphibia: Urodela: Proteidae).

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Abstract: The blind cave salamander, or olm, *Proteus anguinus*, inhabits caves in the Dinaric Karst of the Balkan region of Southern Europe. It is the largest cave-adapted (troglomorphic) vertebrate in the world, and the only troglomorphic vertebrate in Europe. Isolated populations of *P. anguinus* probably represent several species. Most of these are troglomorphic "white" forms, with little or no pigment and vestigial eyes, and are currently assigned to the subspecies *P. a. anguinus*. A single population of pigmented, non-troglomorphic "black" *Proteus*, with developed eyes and dark pigment, is currently assigned to a separate subspecies, *P. a. parkelj*, that is thought to resemble the common ancestor from which the troglomorphic olms evolved (Sket and Arntzen, 1994). Biochemical and molecular studies (Sket and Arntzen, 1994; Goriki and Trontelj, 2006), however, reveal that the "black olm" is more closely related to a geographically adjacent population of "white olm" than that population of white *Proteus* is to other populations of white *Proteus*. Thus, either a) the troglomorphic form has evolved multiple times independently, or, more parsimoniously, b) the black form evolved from a white ancestor (cf. Ivanovi et al., 2013). Recent research on the developmental genetics of cave adaptations in the Mexican Blind Cave Fish, *Astyanax mexicanus* (Jeffery, 2005), allows us to hypothesize the evolutionary developmental mechanism by which such transformations could have occurred in *Proteus*. Testing this idea could contribute to our understanding of how major transformations come about in morphological evolution but will require access to embryonic material of both subspecies of *Proteus*. Goricki, S, P Trontelj (2006) Gene 378:31-41. Ivanovic, A, G Aljancic, JW Arntzen (2013) Contributions to Zoology 82:107-114. Jeffery, WR (2005) J. of Heredity 96:185-196. Kos, M, B Bulog, ASP Roehlich (2001). Cell Tissue Res 303:15-25. Sket, B, JW Arntzen (1994). Bijdragen tot de Dierkunde 64:33-53.

EVD4-1 2:30 pm

The domestication of the neural crest – A developmental perspective on the origins of morphological variation in mammalian breeds and land races.

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Abstract: Studies on domestication are blooming, but the developmental bases for the generation of domestication traits and breed diversity remain largely unexplored. Some phenotypic patterns of human neurocristopathies are suggestive of those reported for domesticated mammals, and disrupting neural crest developmental programs have been argued to be the source of traits deemed the 'domestication syndrome'. These character changes span multiple organ systems and morphological structures. But the distribution of such traits in the phylogeny of domesticated mammals is not universal, with canids being the only group showing a large set of predicted features. Modularity of traits tied to phylogeny characterizes domesticated mammals: through selective breeding, individual behavioral and morphological traits can be reordered, truncated, augmented, or deleted. Similarly, mammalian evolution on islands has resulted in suites of features much like those found in domesticated species. Some morphological features of domesticated mammals that were considered to be the result of juvenilesation have proven not to be so. This does not exclude the potential relevance of heterochrony in the evolution of domesticated species and breeds, as shown by new cranial and postcranial data on domesticated dogs and other species. There are many postnatal markers of growth, which together with morphometric studies of skull form, serve to examine local cases of developmental repatterning. Some features of breeds of domesticated mammals resemble abnormal conditions in humans (e.g., midfacial hypoplasia), but this has not been characterized from a developmental morphology perspective. Many domesticated mammals can serve as valuable models for conducting comparative studies on the evolutionary developmental biology of the neural crest given that series of their embryos are readily available and that their phylogenetic histories and genomes are well characterized.

EVD4-2 2:45 pm

Developmental basis behind the evolutionary origin of the diaphragm.

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Abstract: The diaphragm, a skeletal muscle settled deep in the thorax, represents an evolutionary novelty of the mammalian lineage. In the embryonic development, the diaphragm is differentiated from somitic muscle precursor cells within the pleuroperitoneal fold (PPF), a paired medial protrusion of the lateral body wall. The other vertebrates do not possess muscles corresponding to the diaphragm, and, owing to this difficulty, the evolutionary origin of the diaphragm has not been fully proven yet. Based on comparative morphology of the brachial plexus, we inferred that the diaphragm was acquired through a duplication of the subscapular muscle concomitant with a caudad shift of the shoulder girdle during evolution. Here, we investigated the development of the cervico-pectoral region to elucidate the developmental basis behind the evolutionary origin of the diaphragm. First, we compared the transformation of the lateral body wall during development between mouse and chicken embryos. In the mouse, the PPF initially developed at the cervical level slightly cranial to the base of forelimb bud, and later became encapsulated within the thorax. An equivalent movement was observable in the chicken embryo. We demonstrated that the cells of the somatopleure at the cervical somite levels later become distributed within the thorax in the chicken embryo, through experiments of homotopic transplantation of the somatopleure of quail embryos into chicken embryos. Therefore, the novel developmental mechanism for the diaphragm was principally the repatterning of the muscle precursor cells in the cervical lateral body wall. From this perspective, we analyzed the difference in expression pattern of the Hox4–6 paralogous group genes between mouse and chicken embryos. *Hoxc5* in particular expressed differently in the lateral body wall between these species, and its expression at the PPF and cranial part of the forelimb bud in the mouse potentially reflects the evolution of the diaphragm.

EVD4-3 3:00 pm

A cryptic sacral series that varies in count but not size defines the modular organization of the vertebral column in odontocete cetaceans.

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Abstract: Almost all living mammals are terrestrial quadrupeds, and their vertebral columns resemble those of ancestral taxa in both organization and count. Mammals with extreme adaptations allow new insights into the possible range and developmental control of column transformation over evolutionary time. Odontocete cetaceans are unusual in the apparent lack of a sacral series. Vertebral counts of most taxa are extremely elevated, but increases are unequally distributed among series. Surprisingly, high-count taxa are not elongate, because counts vary inversely with vertebral centrum length. Following recent evidence that morphologically de-differentiated columns may be cryptically regionalized, we used spinal nerve origin, vertebral shape, and fetal ossification patterns to identify and characterize possible sacral vertebrae in odontocetes. We used the pudendal plexus, invariably located at S1 or S2 in quadrupeds, as a proxy for the axial location of the first sacral vertebra. This marker and the anterior boundary of the tail delimit a field within the lumbar series whose count increases directly with total column count. These vertebrae are also separable from anterior lumbar using geometric morphometrics, and ossify earlier in development than either anterior lumbar or caudal vertebrae. We conclude that the sacral series is still regionalized, and that lumbar, sacral, and anterior caudal vertebrae are integrated into a developmental module that undergoes a shared rate of somitogenesis distinct from that of other series. We propose that odontocete column reorganization occurred first by loss of primaxial : abaxial interaction at the sacrum, then by integration of lumbar, cryptic sacral, and anterior caudal vertebrae into a shared module, and finally by repeated, convergent increases to the count of this novel module. These data lend strong support to the currently debated hypothesis that vertebral count and identity assignment are independently regulated.

EVD4-4 3:15 pm

Anatomical tests of *Hox* gene function in a derived vertebrate body form: “Deregionalization” and the role of *Hox10* in the evolution of snakes.

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Abstract: The roles of *Hox* genes in regional patterning of the vertebrate A-P axis are well understood for model taxa and have been used to infer *Hox* modification in the evolution of novel body forms. The function of *Hox10* paralogs to produce a distinct, ribless lumbar region of the presacral vertebral column is documented in *Mus*, and examination of *Hox10* expression in snakes suggests that rib suppressing functions are secondarily inhibited, resulting in rib expression and loss of a lumbar region in the evolution of the snake body form. The ancestral presence of a ribless lumbar region in the lineages leading to snakes and the distribution of lumbar regions within Squamata have never been determined, however. To compare experimental results with evolutionary histories of lumbar regionalization, we characterized posterior presacral axial morphology as discrete characters (ribless lumbar, fused terminal ribs, free ribs) in 130 species of extant and fossil lepidosaurs and sauropterygians. We mapped morphologies onto comprehensive molecular and morphological phylogenies of Lepidosauria, and used Maximum Likelihood and Maximum Parsimony analyses to reconstruct ancestral node values for Squamata and constituent clades, including snakes. Lumbar regions occur in multiple clades; however, ancestral state reconstructions do not unambiguously support a hypothesis of secondary loss of a ribless lumbar region in the evolution of snakes, regardless of tree

topology or reconstruction method. Instead, snakes are either nested deeply within a clade that lacks a lumbar region regardless of body form, or the ancestral condition for the clade is equivocal. Our results do not support evolutionary polarities of *Hox10* function inferred from comparing *Mus* to snakes, and instead suggest more complicated histories for the roles of *Hox10* in patterning the vertebral column. This research is funded by a Wellcome Trust ISSF Joint Grant to JJH.

EVD4-5 3:30 pm

Size, not age, predicts feeding morphology and kinematics among guppy offspring and juveniles.

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Abstract: Large offspring size is routinely selected for in highly competitive environments, such as in low predation populations of the Trinidadian guppy (*Poecilia reticulata*). Low predation guppy environments have low predator density, large guppy biomass and limited supply of benthic algae encrusting the rocky floor. Large offspring are more successful than their smaller counterparts when competing for such limited resources, but the functional mechanisms underlying this advantage are unknown among guppy neonates. We measured cranial musculoskeletal morphologies and jaw kinematics during scraping in neonates and postnatal juveniles from two low-predation (LP) and three high-predation (HP) populations of Trinidadian guppy. Feeding morphology and jaw kinematics vary substantially with guppy neonatal size. Percentage of cranial elements ossified varies over 4-fold from smallest (20%) to largest (90%) neonates. The surface area of the jaw-closing muscle, the adductor mandibulae, scales with positive allometry relative to body length ($L^{2.72}$) indicating growth of the muscle outpaces growth of the body. Maximum gape also scales with positive allometry ($L^{1.20}$), indicating larger neonates are capable of greater jaw excursion. Rotation at the intramandibular joint, but not the quadratoarticular joint, increases with body length among guppy offspring. Average IMJ rotations of neonates range from 11.7° in the smallest HP neonates to 22.9° in the largest LP neonates. Additionally, we find that feeding morphology and kinematics continue to scale with size among juveniles, such that 10-day old juveniles from the highest predation populations are equivalent to newborn offspring from low predation populations. We show that larger LP offspring possess more mature feeding morphologies and kinematics at birth, and that HP juveniles acquire similar traits when grown postnatally to equivalent sizes of LP neonates.

EVD4-6 3:45 pm

Modelling human skull development.

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Abstract: Introduction: During the first year of life the human skull undergoes rapid morphological changes in both size and shape. Understanding the biomechanics of skull growth and in particular the relationship between forces induced by the growing brain during normal skull development would be useful. The aim of this study is to explore these relationships by developing a computational model of human calvarial growth. Methods: A 3D printed physical model and an equivalent finite element model (FEM) were developed from a micro-computed tomography scan of a newborn infant skull. Both models were created to investigate skull growth from birth by simulating brain volume expansion with the goal of replicating observed changes in *in vivo* head measurements. The physical model was used to validate the FEM at ages 0, 1 and 2 months, after which a second FEM was created which predicted growth from 0 to 12 months in an actual skull and compared to clinical CT scan data. Parameters considered included: skull width, skull length and circumference. Results: In both the physical model and FEM, cranial measurements increased gradually with age in line with reported *in vivo* measurements. For example, over 2 months the 1st FEM predicted an increase of 10%, 9.6% and 9.6% compared to 9.9%, 5.2% and 8.2% found in the physical model for width, length and circumference. The 2nd FEM predicted increases of 21.1%, 27.4%, 21.73% in width, length and circumference respectively, which was comparable to 23.3%, 24.2% and 25.9% reported in the literature. Over the 12-month growth period considered, the largest difference between the 2nd FEM's predicted values and *in vivo* measurements was 11.4%. Conclusions: Despite the limitations of all three models, their predicted behaviours compare well with the available *in vivo* data. The next stage of the work involves an investigation into changes in skull development in patients affected by different forms of craniosynostosis.

EVD5-1 4:30 pm

Divergence and elaboration of skeletal musculature in early vertebrates.

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Abstract: Jawed vertebrates possess two distinct groups of skeletal muscles in the trunk, epaxial and hypaxial muscles, primarily defined by the pattern of motor innervations. Of these, the hypaxial group includes muscles with highly differentiated morphology and function, such as the muscles associated with paired limbs and girdles and the tongue muscles. During embryogenesis, these muscles are formed by the extensive distal migration of precursor cells from ventral edges of the somites, a developmental process in which the paired box transcription factor Pax3 plays a key role. In order to clarify the evolutionary mechanisms underlying the variety of hypaxial musculature, we have compared the morphology and molecular signature of the skeletal muscles of several species that diverged

early in vertebrate evolution. The cyclostome lamprey lacks many of morphological features of the gnathostomes, such as jaws, paired fins and epaxial/hypaxial distinction of the trunk skeletal musculatures, but possess the hypobranchial muscles that are apparently homologous to the gnathostome tongue muscles. On the other hand, the elasmobranchs possess paired fins and other gnathostome-like body plan, yet the myogenetic pathway of each muscle has yet to be clarified. Using these animals, we examined the expression of developmental markers and delineated the temporal order of differentiation of various skeletal muscles, such as the hypobranchial, posterior pharyngeal and cucullaris (trapezius) muscles, all located near the head-trunk interface. Our analysis has provided new insights regarding cellular and molecular characteristics of each musculature and illustrated how they have contributed to the complexity and diversification of vertebrate morphology.

EVD5-2 4:45 pm

A single mutation reveals latent capacity for limb-like development in the zebrafish.

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Abstract: The diversification and specialization of the paired appendages are hallmarks of vertebrate evolution. In the lineage leading to tetrapods, the appendicular skeleton was elaborated along the proximal-distal (PD) axis by adding articulated skeletal elements to form the stylopod (humerus), zeugopod (radius/ulna), and autopod (wrist/hands) of the limbs. This tripartite skeletal pattern has remained constant during the 360 million years of tetrapod evolution. In contrast, the teleost fish lineage shows a reduced appendicular skeletal pattern with a diminutive endochondral skeleton, consisting of only proximal radials and small, nodular distal radials along the PD axis. This pattern is canalized and has persisted over 250 million years of teleost evolution. Using a forward genetic approach in the zebrafish, we have discovered an adult-viable, dominant mutation that results in the acquisition of supernumerary radial bones located between the proximal and distal radials. Unlike the proximal radials, these extra elements have both proximal and distal growth zones and articulate with proximal and distal radials. Ontogenetic analyses reveal that the new elements develop from the branching and splitting of cartilaginous condensations in a fashion similar to that seen in tetrapod limb development. Unexpectedly, the extra elements are sometimes directly connected to musculature, which is not observed in wild type radials. An analysis of early development shows modification of known limb developmental gene networks in mutant fins. The genetic alteration in this mutant reveals the latent capacity for skeletal elaboration in fins of fishes and may inform our understanding of 'limbness' and the fin to limb transition.

EVD5-3 5:00 pm

Establishing proportion: a hypothesis for the role of the vasculature in zebrafish fin length mutants.

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Abstract: The zebrafish (*Danio rerio*) is a unique research model that can be used to explore regulation of proportional growth during vertebrate development. In adult wild-type zebrafish, the relative proportion of fin to body length is constant, even following fin amputation and subsequent regeneration. We studied the *Schleierschwanz* (*Schw*) mutant zebrafish, which displays long fins as a dominant Mendelian trait. We found that *Schw* exhibits overgrowth of all fins and barbs, with an average caudal fin length: body length ratio of 0.49 as compared to 0.21 in wildtype fish. We further characterized the *Schw* mutant by studying its vasculature. Introduction of the *Schw* mutation into a transgenic line, in which green fluorescent protein is expressed under the control of a vascular endothelial-specific promoter (*fli::GFP*), revealed that caudal fins in *Schw* contain arteries and veins that are over twice the diameter of similarly located vessels in wild type fish. In addition, preliminary particle image velocimetry (PIV) analysis of blood flow in the caudal fin tips revealed that although arterial blood velocity does not differ between mutant and wildtype, the velocity of venous blood is significantly slower in mutant individuals (5.39 mm s⁻¹ and 1.55 mm s⁻¹, respectively). This appears to result in a backlog of blood in the distal tips of the caudal fins in *Schw* mutants. As a result of our findings, we postulate that greater blood flow to the fins may result in longer fins by increasing exposure of fin tissues to circulating growth factors or by altering signaling from vascular smooth muscle cells. The *Schw* model may provide insight into underlying causes of fin length differences in natural populations of fish and in proportion systems, like limbs and antlers, in other vertebrates.

EVD5-4 5:15 pm

How is preaxial polarity established in limb development? A comparison of larval and direct developing salamanders to other tetrapods.

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Abstract: The pattern of limb development in extant tetrapods is highly conservative in a number of aspects, including overall patterns of gene expression as well as skeletal condensation. Tetrapods exhibit "postaxial polarity" –

digital cartilages condensate in a sequence of IV-V-III-II-I inside of a preformed “paddle”. This paddle allows expressed genes to diffuse and to establish gradients across the limb field, which produce positional information and regulate the polarity of the developing limb. However, salamanders are the only extant tetrapod clade showing a reversed pattern. Their digital cartilages condensate in a sequence of II-I-III-IV-V, a pattern called “preaxial polarity”. Furthermore, a striking interspecific diversity can be seen in the ontogenetic timing of limb and digit development. Most salamanders with free-swimming larvae, e.g. the Mexican axolotl, bud their digits one by one, whereas in the direct developing plethodontid salamander *Desmognathus aeneus* limb development undergoes a paddle stage comparable to other tetrapods. Although some classic limb developmental genes have already been investigated in early limb bud stages of axolotls, it remains unclear how the positional information and polarity of the digits are established. Furthermore, limb development via a paddle stage in *D. aeneus* has only been described morphologically, but gene expression has not been investigated. We morphologically described limb development of four more species of the family Plethodontidae, which all show a paddle stage during limb development regardless of their developmental strategy (larval or direct development). Furthermore, we investigated gene expression patterns of some more limb development genes in the axolotl and compared them to gene expression patterns in plethodontid salamanders. The data show some obvious differences to other tetrapods and provide new insights into mechanisms underlying preaxial polarity in salamander limb development.

EVD5-5 5:30 pm

Probing the cellular and genetic mechanisms involved in producing bone length variation using the Longshanks mouse.

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Abstract: The main molecular and cellular processes involved in limb development are relatively well known, however, the aspects of these processes that generate continuous, selectable variation in bone length within a population are still poorly understood. To study the cell and molecular mechanisms of variation in this complex trait, our research group selectively bred mice (Longshanks mice) to increase relative tibia length by approximately 15%. We performed histomorphometry and gene expression analyses in the proximal tibial growth plate to study the mechanisms underlying bone length variation. Histomorphometry shows that the proliferative zone is larger and has more cells in Longshanks compared to random-bred Control mice, whereas there is no difference in hypertrophic chondrocyte size and number. These data suggest that strong selection for increased tibia length produces changes in chondrocyte proliferation, with downstream effects on the rates of hypertrophy and apoptosis. Analysis of gene expression between Longshanks and Control proximal tibiae using RNA sequencing identified a few genes that are significantly differentially expressed, and which are known to be involved in growth plate function, such as *Ifi202b* and *Ifi204*, *Frzb*, *C1qtnf3* (cartonectin) and the transcription factor *Stat1*. Surprisingly, there was little to no difference in genes known to be involved in mediating the chondrocyte life cycle and chondrocyte differentiation, such as *lhh*, *PTHrP*, *Bmps*. Our results suggest that the main mechanism producing longer bones in Longshanks is an increase in chondrocyte proliferation and bone apposition rate. This process seems to be regulated by only a small number of genes previously known to be involved in the growth plate.

EVD5-6 5:45 pm

The role of *Hox* in pisiform and calcaneus ossification and the nature of the zeugopod/autopod boundary.

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Abstract: The wrist and ankle, or mesopodium, form at the boundary between the zeugopod and autopod and are composed of short nodular bones that typically lack growth plates. *Hoxa11* and *Hoxa13* are expressed in mutually exclusive proximal-distal domains that demarcate the zeugopod/autopod boundary. Similarly, *Hoxd* genes are deployed in two distinct phases during limb development. The early phase corresponds to proximal segments including the zeugopod and a late phase occurs in the digits. This arrangement produces a gap of low *Hoxd* expression that generally corresponds to the mesopodium. In contrast to the other bones of the wrist and ankle, the mammalian pisiform and calcaneus form true growth plates. We show that these bones develop within the *Hoxa11* and *Hoxd11* expression domains. We also observe that the pisiform growth plate becomes disorganized with *Hoxa11* or *Hoxd11* loss-of-function indicating a direct role for *Hox11* in its development. *Hoxa13* loss-of-function has minimal effect on the pisiform and proximal calcaneus as these bones still form secondary centers and undergo longitudinal growth. Consideration of the phenotypes resulting from hypodactyly (*Hd*) and synpolydactyly homolog (*Spdh*) mutations, which result from altered HOXA13 and HOXD13 proteins respectively, confirms that *Hox13* plays a limited role in the development of the pisiform and calcaneus and suggests that they lie within the early phase of *Hox* expression. Therefore, with respect to patterns of ossification and gene expression, these bones share much more in common with the zeugopod than the autopod. Such an interpretation fits with the timing of autopod origins during tetrapod evolution. This work is supported by the NSF (BCS-1540418) and a Hill Fellowship, Department Anthropology, Pennsylvania State University.

Contributed Session — Feeding (FED)

FED1-1 2:30 pm

Assessing the role of the rostrum in skull variation and feeding performance among billfishes: a 3-D Geometric Morphometric approach.

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Abstract: Feeding is perhaps one of the major drivers of skull diversification and the acquisition of novel structures can amplify this diversity. However, new structures can be costly, limiting structural space and sometimes jeopardizing organismal performance. Billfish are a group of fishes characterized by the elongation of their upper jaw. This structure utilized as a feeding weapon is morphologically diverse within the group, offering a good opportunity to investigate how changes in rostrum morphology could influence skull variation. In this study we investigated the role of the rostrum and potential trade-offs in cranial architecture by the use of 3-D geometric morphometrics. Subsequent implications of rostral morphology in billfish feeding performance were also evaluated. A total of 55 digital landmarks were positioned along the skulls of five billfish species and wahoo. Warping analysis showed most of the variation to occur between swordfish and istiophorids. Swordfish had an abrupt reduction in skull dimensions and an elongation of the rostrum. Within istiophorids, most of the variation was found between blue marlin and shortbill spearfish, not only in rostrum length, but also in relative lower jaw length. Billfish species with relatively long rostrums showed relatively short lower jaws. No trade-offs were found between eye size and muscle size suggesting that the eye may be under selective pressure to remain the same. The possible implications of these results are discussed within an ecological context.

FED1-2 2:45 pm

Evolution of mysticete-like filter feeding in plesiosaurs of the austral Late Cretaceous.

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Abstract: The marine reptiles of the Cretaceous of the southern hemisphere have puzzled paleontologists for decades. Despite abundant fossil material, basic questions of morphology and taxonomy of the austral elasmosaurs (Plesiosauria) have defied repeated analysis, largely due to the bizarre anatomy of the animals involved. Here we report a new synthesis of cranial fossils from Antarctica, Chile, and New Zealand, allowing the first confident cranial reconstruction of the entire skull of a derived member of the Aristonectinae. The cranial anatomy of *Morturneria seymourensis* is radically derived relative to all other plesiosaurs, possessing an unprecedented suite of dental and oral cavity adaptations. Both the upper and lower dentition form a sieving oral battery that is unique among vertebrates, yet probably functioned like baleen in straining food particles from water ejected from the oral cavity. The volume of the oral cavity is increased enormously by a posteriorly displaced jaw articulation and broad, hooped mandible. The palate is also highly vaulted, a condition unique among plesiosaurs. Several osteological correlates demonstrate the presence of a large, distensible gular pouch. This highly derived suite of adaptations is shared by extant mysticete cetaceans, and we hypothesize that it functioned in a similar manner. This is the first identification of whale-like sieve feeding in any marine reptile, a condition once claimed to be anatomically impossible. Further review of southern hemisphere elasmosaurs suggests significant taxic and trophic diversity, revealing a Late Cretaceous circumpolar marine ecosystem populated with filter-feeding plesiosaurs highly reminiscent of the mysticete whales living there today.

FED1-3 3:00 pm

Bioinspired design: A novel mechanism of filtration based on manta ray feeding.

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Abstract: Filtering particles from fluids is ubiquitous, both in nature and in engineered systems. In particular, filter-feeding is used to capture small (20-2000 micron) food particles in a wide variety of aquatic organisms from sub-millimeter bryozoans to 12 m whale sharks. Intriguingly, mobulid fishes (mantas and devil rays) appear to use a particle filtration mechanism that is distinct from previously described systems. Mobulids are obligate ram suspension feeders who can filter particles without any noticeable clogging along their filters. We have created bioinspired physical models of manta ray filters to identify the basic hydrodynamic principles of filtration in three biologically relevant variations: smooth lobe filters, denticulate lobes, and lobes with finger-like projections. The location and form of these morphological structures suggest that they play an important role in controlling turbulence and boundary layer separation at the filter pore. We have documented a new modality of filtration in a vertebrate system, cyclonic filtration, that works in conjunction with cross-flow filtration to filter particles both larger and smaller than the filter pore size while also eliminating clogging at the filter surface.

FED1-4 3:15 pm

Ontogeny of a cypriniform filter-feeding novelty.

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Abstract: Silver carp, as well as a number of other Asian carp, have garnered recent interest as invasive species well-established within several American rivers and threatening to enter the Great Lakes. Part of the reason for their success has been their capacity to feed so efficiently within eutrophic environments. While previous research has described the structure and function of the epibranchial organ (a snail-shaped structure comprised of highly modified branchial arches used to concentrate material filtered from the water column) other aspects of their feeding anatomy have been ignored. Although concentration of phytoplankton is important for efficient feeding, the actual filtration mechanism at the level of the gill rakers has not been investigated within a functional context. This is a particularly glaring omission given that silver carp possess highly derived gill rakers that interdigitate with extended ventral folds of the palatal organ. The palatal organ is an important structure located on the dorsal pharyngeal roof. Previous work has shown that it is important in a specialized type of feeding that characterizes goldfish and carp, in which particulate matter is captured by localized protrusion of this muscular structure. Recent work in our lab has revealed that the overwhelming majority of cypriniform species examined have a muscular palatal organ, however the specialized nature of the palatal organ of the silver carp rivals anything previously described. It has been suggested that the large palatal organ is simply used as a piston pump to drive water through the gill rakers. Given the complex muscular architecture of each palatal fold this proposed mechanism seems overly simplistic.

FED1-5 3:30 pm

Forelimb morphology determines prey processing style in pinnipeds (Mammalia, Carnivora).

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Abstract: Living pinnipeds show a range of forelimb morphologies that reflect their method of aquatic locomotion. Otariids (fur seals and sea lions) have hydrofoil-shaped forelimbs used to propel themselves underwater, whereas many phocids (true seals) have less aquatic-specialised forelimbs with dexterous digits and robust claws, and accordingly rely on their hind limbs to generate propulsion. In terrestrial and semi-aquatic mammals, the forelimbs frequently play an important role in feeding behaviour. We aimed to discover whether, and to what degree, pinnipeds use forelimbs to deal with prey. We investigated skeletal and muscular forelimb anatomy using skeletal specimens, dissections and MRI/CT scans. We then related morphology to foraging behaviours observed during field observations and captive feeding trials, as well as data from the literature. We found marked differences in prey processing behaviour that correlate with forelimb anatomy. Phocine seals, which have the least modification of forelimbs relative to their ancestral (i.e. terrestrial) condition, resemble smaller, semi-aquatic mammals in securing prey in their clawed forelimbs while tearing off pieces using their teeth. By contrast, most otariids do not use their forelimbs and instead process large prey by holding it in their teeth and shaking it at the surface, breaking it into swallowable pieces. There is also a trend among monachine phocids away from clawed forelimbs and towards more "otariid-like" flippers (including leopard seals), apparently with similar functional limitations. Overall, living pinnipeds demonstrate the morphological transition from clawed, dexterous forelimbs to the more derived, flipper-like anatomy considered typical of marine mammals. The link between pinniped forelimb morphology and other aspects of their biology may plausibly extend to fossil species, and thus provide new insights into how and when their ancestors adapted to life in the sea.

FED1-6 3:45 pm

Independent transitions to a more goose-like beak in waterfowl (Aves: Anseriformes) correlate with a performance trade-off between terrestrial and aquatic feeding.

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Abstract: The evolution of beak shapes in birds to match a particular diet is a classic example of adaptation. Yet, the correlation between beak shape and diet has been tested in relatively few groups. Additionally, in most cases the precise relationship between beak morphology and feeding function remains unclear. The bird order Anseriformes, which includes ducks and geese, is an ideal group in which to test the relationship between beak structure and function: waterfowl exhibit diverse beak shapes and their diets are among the best documented of any bird order. I collected data on 3D beak curvature from museum specimens representing 49 species in Anseriformes (including two extinct forms) and 13 species in Galliformes, the sister group to Anseriformes, using a recently published stereo camera method. For 43 of these species I also compiled diet data from the literature, classifying each dietary entry to create several continuous characters representing dietary composition (proportion animal, seeds, herbivory, terrestrial, etc.). Geometric morphometric analysis reveals that the major axis of shape variation describes convex ("goose"-like) versus concave ("duck"-like) curvature of both the culmen (upper ridge) and tomium (biting edge) of the beak. Additionally, models of trait evolution show independent transitions toward a more goose-like beak from a more duck-like beak. Of all the dietary characters, the major axis of shape variation correlates most strongly with whether food items are acquired in an aquatic or terrestrial environment. This parallels a previously described performance trade-off in waterfowl between filter-feeding (aquatic) and grazing (terrestrial), strengthening the argument that a more convex culmen and tomium represent adaptations to grazing. The results of this study additionally raise the

possibility that performance trade-offs may be a principal driver of major axes of shape variation in functional systems more generally.

FED2-1 9:30 am

XROMM and VROMM studies of suction feeding in fishes.

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Abstract: Suction feeding in actinopterygian and chondrichthyan fishes relies on coordinated and highly three-dimensional motion of skeletal elements. We can now quantify these motions by using X-ray Reconstruction of Moving Morphology (XROMM) to produce accurate animations of 3-D skeletal shape and in vivo movement. In bamboo sharks we used marker-based XROMM (with conical carbide markers) to track the motions of the cranial cartilages. Long-axis rotation (LAR) cannot be detected from markers alone, but rigid-body animation in XROMM yields full 6 degree-of-freedom motion, including LAR. For Meckel's cartilage we found 10-15° LAR in one direction (supination) prior to peak gape, and then 20-25° of fast pronation after peak gape. The ceratohyal also showed slow LAR of 10-20° before peak, and rapid counter-rotation of 10-40° after peak gape. The hyomandibula showed 10-50° of rapid LAR in just one direction. In ray-finned fishes we used spherical tantalum markers for XROMM animation of cranium, maxilla, mandible, suspensorium, operculum, hyoid bar, urohyal and pectoral girdle. We generated a dynamic digital endocast from the XROMM skeletal animations to measure the instantaneous rate of buccal volume expansion and instantaneous suction power. We mapped cranial muscles onto the XROMM skeletal animations to measure muscle strain, and measured body muscle strain with fluoromicrometry. In largemouth bass we found that the cranial muscles generate a negligible amount of power, and instead more than 95% of the power for high-performance strikes comes from axial muscles. Additionally, by combining XROMM with kinematic modeling we find that a 3-D, 4-bar model provides a good representation of opercular linkage kinematics in largemouth bass and significantly outperforms a planar, 4-bar model. A new method, Video Reconstruction of Moving Morphology (VROMM), shows promise for XROMM without X-rays, particularly for superficial bones such as the cranial bones of actinopterygians.

FED2-2 9:45 am

Comparative biomechanics of biting vs. suction feeding in fish.

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Abstract: Suction feeding and biting are the two most common feeding modes in living aquatic and terrestrial vertebrates respectively. However, the evolution of biting for terrestrial feeding in tetrapods from their aquatic suction feeding ancestors remains poorly understood. This is partly due to a lack of comparative data from living functional analogues of fossil taxa. Here, we use comprehensive three dimensional finite element analysis to investigate the mechanical performance of the lower jaw in three extant fishes: *Esox lucius* (Actinopterygii: Teleostei), *Anguilla anguilla* (Actinopterygii: Teleostei) and *Polypterus senegalus* (Actinopterygii: Polypteriformes). High speed video footage demonstrates that *Esox* is primarily a suction feeder, whereas *Anguilla* is a known biter. *Polypterus* is the most basal living ray-finned fish and a widely used extant analogue of early tetrapods. We use stress metrics to compare mandibular structural strength, and strain energy to determine the mechanical efficiency of the lower jaw. The jaws of *Anguilla* are stronger and more efficient than those of *Esox*; we interpret these differences as a result of selection for increased bite force production in *Anguilla* and the need for the lower jaw to withstand these higher forces, suggesting clear differences in jaw mechanics between a biter and suction feeder. Whilst broader studies are needed, functional data from extant taxa could help elucidate feeding function in fossils. *Polypterus* is intermediate between *Esox* and *Anguilla* in terms of both jaw strength and efficiency. This suggests that *Polypterus* is capable of using a mixture of biting and suction feeding for prey capture, which implies that stem tetrapods may have functioned in a similar manner. The capacity for biting and terrestrial-style feeding likely evolved early on in the tetrapodomorph lineage while the ancestors of tetrapods were still aquatic.

FED2-3 10:00 am

Feeding behavior variation in polyphenic bluegill.

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Abstract: Polyphenic populations are a valuable resource for understanding the relationship between form and function. Morphological variation within a population can have dramatic impacts on performance and subsequently fitness. In Lake Waban (Wellesley, MA) bluegill (*Lepomis macrochirus*) have diverged into two ecomorphs which occupy pelagic and littoral habitats. Based on morphological variation of the oral jaws and diet studies, we

hypothesized that littoral individuals would use more suction during feeding than pelagic fish. To address this hypothesis we measured pressure and kinematics during prey capture on earthworms, mealworms and brine shrimp. We found that littoral fish used more suction when feeding on all prey types and varied their feeding behaviors dependent on prey type. Similarly, the littoral ecomorph traveled a greater distance during feeding, suggesting that they use more ram than the pelagic fish. Pelagic bluegill exhibited a stereotyped feeding behavior for all prey types, which suggests that they have reduced modularity during feeding. These results give further credence to the divergence in behavior and morphology that is seen when comparing two phenotypes of bluegill. Future studies will investigate differences in muscle morphology and mechanics between these phenotypes.

FED2-4 10:15 am

Where does the vertebral column bend during suction feeding in fishes? A comparative study of axial bending during cranial elevation.

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Abstract: During suction feeding, many fishes use their epaxial muscles to generate a substantial amount of power to produce cranial elevation. When the muscles contract, they reduce the angle between the head and body, causing the axial skeleton to bend dorsoventrally. Axial bending increases cranial elevation and improves feeding performance, but is not well studied. The goal of this study is to locate where the vertebral column bends during suction feeding and relate it to the axial morphology of different species. We collected and analyzed live feeding data from three species (largemouth bass, pacific staghorn sculpin, and striped surfperch) using XROMM and VROMM. We used joint coordinate systems to measure relative motion between the neurocranium and body plane to determine the degree of cranial elevation and the location of the axis of rotation (AOR). We also analyzed the morphology of the axial skeleton. We found that largemouth bass had AORs centered around vertebral joints 2 and 3 (42 and 58% of strikes, respectively). Striped surfperch had AORs centered around joints 1, 2, and 3 (25, 56, and 19%). Finally, AORs of staghorn sculpin were located in joints 3 through 7. Surfperch and bass AORs were associated with spaces between the neural spines and epineural bones. Moreover, surfperch and sculpin AORs were in the anterior vertebrae where the zygapophyses articulate. Despite the similar locations of the AORs of largemouth bass and striped surfperch, there were significant differences in the amount of cranial elevation they produced. As such, more posterior AORs are not necessarily associated with greater cranial elevation. This is particularly evident in staghorn sculpin, in which the same AOR (joint 6) produced some of the highest and lowest cranial elevations (35° and 12°). Given the great deal of interspecific variation of the axial skeleton, it is important to investigate the role of these different morphologies in suction feeding.

FED2-5 10:30 am

Built to bite? Bite performance based on 3D-reconstructions in European glass eels (Teleostei: Anguilliformes).

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Abstract: In the yellow eel stage of both the European and Japanese eel (*Anguilla anguilla* and *A. japonica* respectively), two phenotypes can be found: narrow- and broad-heads. This dimorphism has been linked to dietary differences, with the broad-headed phenotypes feeding on hard prey and the narrow-headed ones feeding on soft prey. The broad heads are therefore associated with larger adductor mandibulae muscles, which increase their bite force. Next to this, they exhibit an elongated lower jaw with a larger coronoid process, providing a larger surface to which the adductor mandibulae can attach. Interestingly, recent research showed that broad- and narrow-headed phenotypes are already present in the non-feeding glass eel stage of the European eel, the predecessor of the yellow eel stage. It was then hypothesized that broad-headed glass eels might be better suited to start feeding on hard prey. Here, we wanted to test this hypothesis by studying the morphology of broad- and narrow-headed glass eels. To study the morphology of the glass eels, heads of 5 narrow- and broad-heads were CT-scanned. These scans were then used to make 3D-reconstructions of the cranial musculoskeletal system. Next to this, a newly developed 3D-bite model was used to assess the bite force of the glass eels based on these reconstructions. We found that broad-headed glass eels are already characterized by larger adductor mandibulae muscles, which were associated with higher bite forces compared to the narrow-headed ones. The measured bite forces were still very low, which could be expected since the glass eels are not actively feeding yet. Nevertheless, these results imply that broad-headed glass eels would be indeed better suited to start feeding on hard prey, which could eventually result in the dimorphism observed in the yellow eel stage.

FED2-6 10:45 am

Premaxillary protrusion in Lampriformes: innovations and radiations.

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Abstract: Jaw (premaxillary) protrusion is thought to be a key innovation correlated with the subsequent radiation and diversification of fishes. Extreme amounts of protrusion are associated with suction prey capture, often on highly

elusive prey. Notable examples of this are the sling-jaw wrasse *Epibulus insinuator* and the cichlid *Petunia splendida*; wrasses and cichlids both being extremely speciose clades of fishes. Interestingly, king-of-the-salmon or ribbonfish, *Trachipterus altivelis* (Lampriformes), also are capable of extreme jaw protrusion. The Lampriformes as a group are not terribly species-rich, yet multiple members appear to show the capacity for impressive jaw protrusion. Here we present findings regarding the anatomy of ribbonfish and their relatives, as well as the implications for jaw protrusion and prey capture in a group of fishes not easily studied via traditional functional morphological tools. Using a predictive model based upon morphological metrics, we compare protrusion ability within Lampriformes and across the Acanthomorpha, highlighting (extant) species and clades with particularly impressive premaxillae. Based upon available data, the ribbonfish may be the capable of the most extreme protrusion recorded to date. However, the link between premaxillary protrusion and subsequent species radiations is less clear.

FED3-1 11:30 am

Functional diversity and evolution of dicynodont (Therapsida: Anomodontia) jaw mechanics.

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Abstract: Dicynodont therapsids are one of the most successful synapsid clades aside from mammals. The dicynodont skull and mandible are highly modified relative to other therapsids to allow a palinal movement of the mandible. The basic operation of the dicynodont feeding system has been reconstructed for three taxa: *Pristerodon*, a basal dicynodont that retains 'postcanine' teeth, the highly autapomorphic *Lystrosaurus*, and the Triassic *Kannemeyeria*. Dicynodont skulls show high morphological disparity, much of which relates to the detailed morphology of jaw muscle attachment areas, but its functional implications are unexplored. We reconstructed m. adductor mandibulae externus medialis (= m. temporalis in mammals) and m. adductor mandibulae externus lateralis (a masseter analogue) in 32 dicynodonts and basal anomodonts by mapping origins and insertions in lateral view. We identified and connected centroids of each origin and insertion to create muscle vectors, and calculated mechanical advantage (MA) for each muscle in relation to a mesial bite point at the beak. Dicynodonts show a large range of mandibular MA values. Muscular MA values in dicynodonts are higher than in basal anomodonts, suggesting adaptive evolution of a more efficient herbivorous feeding mechanism. Among dicynodonts, MA ranges varied broadly with skull and jaw proportions. Genera with larger attachment sites for both muscles and deeper mandibles, such as *Daptocephalus*, *Lystrosaurus*, and *Angonisaurus*, show high MA values. In contrast, most kannemeyeriiforms present lower MA values caused by rostral displacement of the mAMEM and mAMEL insertions and low adductor angles. These notable transitions to lower adductor angles and MA values suggest a likely recruitment of m. pterygoideus musculature acting to induce a more orthal feeding stroke in the derived kannemeyeriiforms. Our results demonstrate that the radiation of dicynodonts was accompanied by a functional diversification of their feeding system.

FED3-2 11:45 am

Modelling microscopic tooth wear using finite elements: indicating how abrasive particles interact with enamel surfaces.

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Abstract: Recent research on the etiology of microscopic dental wear has focused primarily on the agents causing wear and has not addressed the processes by which wear is formed. Here, we use finite element analysis (FEA) to investigate the process by which phytoliths cause dental wear to form on the micro scale, and how phytolith size, attack angle, and force with which it impacts the enamel can change the wear signature (e.g. microwear). A parametric FE model consisting of two enamel blocks with a spherical phytolith was constructed. Non-linear, elastic, contact simulations were run where ingesta characteristics and masticatory were taken into account. The upper enamel block was displaced the following manner: downwards towards the lower enamel block, compressing the phytolith(s), laterally, shearing the phytolith across the enamel's surface, upwards to its original height, and laterally to its original starting position. The lower enamel block remained stationary, and the phytolith was constrained at its center with weak spring elements. The generated wear surfaces were quantified using 3D surface texture method following ISO 25178. Results indicate that changes in phytolith size affect the size of the pit formed on the enamel's surface, but cannot make a pit look like a scratch. Decreases in attack angle cause pits to become elongated and if elongated enough, become scratches. Increases in phytolith concentration and indentation force cause higher levels of enamel wear, resulting in deeper, wider pits. These results show how factors unrelated to diet such as masticatory kinematics and bite force may play as important a role in pit and scratch formation as diet itself. In addition, the intensity of the dental microscopic wear signature (depth and number of pits, length and number of scratches) is sensitive to attack angle, particle size, particle concentration, and bite force. This research is funded by the Max-Planck-Society.

FED3-3 12:00 pm

Tooth form and function of extinct durophagous reptiles, the Placodontia.

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Abstract: Dental morphology is one of the key characters for identifying the Placodontia, a group of extinct marine reptiles from the mid to late Triassic. Based on tooth morphology most placodonts were durophagous - predators of hard-shelled prey. The teeth are typically described as “low” or “blunted” in groups at the root of the tree and “hemispherical” or “flatter” in more nested groups. In addition to these qualitative descriptions of changes across the phylogeny, changes in tooth size, position, and replacement rate have also been documented. We are interested in quantifying differences in occlusal morphology over time and in understanding how these changes might have affected feeding. Variation in occlusal morphology can have an effect on tooth function, and we can predict a functionally ‘optimal’ shape for crushing teeth based on functional trade-offs: a flat or shallowly convex tooth which can both crush prey items and resisting tooth failure. Teeth that vary from the predicted morphology may suggest a different diet or indicate that some other aspect natural history, apart from pure function, is at play. To quantify tooth morphology we measured the functional radius of curvature (RoC) of the occlusal surface by fitting spheres to 3D surface scans. We found that palatine teeth tend to be flatter (large RoC) than maxillary teeth (small RoC). We also observed that stem taxa, which have faster, less organized replacement rates, have pointier teeth more prone to failure, than nested taxa which had teeth closer to the ‘optimal’ morphology and slower, more organized replacement rates. Within one well-nested clade, the placochelyids, the rear-most palatine teeth have a more complex morphology than predicted, with an overall concave occlusal surface and a small, medial cusp. These findings are in keeping with the theory that placodonts were specialized durophagous predators, with teeth modified to break hard prey items while resisting tooth failure.

FED3-4 12:15 pm

Quantifying textures of tooth wear for dietary analysis of fishes, sharks and whales.

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Abstract: Changes in trophic niche and/or diet are central components of many evolutionary scenarios, yet good evidence of what extinct taxa ate can be hard to come by. Analysis of tooth wear and microwear has a proven track record in analyses of dietary change and for testing hypotheses of trophic differences between vertebrate taxa, but microwear analysis has been applied almost exclusively to terrestrial mammals, particularly ruminants and primates. More recently, quantitative approaches, particularly 3D texture analysis, have been developed and applied more broadly to investigate trophic niche and test hypotheses of evolutionarily significant dietary change in a wider range of vertebrates. Recent and ongoing studies include early stem-mammals and a variety of aquatic vertebrates – sarcopterygian and actinopterygian fishes, chondrichthyans, and cetaceans. By calibrating differences in tooth wear and microtextures in fossils against extant taxa with known diets, these analyses are providing powerful new insights into aspects of niche partitioning, competition, and adaptive radiations in aquatic vertebrates that were previously beyond what the fossil record could reveal.

FED3-5 12:30 pm

Ecomorphological relationships between tooth morphology and diet in varanid lizards (Squamata: Varanidae).

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Abstract: The ecomorphological relationships between tooth shape and diet have not been quantitatively demonstrated in reptiles. Previously, ziphodont teeth, which are blade-like and often denticulate teeth, have been suggested to indicate a broad carnivorous diet. However, in the only group of extant ziphodont reptiles, varanid lizards, diet is highly variable and often species-specific. We predicted that variation in tooth morphology between varanid species would be reflected in dietary preferences, as dentition plays an important role in prey capture. Here, we used a quantitative multivariate redundancy analysis to find which morphological variables explained a significant portion of observed dietary data in varanids. We collected linear variables and geometric morphometric landmarks from over 150 specimens in 41 species of varanids, including members from every subgenus. Gut content abundances were collected from the literature. Results of our combined linear and geometric morphometric analysis indicate that 4 significant ecomorphological axes are present in the data governed by the relationships between 4 significant morphological variables. Using these results, varanid species can be categorized as belonging to one of 8 ecomorphs based on diet and morphology. Identified ecomorphs include 1) specialists on vertebrates, 2) terrestrial invertebrates and reptiles, 3) both terrestrial invertebrates and vertebrates, 4) general aquatic prey and terrestrial invertebrates, 5) molluscs, 6) fish, and 7) crustaceans, as well as 8) generalists that do not have a strong prey preference. Separate analysis of only the linear dataset also indicates that the preference for larger vertebrate prey is related to larger tooth denticle size. Using these ecomorphological axes, we can reconstruct the likely diets of species with unknown dietary preference data. The strength of these results suggests that species-specific ecological data can be recovered from morphological datasets.

FED3-6 12:45 pm

A high-fidelity, 3D model of the skull of *Alligator mississippiensis* (Archosauria: Crocodylia) and its significance for vertebrate feeding biomechanics.

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Abstract: Accurate modeling of cranial morphology, muscular conformation, and feeding performance is critical to understanding the functional morphology and evolution of the vertebrate skull. Although the primary components of jaw muscle, bite, and joint forces are oriented dorsoventrally during biting, the oft-overlooked mediolateral and rostrocaudal components of muscle forces are particularly important for platyrostral animals such as crocodylians. Accurate three-dimensional anatomical data are therefore crucial to understanding cranial function of not only crocodyliforms but also most other taxa with complex cranial musculoskeletal systems. This study uses CT-derived biomechanical models to characterize the ontogeny of muscle forces, moments about joint axes, and joint forces in the American Alligator. We made finite element and free body models to estimate how individual muscles contribute to bite force as well as joint forces. Muscle attachments and physiologies were modeled according to dissections and previous work. Despite challenges in modeling muscle wrapping and soft-tissue attachments, modeled bite forces still approach those measured *in vivo*, supporting this approach. Thus, we can use these hi-fi models to explore the functional environment of alligator, crocodyliform, and vertebrate skulls in ways not previously possible. For example, we show quantitative support for the ontogenetic shifts in jaw muscle orientation as alligator skulls flatten with age. We found the pterygomandibular joint is loaded with a greater magnitude than the primary jaw joint, suggesting crocodylians may employ a dual craniomandibular joint system. Finally, contrary to the loading of mammalian TMJs, we found the working-side jaw joint is loaded in tension during unilateral biting. These robust, three-dimensional methods now allow us to accurately test hypotheses about the loading environment of the skull, its joints, and skeletal tissues during gape cycles, ontogeny and macroevolution.

FED4-1 2:30 pm

Hierarchical variation in EMG signal in oral vs. pharyngeal muscles.

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Abstract: Variation in EMG signals of the oropharyngeal muscles can be partitioned into hierarchical components ranging from the cycle, through sequence, experiment (e.g., day), individual and species. By integrating data on mammalian oropharyngeal muscles from the FEED database, it is possible to compare the relative significance of different components of variation among anatomical groups of muscles. In particular, there are significant differences in function and evolutionary history among (1) the muscles of the oral floor/suprahoid muscles; (2) the muscles of mastication; and (3) the infrahyoid muscles. We measured both the time of peak activity and the relative amplitude at peak activity for multiple muscles in each of these anatomical groups for various mammalian species. Among the pharyngeal muscles, the suprahoid muscles were more variable than the infrahyoid muscles. The pharyngeal muscles demonstrated the most variation among individuals and then within a given muscle (duplicate electrodes). For the muscles of mastication, the cycle accounted for the largest portion of the variation in peak timing followed by sequence or species depending on the muscle. Variation in peak activity was accounted for primarily by variation at the level of the cycle and sequence. While the pharyngeal and masticatory muscle datasets vary in species and ontogenetic stage, the comparison of variance components among these anatomical muscle groups suggest future testable hypotheses relating to oropharyngeal muscle function, feeding plasticity, and performance across mammals. Supported by NIH:DC9980, NSF:DBI – 1062332, NSF:BCS-0552285.

FED4-2 2:45 pm

The relationship between kinematics and performance in mammalian swallowing.

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Abstract: An organism's performance is controlled by a hierarchy of mechanisms, from the CNS, through muscle activity, which produces kinematics. Here, we use mammalian swallowing to assess the relationship between kinematics and performance. Swallow performance falls into discrete categories: swallows without error and those with corrected error. We tested the hypotheses that correcting performance errors was correlated with kinematics changes and that the variation would be higher in the corrected swallows. Infant pigs, with radio-opaque markers in the hard and soft palates, the tongue, the hyoid and the epiglottis, were recorded, via videofluoroscopy at 100 fps, drinking milk. Swallows were scored using the Infant Mammalian Penetration Aspiration Scale (IMPAS). IMPAS = 1 are swallows without error and IMPAS = 2 are swallows with corrected errors. This study included three animals with both IMPAS 1 & 2 swallows, and 218 swallows. A repeated measures design in a mixed GLM model was used to test for differences among our measurements between the two performance scores. The duration of the swallow cycle was different between swallows IMPAS 1 and 2 ($p < 0.00$). The range in movement of the posterior tongue, epiglottis, and hyoid were more variable in swallows IMPAS = 2 than swallows IMPAS = 1 ($p < 0.00$). Despite differences in duration of the swallow cycle and differences in variation of the range of movement of structures directly implicated in the swallow, relative timing of movement, the movement and location of one structure relative to the others at the same time, was not different ($p = 0.11$). For swallows with corrected errors, variation is increased in the duration of the swallow cycle and the range in movement of structures implicated in swallows compared to swallows without error. It is possible that these changes are due to the mechanisms employed in swallows where error is corrected, which

informs us on how kinematic changes can lead to performance changes.

FED4-3 3:00 pm

Variation in tongue and bolus shape and its relationship to airway protection in infant mammals.

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Abstract: Obligate liquid feeding using a lingual suction pump is a mammalian behavioral synapomorphy of infants. Owing to the anatomical relationships between the trachea and the esophagus, the path of the liquid bolus during the swallow crosses over the entrance to the airway. Thus, control of the movement dynamics of the liquid bolus as it is propelled from the oral cavity into the pharynx is crucial for maintaining airway protection. In this study we tested the hypothesis that, following sensory nerve lesion, changes in tongue shape and bolus shape prior to movement of the bolus from the oral cavity to the pharynx affect airway protection. Four infant pigs were trained to drink milk with barium. The right recurrent laryngeal nerve, which provides sensory supply to the lower trachea, was lesioned in each animal. Swallows were recorded using highspeed videofluoroscopy, pre- and post-lesion, and subsequently assessed for airway protection. Bolus and tongue surface shape were digitized in the frame prior to onset of movement of the bolus across the airway. Bolus shape was analyzed using elliptical Fourier analysis and principal components, and tongue surface shape analyzed with second order polynomial fitting. Although bolus shape and tongue shape varied significantly among individuals, within individuals, consistent, statistically significant patterns of change in bolus shape and in tongue shape exist both pre- and post- lesion, and between swallows with and without adequate airway protection. Variation in bolus dynamics and tongue behaviors is hierarchically partitioned. Within individuals, tongue control is key to bolus control, and safe swallow. A better understanding of the kinematics of the muscular tongue is needed to understand how infant mammals protect the airway while swallowing milk. This work was supported by NIH R01 009980.

FED4-4 3:15 pm

Dental morphology, diet and the dynamics of morphological evolution across marsupials and placentals.

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Abstract: Dietary inferences are a key foundation for paleoecological, ecomorphological and macroevolutionary studies because they inform us about the direct relationships between the components of an ecosystem. Our goal was to design a quantitative phylogeny-free method to infer the typical diet of a species that could be also applied to macroevolutionary questions. Thus, we designed a multidimensional approach called Multi-Proxy Dental Morphology Analysis (MPDMA), which captures the variability of diet and dietary morphospaces. Marsupials and placentals have experienced extraordinary adaptive radiations since their divergence in the Late Jurassic. Thus, they provide a unique opportunity to quantitatively both to test the power of MPDMA and to show whether diet specialization drives the evolution of dental morphology towards functional optima. We three-dimensionally scanned 32 marsupial and 115 placental species and qualitatively classified their diets. Orientation patch count (OPCR), slope diversity and the relief index were calculated from the dental 3D scans, and multivariate statistical analyses were used to test for discriminatory power. MPDMA demonstrates significant morphological differences across diets ($P < 0.05$) in a dataset including all species and in separate datasets including all individual orders save rodents ($P = 0.321$). Additionally, it correctly discriminates diet for 66 to 82% of the specimens in the dataset, including and excluding rodents respectively. Here, we quantitatively show for the first time how marsupials and placentals with the same dietary specializations overlap strongly in ecomorphospace, which suggests convergent phenotypic evolution in these two clades. Additionally, MPDMA highlights evolutionary changes within a given phylogeny. The coverage as well as movement across the plots of species belonging to different paleocommunities illustrates processes of diversification and ecomorphological evolutionary patterns such as niche competition.

FED4-5 3:30 pm

Primate chewing biomechanics revisited using Finite Element Analysis of the mandible.

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Abstract: Both biomechanics and teeth characteristics (morphology and wear) have been shown to be crucial to understand diet and evolution in primates. However, the relationship between these two types of data still remains unknown. In this work, biomechanics of the primate jaw were analysed using a classical two-dimensional lever approach together with a Finite Element Model. The aim was to analyse if there is a correlation between some biomechanical indicators of the jaw—such as bite force, mechanical advantage, von Mises Stress, etc.—and geometrical and physical properties of the teeth such as radius, enamel thickness, failure loads of the teeth, etc. If this correlation exists, that would allow researchers to predict the biomechanical behaviour of other taxa—especially extinct taxa—from physical characteristics of the teeth. Classical biomechanics were used to estimate muscular and biting forces as a load response in the models whereas FEA generated stress distribution patterns from the models.

Recent procedures to compare quantitative FEA results from different models were used combining the Stress distribution maps and the values for the whole model. That includes exploratory methods such as box-plots and Principal Component Analysis. Phylogenetic signal was tested by means of Bloomberg's K. The physical properties of the teeth (enamel thickness or failure loads) were obtained from the literature. As a whole they suggest that there is a relationship between some biomechanical parameters with enamel thickness and tooth radius as well as with the critical loads of tooth failure. The use of exploratory methods on the biomechanical variables helped to understand the oral behaviour of the primates, as well as the biomechanical performance.

FED5-1 4:30 pm

Loss of a tongue muscle improves prey-capture performance in salamanders.

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Abstract: Many salamanders in the family Plethodontidae have evolved a high-powered elastic tongue projection mechanism, allowing them to project their tongue with high acceleration and power. Within plethodontids, the musculature of the tongue projection apparatus varies in its degree of complexity. The subarcualis rectus projects the tongue from the mouth, the rectus cervicis retracts the tongue, and the genioglossus rotates the tongue pad. The genioglossus muscle connects the tongue pad to the tip of the mandibles in the ancestral state that is retained in some taxa, and this may limit projection distance and tongue aiming relative to the head. Within the clade of plethodontids, tribe Bolitoglossini has lost the genioglossus muscle. In other taxa, the genioglossus is elongated, originating more posteriorly on the mandible. We examined how the presence or length of this muscle affects tongue projection performance. Using morphological examination and high-speed imaging, we compared tongue projection of salamanders with varying length or presence of the genioglossus muscle across the family Plethodontidae. We found that the presence of the genioglossus muscle reduces tongue directional versatility and that it may limit tongue projection length. These results provide insight into some of the constraints on salamander feeding performance and aiming ability.

FED5-2 4:45 pm

Robust hyobranchial apparatus yields increased aquatic feeding performance in newts.

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Abstract: Salamanders use the hyobranchial apparatus to capture prey via tongue projection on land and suction feeding in water. Within the Salamandridae, salamanders are ecologically and morphologically diverse and can be terrestrial, semi-aquatic, or aquatic. The purpose of this study was to quantify suction feeding performance in aquatically feeding salamandrids and to determine how differences in morphology affect feeding performance. We predicted that newts with more robust hyobranchial apparatus morphologies would have increased aquatic feeding performance. High speed video of five aquatic and semi-aquatic newts were analyzed using kinematics and inverse dynamics of aquatic feeding events. Dissections and cleared and stained specimens were used to obtain morphological data of the feeding apparatus and relevant musculature. The fully aquatic newt, *Paramesotriton labiatus*, was found to have increased feeding performance when compared to other salamandrids. Maximum velocity and acceleration of mouth opening exceeded the performance of other salamandrids by two and four times, respectively. Also, hyobranchial depression velocity peaked at 0.22 m/s, almost twice that of other aquatically feeding newts, and acceleration was four times greater, peaking at 49 m/s/s. Increased hyobranchial depression velocity was found to be correlated with more robust hyobranchial apparatuses, including broader ceratohyals and second ceratobranchials. Differences in performance could be due to functional trade-offs in semi-aquatic species that must perform various feeding modes in multiple habitats.

FED5-3 5:00 pm

Aquatic prey capture in snakes: the link between morphology, behavior and hydrodynamics.

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Abstract: Aquatic animals have to face the physical constraints imposed by the mechanical properties of the fluid through which they move. Movement under water is resisted by drag and acceleration reaction forces, which can impair the displacement of the animal. The forward strike during prey capture will generate a pressure wave that can trigger the escape response of a mobile prey and thus decrease the capture success. Most animals have circumvented these constraints by developing a suction feeding system, but some animals cannot because of anatomical limits. As the physical constraints are highly dependent on the shape of the object, we hypothesize that the animals that cannot perform suction will have morphologically converged to be more streamlined. Moreover, we hypothesize that the behavior of species that do not present a streamlined head will aim to reduce the hydrodynamic forces associated with a strike under water. We chose snakes as biological model to test our hypotheses, as these animals cannot use suction and have evolved aquatic life-styles convergently. We predict that the head shape of aquatic snake species is more streamlined in comparison with that of non-aquatic species. The variability in the head shape of aquatic snakes is large and some species have a large, massive head. We suggest that these species have adapted their behavioral strategies to efficiently capture prey. To test our predictions, we compared 3D scans of the head shape of 83 species. We also developed a 3D printed model to mimic a snake attack under water in a

laboratory experiment, characterizing the fluid flow associated with different head shapes and different behaviors using flow field velocimetry and force measurements.

FED5-4 5:15 pm

Masticatory jaw movements in two species of musteloid carnivorans with divergent dietary specializations: an XROMM and EMG study.

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Abstract: Despite decades of research on mammalian mastication, there are still surprising gaps in our understanding of the functional implications of diversity in craniodental morphology among mammals. To begin to address these limitations, we used X-ray Reconstruction of Moving Morphology (XROMM) and electromyography (EMG) to quantify jaw movements and jaw adductor activity patterns during mastication in two species of musteloid carnivorans. Ferrets (Mustelidae: *Mustela putorius furo*) possess many ancestral carnivoran traits, including a hypercarnivorous diet, tall shearing dental cusps, a “fixed” hinge-like temporomandibular joint (TMJ), and an unfused mandibular symphysis. In contrast, kinkajous (Procyonidae: *Potos flavus*) specialize on a frugivorous diet, have broad flat teeth, and possess an ossified or fused mandibular symphysis. We show that both species exhibit nearly-simultaneous activity of almost all jaw muscles, producing rapid vertical jaw adduction, but the morphological differences in their dentition and jaw contribute to notable differences in movement. In ferrets, the unfused mandibular symphysis allows the hemimandibles to move semi-independently. The working-side (WS) dentary translates laterally and rotates around its Y and Z axes to allow vertical occlusion of the cheekteeth—movements which would dislocate the contralateral TMJ if the symphysis were rigid. Kinkajous differ from known carnivorans in that a late burst of their WS deep masseter produces transverse translation of the jaw at the end of the closing phase. This likely necessitates symphyseal fusion while facilitating grinding of fruit with the horizontally-occluding cheekteeth. These data improve our understanding of the functional significance of mandibular symphyseal structure and shed light on the integrated evolutionary patterns of both adaptation and constraint associated with dietary specialization—patterns which may also be present in other mammalian taxa.

FED5-5 5:30 pm

Fibre type composition in the masticatory muscles of wolves (Carnivora: *Canis lupus*) and domestic dogs: implications for canine chewing efficiency and feeding ecology.

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Abstract: Bite force generation and chewing efficiency depend on the mass, fascicle architecture and fibre type composition of the jaw-moving muscles. The masseter, temporalis and medial pterygoid muscles of carnivores and some other mammals consist of the slow contracting and enduring type I fibre and the fast contracting and fast fatiguing IIM fibre. Here we compare the muscle fibre type composition of the wolf, *Canis lupus* L. 1758, to that of its domestic form, the dog (*C. lupus* f. *familiaris*), to assess whether the relaxation of selection pressures as the result of the domestication process had any bearing on muscle morphology and function. To this end, the intraspecific and regional distribution of the two fibre types was analysed in the temporalis-masseter muscle complex of ten wolves originating from the German resident population. The comparative sample constituted muscles from 17 dog breeds. Using an immunohistochemical protocol we found that the proportion of type I fibres increased from more superficial to deeper portions of the muscles in both wolves and dogs. Yet, on average the proportion of slow fibres in the temporalis and masseter muscles was significantly higher in wolves (20% in both muscles) than dogs (14% and 15%, respectively). These results concur with previous studies showing that the deep slow contracting muscle portions serve as stabilizers, while the superficial fast contracting muscles are both mobilizers and stabilizers. Moreover, the higher percentage of slow fibres in wolves compared to dogs suggests that the former are capable of a more stable and enduring bite which is particularly important when subduing prey and in processing of bone and meat. In dogs, in turn, the reduction in relative type I fibre proportion is likely linked to a diminished chewing efficiency as a result of a diet of processed and starch-rich foods.

FED5-6 5:45 pm

Exploring the value of anatomy ontologies: testing the Mammalian Feeding Muscle Ontology.

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Abstract: In recent years large bibliographic databases have made much of the published literature of biology

available for searches. However, the capabilities of the search engines integrated into these databases for text-based bibliographic searches are limited. To enable searches that deliver the results expected by comparative anatomists, an underlying logical structure known as an ontology is required. An ontology is a set of terms that are organized into a network structure that can be operated on by computer. The Mammalian Feeding Muscle Ontology (MFMO; <http://purl.obolibrary.org/obo/mfmo.owl>) is an anatomy ontology (AO) focused on anatomical structures that participate in feeding and other oral/pharyngeal behaviors. The MFMO is an outgrowth of the Feeding End-User Database (FEED) Project (Wall, et al., 2011; <http://feedexp.org>), an ongoing effort to develop an online repository for data from physiological studies of feeding in mammals. Further, it provides a template for muscles that will be useful in extending any anatomy ontology. Currently the MFMO is integrated into FEED and also into two literature-specific implementations of Textpresso, a text-mining system that facilitates powerful searches of a corpus of scientific publications. We evaluate the MFMO by asking questions that test the ability of the ontology to return appropriate answers (competency questions). We compare the results of queries of the MFMO to results from similar searches in PubMed and Google Scholar. Our tests demonstrate that the MFMO is competent to answer queries formed in the common language of comparative anatomy, but PubMed and Google Scholar are not. Overall, our results show that by incorporating anatomical ontologies into searches, an expanded and anatomically comprehensive set of results can be obtained. Supported by NSF DBI-0960508, NSF - DBI 1062350, EF-0423641, and a Collaboration Exchange Grant from Phenotype RCN to RED.

Symposium — Life Underground: Morphological Consequences of Fossoriality (FOS)
Organizers: Christy Hipsley, Emma Sherratt, Hillary Maddin

FOS1-1 9:30 am

Introduction to the Symposium.

Maddin HC, Carleton University hillary.maddin@carleton.ca

FOS1-2 9:45 am

The influence of fossoriality on cranial architecture in caecilian amphibians (Gymnophiona).

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Abstract: Fossoriality, wherein the head is employed as the primary locomotor organ (i.e., head-first burrowing), has evolved multiple times independently within Tetrapoda. Among these, caecilians have been shown to exert some of the greatest forces against the substrate during burrowing, and this has been attributed to their unique mode of hydrostatic locomotion. In order to gain a clearer understanding of the features associated with their forceful mode of fossoriality, the skulls of caecilians were examined from both morphological and mechanical perspectives. Examination of cranial architecture reveals elements of the dermal skull form extensive lap joints with adjacent elements in the anteroposterior direction, whereas overlap between elements in the mediolateral direction is minimal or absent. Dense networks of collagen fibres span the joint surfaces. In addition, nostrils are rimmed with cartilage throughout life, and joints between certain elements (e.g., maxillopalatine and braincase) are filled with cartilaginous plugs, also predominantly oriented in the anteroposterior direction. Results of finite element analysis support the hypothesis that cranial joints together with strategically placed cartilages form a complex dampening system, capable of reducing the transmission of compressive forces to the braincase and throughout the dermal skull produced during head-first burrowing. These features contrast somewhat with those known for other fossorial tetrapods, and may thus represent important adaptations associated with the style of burrowing observed within the caecilian lineage.

FOS1-3 10:00 am

Eyes underground: The degradation of vision genes in subterranean environments.

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Abstract: Vertebrates that have adapted to a subterranean niche experience various extreme conditions, which include a drastic reduction in light exposure. Evolutionary theory predicts that commitment to life underground for millions of years should relax selection on, or select against, traits involved in detecting light, resulting in the degradation of photosensory systems and their underlying genes. Here we test this hypothesis by examining the functionality of 65 vision genes in three fossorial mammals with varying commitments to underground life: the star-nosed mole (*Condylura cristata*), naked mole-rat (*Heterocephalus glaber*), and Cape golden mole (*Chrysochloris asiatica*). We show that the highly subterranean naked mole-rat and golden mole have a greater abundance of visual pseudogenes than the facultatively subaerial star-nosed-mole, and the loss of genes is mostly restricted to those that function in bright-light. We provide evidence of complete loss of cone photoreceptors in the golden mole, the first genomic confirmation of pure-rod retinas in a terrestrial vertebrate. We then estimated the timing of vision gene loss and found that it largely postdates inferred adaptations for fossoriality. This suggests that vision pseudogenes can be used to estimate the minimum age of adaptation to a subterranean environment in vertebrates with a limited or absent fossil record. We then show that the loss of bright-light visual genes also occurred early in the history of xenarthrans (sloths, armadillos, anteaters) potentially suggesting an early subterranean bottleneck in this clade. We

further demonstrate that genes related to melatonin production and reception also have degraded in xenarthrans, providing further support for this hypothesis.

FOS1-4 10:15 am

Ontogenetic allometry constrains cranial shape of the head-first burrowing worm lizard *Cynisca leucura* (Reptilia: Squamata: Amphisbaenidae).

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Abstract: Amphisbaenians are fossorial, predominantly limbless squamates with distinct cranial shapes corresponding to specific burrowing behaviors. Little is known of their cranial osteology, which represents a critical loss of information as the majority of morphological investigations of squamate relationships are based on cranial characters. We investigated cranial variation in the West African Coast Worm Lizard *Cynisca leucura*, a round-headed member of the family Amphisbaenidae. Using geometric morphometric analyses of three-dimensional computed tomographic scans, we found that cranial osteology of *C. leucura* is highly conserved, with the majority of shape changes occurring during growth as the cranium becomes more slender and elongate, with increasing interdigitation among the dermal roofing bones. The ventral cranium, however, remain loosely connected in adults, likely as a protective mechanism against repeated compression and torsion during burrow excavation. Intraspecific variation was strongly correlated with size from juveniles to adults, indicating a dominant role of ontogenetic allometry in determining cranial shape. Given the fossorial habits of *C. leucura*, we hypothesize that cranial allometry is under strong stabilizing selection to maintain optimal proportions for head-first digging, thus constraining the ability of individuals to respond to differing selection pressures including sexual selection and variation in diet or microhabitat. For species in which digging performance is less important (e.g., in softer sand), allometric associations during growth may be weakened, allowing changes to the ontogenetic trajectory and subsequent morphological traits. Such developmental dissociation between size and shape, known as heterochrony, may be implicit in the evolution of the other amphisbaenian cranial shapes (shovel, spade and keel), which may themselves be functionally optimized for their respective burrowing techniques.

FOS1-5 10:30 am

Cranial and postcranial specializations for fossoriality in the Permian dicynodont family Cistecephalidae.

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Abstract: Burrowing was a common behavior in small-bodied Permo-Triassic synapsids, as evidenced by an extensive ichnological record and the preservation of in situ skeletons in burrows. However, while some form of den construction may have been prevalent among early synapsids, only a single clade, Cistecephalidae, is currently thought to include obligately fossorial taxa. Evidence for obligate fossoriality in cistecephalids is based on their limb anatomy, which is convergent on that of modern fossorial mammals in the possession of a massive olecranon process, flattened phalanges, and a robust humerus with well-developed supinator process. Here, we present new data on fossorial adaptations in cistecephalids. Cranial adaptations for fossoriality in cistecephalids have received little study, other than general recognition of their broad, flattened skull. However, cistecephalids exhibit significantly more complex cranial sutures than other dicynodonts. The naso-frontal suture of *Cistecephalus* has a mean degree of interdigitation (measured as path/point length) of 3.61 vs. 1.89 in *Diictodon* (a taxon found in burrows) and 1.26 in *Dicynodon* (not found in burrows), and other cistecephalid snout sutures show similar values. We argue this high sutural complexity is related to strain from the surrounding substrate, as in extant head-based fossors such as amphisbaenians. Although some derived cistecephalid taxa mirror extant fossors in reduced orbit size, others retain large orbits and show evidence of binocular vision, indicating significant diversity in behavior within this family. Placing cistecephalid burrowing specializations in a phylogenetic context highlights their uniqueness among dicynodonts: a new specimen of *Myosaurus* (the sister-taxon of Cistecephalidae), including the first skeleton known for this taxon, shows almost none of their peculiarities, with the only possible exception being a shared reduction in the number of cervical vertebrae to 5.

FOS1-6 10:45 am

Morphological specialization and kinematic flexibility in mole burrowing (Mammalia: Talpidae).

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Abstract: The interplay between morphological specialization and kinematic flexibility is important for organisms that move between habitats with different substrates. Burrowing is energetically expensive and requires substantial interaction with soil to both break it apart and move it. Moles (Talpidae) have evolved extraordinary forelimb morphologies including an extremely enlarged teres major (75% of total forelimb muscle mass) that spans the shoulder joint, and an unusually long olecranon process on the ulna for attachment of the elbow extensors. Enlarged elbow extensor moment arms have been hypothesized as being important during scratching in other digging mammals. Despite these apparent specializations, moles exhibit different digging behaviors depending upon the compactness of the soil. In loose soil they perform lateral strokes to move the soil aside, but in very compact soil they scratch the soil to loosen it. Using marker-based X-ray Reconstruction of Moving Morphology (XROMM), we tested

the hypotheses that in Eastern moles (*Scalopus aquaticus*) the shoulder is the primary joint involved in lateral strokes, while the elbow joint plays the larger role in scratching. Unexpectedly, we found that both lateral strokes and scratching are primarily driven by movement at shoulder joint. This suggests that the massive teres major is the primary source of muscle force during both lateral strokes and scratching. We also found that the end of the lateral strokes has an additional increment of elbow extension compared to scratching. This enables moles to move and compress soil to open a tunnel with a single stroke. Burrowing by scratching in compact soil requires the moles to clear the tunnel by moving soil to the surface. Our work provides an example of how kinematic flexibility of a very specialized forelimb allows an animal to make use of very different substrates.

FOS2-1 11:30 am

Ontogeny of a burrowing morphology - examples from anurans and caecilians (Lissamphibia: Anura and Gymnophiona).

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Abstract: In general, burrowing taxa show a broad range of different morphological specialisations that are usually absent or less elaborate in their surface-dwelling relatives. In amphibians these include a more stout body shape, modified limbs, more heavily ossified skeletal elements and keratinized tubercles. Most amphibians have a biphasic life cycle in which an aquatic larval stage and a more terrestrial adult stage are punctuated by a profound metamorphosis. Larval and adult morphologies are each adapted to very different environments and feeding strategies and the feeding apparatus becomes temporarily non-functional during metamorphosis. Most amphibians metamorphose rapidly to quickly transition this maladapted phase and juvenile skeletons, though functional, are usually only incompletely ossified. In addition to the constraints imposed by metamorphosis, emerging metamorphs of burrowing amphibians need to commence a burrowing lifestyle, which in turn necessitates a more rigid and more heavily ossified skull than usually found in amphibian metamorphs. I present data on the development of burrowing and fossorial frogs (*Hemisus*, *Breviceps*) and caecilians (e.g. *Ichthyophis*, *Gegeneophis*, *Boulengerula*) that highlight some of the challenges faced by burrowing amphibians and how these have been addressed.

FOS2-2 11:45 am

Morphological diversity of the pectoral girdle and anterior body axis in Amphisbaenia.

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Abstract: The fossorial Amphisbaenia, or worm lizards, are characterized by extensive body elongation, limb loss, and the reduction of the appendicular skeleton. Despite the superficially uniform appearance there is a high degree of variation in the amphisbaenian postcranium, but so far there have been only a few attempts to assess this variability in a both taxonomically and phylogenetically comprehensive framework. Here we present the first results of our analysis of the anterior body axis and the pectoral girdle, which is part of an ongoing, extensive assessment of amphisbaenian osteology using micro-computed tomography. In contrast to previous claims, shoulder girdle elements or remnants thereof are not only found in blaniids, bipedids and trogonophids, but also in several genera of amphisbaenids. Also, we found clavicles, scapulocoracoids and parts of the sternum in the enigmatic genus *Cadea*, which was formerly considered to be amphisbaenid but now is thought to be closely related to blaniids, the latter showing a similar number of elements. Our data suggest that the reduction of pectoral elements occurred many times independently, and also within the different major clades. In addition, we recorded substantial variation in the morphology of the cervical and anterior thoracic vertebrae, and found that this variation is, at least in part, phylogenetically informative, fitting recently proposed hypotheses of relationships. Especially some African amphisbaenids show a highly derived cervical morphology, which seems to be related to the evolution of shovel-headed skull shapes and associated digging styles. The variable position of the pectoral elements relative to the cervical region, which can be especially seen in bipedids and some trogonophids, suggests developmental plasticity and potential frame shifts during amphisbaenian evolution.

FOS2-3 12:00 pm

Evolution of cranial features associated with the "freight-train" burrowing of uropeltid snakes.

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Abstract: The head-first burrowing style employed by uropeltid snakes is a unique form of internal concertina locomotion. Uropeltids have a hyper-mobile cranio-vertebral joint and form tight curves with their anterior vertebrae, using those to push off tunnel walls and drive the skull directly forward through substrate. This burrowing style is expected to generate strong forces at the tip of the premaxilla, with stress propagated longitudinally along the nasals, frontals, parietals, and fused braincase. However, this "freight train" digging was characterized through study of more recently derived uropeltids, which exhibit a higher degree of fusion and modification of skull elements. Considerably less is known about more basally positioned taxa, which were described primarily from dried skeletons. In order to access anatomical regions normally obscured in traditional skeletal preparation, alcohol preserved skulls of *Melanophidium punctatum* and *Teretrurus sanguineus* were subjected to micro-CT and individual bones were digitally disarticulated and described. Compared to more crown-ward taxa such as *Uropeltis*, *M. punctatum* and *T. sanguineus* present not only a larger number of separate skull elements, but a greater amount of sutural space

between bones. In *M. punctatum*, few of the non-braincase elements make direct contact and some are widely separated by thick regions of soft tissue. Given the variation in bone relationships across uropeltids, basally positioned species may exhibit more cranial kinesis than has been presumed for the clade, and may lack the highly specialized version of "freight train" burrowing seen in crown-ward taxa. Of broader importance, the anatomical differences apparent between dried and alcohol preserved skulls may have consequences for the validity of biomechanical studies, such as Finite Element Analysis, based on scans of traditional skeletal preparations, or lacking sutural data.

FOS2-4 12:15 pm

Blind, naked, and feeling no pain: sensory neurobiology of the naked mole-rat (Mammalia: Bathyergidae).

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Abstract: Around the world and across taxa, subterranean mammals show remarkable convergent evolution in morphology (e.g. reduced external ears, shortened limbs and tails). This is true of sensory systems as well. Subterraneans have lost object vision and high frequency hearing. The naked mole-rat (*Heterocephalus glaber*) displays these typical subterranean features, but also has unusual characteristics even among other subterranean mammals and even other mole-rat species. Naked mole-rats are cold-blooded, completely furless, very long-lived (> 30 years) and eusocial (like bees). They also live in large colonies, which is very unusual for subterraneans. We are studying yet other unusual characteristics. First, the naked mole-rat is the only mammal whose pheromone-detecting vomeronasal organ (VNO) shows no postnatal growth, and sexual suppression is not mediated by urinary signals as in other rodents. Second, the nerve network for processing pain from noxious chemicals (e.g. acid and capsaicin) is reduced and lacks the neurotransmitter, Substance P, that usually signals pain. Naked mole-rats are the only mammals that feel no pain from these substances. Third, brain tissue from naked mole-rats is extremely tolerant to oxygen deprivation, and can recover from up to 30 minutes of anoxia. These features may be a result of this species' "extreme subterranean lifestyle" that combines living underground and living in large colonies. Many respiring animals cramped together in unventilated burrows raises CO₂ levels enough to cause acidosis and chemical pain, and depletes O₂ concentrations low enough to kill other mammals. Coincidentally, Substance P (lacking in the naked mole-rat) also mediates the VNO's vascular pump. The naked mole-rat may be an extreme model of adaptation to subterranean life and provides insights into the complex interplay of evolutionary adaptation to the constraints of subterranean living.

FOS2-5 12:30 pm

Climate change impacts on the fossorial herpetofauna of the globe: integrating models across paleo, contemporary and future timeframes.

Sinervo Barry*, UC Santa Cruz; Miles Donald, Ohio University lizardrps@gmail.com

Abstract: Models predict anthropogenic climate change will generate extinctions in the next century. Current models assume that extinctions will be triggered by severe demographic challenges faced by populations experiencing warming or drying but most models are correlative at best. Here, we develop new ecophysiological species distribution models, predicated on thermal physiology, that can be used to predict extinctions of ectotherms due to climate change. We apply these models to predict extinctions of fossorial reptile taxa in present and future timeframes and compare extinctions in these taxa that are thermoconformers to above ground taxa that are either heliotherms or thermoconformers. We also calibrate extinction models against reconstructed paleodistributions, back to the Eocene, the warmest period in the last 65 million years. Models predict the paleobiogeography of both above ground and fossorial taxa as validated by fossil inferences and inferences derived from phylogenetic patterns as related to the biogeographic origins of taxa at global scales. Fossorial reptile taxa appear to be buffered from the impacts of climate change compared to above ground taxa. This research was funded by an Emerging Frontiers Grant from NSF (EF-1241848).

FOS2-6 12:45 pm

Comparative morphology of the shoulder muscles of Amphisbaenia (Reptilia, Squamata) using iodine-staining and computed tomography.

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Abstract: The bony shoulder girdle of worm lizards, or Amphisbaenia, shows variable degrees of reduction across different clades. Bony and cartilaginous shoulder girdle elements are reduced in all taxa, with Bipedidae showing the least degree of reduction and many Amphisbaenidae and Rhineuridae having completely lost the pectoral girdle. In contrast to the bony elements, little is known about the pectoral muscles of Amphisbaenia, and it remains unclear if they experienced reductions similar to those of the ossified skeleton. Here we present a comparative analysis of the pectoral muscles of *Rhineura floridana*, *Blanus cinereus*, *Bipes biporus*, *Trogonophis wiegmanni*, and *Cynisca leucura*, which are representatives of all the major clades of Amphisbaenia. Specimens were iodine-stained using 20% aqueous IKI solution and scanned using micro-computed tomography. In total, 17 pectoral muscles, nine superficial and eight deeper muscles, could be identified for all taxa except *Rhineura*, in which muscles were strongly reduced. The morphology of the muscles largely compares to that of the lacertid lizard *Meroles*, which was used as

outgroup, whereas adjacent muscles variably tend to fuse in the different species. In *Trogonophis* and *Cynisca*, four superficial muscles, the *M. latissimus dorsi*, the *M. episternocleidomastoideus*, the *M. trapezius*, and the *M. pectoralis* together form an extensive ring structure, which might be considered a synapomorphy of trogonophids and amphisbaenids. The arrangement of the pectoral muscles remains constant in amphisbaenians except *Rhineura*, despite variable degrees of bone reduction. Instead of attaching to bony or cartilaginous elements, muscles arise from or insert into other muscles, skin or cartilage near the ancestral area of bony attachment. Our study presents the first detailed analysis of amphisbaenian pectoral myology, and provides compelling evidence that bone reduction is not necessarily accompanied by similar changes in muscle anatomy.

Contributed Session — General Morphology (GEN)

GEN1-1 9:30 am

Homology of the accessory elements of the hyoid arch within Gnathostomata.

Bockmann F. A., Universidade de São Paulo, FFCLRP; Carvalho M., Universidade de São Paulo, Instituto de Biociências; Carvalho M. R., Universidade de São Paulo, Instituto de Biociências; Rizzato P. P.*, Universidade de São Paulo, FFCLRP rizzatopp@gmail.com

Abstract: In this study, we investigated specifically the homology of the accessory elements of the hyoid arch, called symplectic and inter-hyal, by means of anatomical comparisons among chondrichthyans and actinopterygian polypteriforms, acipenseriforms, lepisosteiforms, amiiforms, and some teleosts at different stages of their early ontogenies, both extant and fossil. The symplectic belongs to the epal series, being articulated with the distal extremity of hyomandibula whereas the interhyal is part of the ceratal series, being usually attached to the distal extremity of ceratohyal. Recently, it has been suggested that a cartilaginous piece lying between the distal tips of ceratobranchials 4 and 5 of actinopterygians, which was usually identified as epibranchial 5, is actually an accessory element associated with ceratobranchial 4. The origin of this element may have a single origin, being a remnant of a series of elements distally attached to ceratobranchials 1–4, a condition totally or partially retained in basal actinopterygians. A closer examination of the anatomy of the osteichthyan hyoid and branchial arches suggests that primitively there are actually two accessory elements in each arch, an anterior, which is associated to epal portion of the arch, and a posterior, which is attached to the ceratal portion. According to this finding, it is proposed that the symplectic is serially homologous to the anterior, epal accessory elements of the branchial arches, which are characteristically present in Polypteriformes and Lepisosteiformes, while the inter-hyal would be serially homologous to the posterior, ceratal accessory elements of the branchial arches, which are more commonly encountered among actinopterygians (including the accessory element of ceratobranchial 4). This work is supported by CNPq and FAPESP.

GEN1-2 9:45 am

Evolution of complex skull shape across the global radiation of extant bats.

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Abstract: Biological shapes and structures are intrinsically linked to an organism's ecological niche, their performance and function, and their integration or modularity within a morphological whole. Many biological shapes are highly complex and multidimensional, making them difficult to model within the framework of established evolutionary theory. Much research on adaptive radiations and macroevolution have proposed that rates of trait evolution are variable through time—clades can be marked by an initial, explosive exploration of trait space, followed by gradual deceleration through time as niche space is claimed by congeners and competitors. Using both traditional and geometric morphometric data, we explore this and related hypotheses during the global radiation of extant bats (Order Chiroptera). Bats are among the most ecological and morphologically diverse mammals, and their skulls are known to exhibit a tight coupling among morphological shape, performance, and ecology. Using a comprehensive dataset that spans skulls from all extant bat families, and a recent, time-calibrated phylogeny of the order, we quantify shape disparity across bats, calculate rates of trait evolution, and explore the trajectory of shape evolution through time. We find a decoupling between rates of trait evolution and speciation, but also that macroevolutionary patterns are both module- and clade-dependent.

GEN1-3 10:00 am

Mammalian neck construction between variation and constraints.

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Abstract: Neck construction in mammals is highly determined by developmental (e.g. fixed number of cervical

vertebrae) and gravitational (e.g. permanent head bending moment) constraints limiting the possibility for adaptive modifications through evolution. However, there exist obvious differences in neck morphology between, for example, small and large, terrestrial or fossorial, upright, jumping, and high browsing mammals which correspond to different functional demands. As positional (i.e., local) identity of the individual vertebrae seems to be highly conserved and invariant across mammals, the extent of the observable evolutionary variation is not yet clear. We analyzed and quantified patterns of variation and conformity of neck morphology across mammals by combining different approaches on osteological and myological data. Cervical scaling parameters and proportions were measured across a variety of species representing all major monotreme, marsupial, and placental groups in order to infer global characteristics of cervical spine variation. In contrast, muscular properties were examined in situ based on contrast enhanced μ CT-scanning for different small mammals representing so called generalized members of their clades. Our results imply that overall neck construction is guided by a fixed set of constructional principles common to all mammals. However, deviation from those 'rules' evolved in several lineages on different constructional levels (cervical scaling, vertebral proportion, muscular topography, and micro-architecture). Although limited in their extent, the combination of these deviations enables the mammalian neck for constructional variation and adaptive modification beyond its constraints.

GEN1-4 10:15 am

How does the transition from lizard body to serpentiform morphology influence the atlas-axis complex in lizards?

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Abstract: Currently, the minimal understanding of comparative anatomy on the neck region represents a significant knowledge gap in understanding these anatomical structures as a whole. The comparative vertebral morphology of the atlas-axis complex in cordyliforms, xantusiid and several skinks is reported here. These lizards are particularly interesting because of their different ecological adaptations and anti-predation strategies, where conformation ranges from the lizard-like body to a snake-like body. This transition to serpentiform morphology shows several evolutionary patterns in the atlas-axis complex depending on the stage of the transition and ecology of animals (e.g., adaptation to burrowing lifestyle or for rapid surface mobility). Moreover, the first intercentrum of African *Chamaesaura* and *Tetradactylus africanus* (serpentiform grass-swimmers) is fully curved anteriorly, underlying the occipital condyle. While this limits ventral skull rotation beyond a certain angle, it locks the skull, which is a crucial adaptation for a sit-and-wait position in grassland habitats that needs to keep the head stabilized.

GEN1-5 10:30 am

Tinkering with the tail: variation in the vertebral column in Ophidiiformes.

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Abstract: Within Actinopterygii, body elongation is the dominant axis of shape variation. Most often, body elongation involves modification to the postcranial axial skeleton, either through adding additional vertebrae or lengthening the vertebral centra. In this study, we examine the vertebral column and body shape of members of the group, Ophidiiformes (cusk eels, brotulas, and pearlfishes). Ophidiiform fishes vary in their degree of elongation, which may be tied to their diverse ecologies. An interesting attribute of elongation in these fishes is a strong tapering caudal region; the degree of tapering also varies across species. Since caudal fin size has been linked to swimming performance, it is likely that extreme body tapering will result in a decrease of propulsive power during swimming. Our goal is to examine how morphological variation in body shape and vertebral column morphology in the caudal region may affect swimming performance. We measured 13 morphological and meristic variables from vertebrae and body shape (e.g., centrum height and length) in 14 species. We tested the relationship between decrease in body depth and centrum height (tapering) and found that while nine species have similar tapering in the body and vertebral column, there are five species, which have more tapering in the body than the vertebral column. Ophidiiformes are highly variable in the decrease in centrum height and length along the caudal region. When controlling for vertebral number, we found that the second moment of area (I) decreased along the caudal region. While I decreases posteriorly along the caudal region for all members of the group, *Brotula* sp., with the most extreme tail tapering, had the lowest rate of decline of I. *Chilara taylori* had the greatest I, indicating relatively stiff posterior vertebrae. This study provides a model for examining how changes to the caudal vertebrae associated with tail tapering might affect the ecology of fishes.

GEN1-6 10:45 am

Body shape transformation along anatomical lines of least resistance in labyrinth fishes.

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Abstract: Body shape transformations punctuate vertebrate evolutionary history. Eel-like forms and torpedo-shaped bodies evolved within ray-finned fishes; elongate limbless forms arose within lissamphibians; and snakes and snake-like lizards evolved within squamates. Previous researchers have shown that varying combinations of changes to dimensions of the body, axial skeleton, and skull can drive transformations in different lineages. But why has a

particular transformation involved change in some body regions but not others? Here, we test the hypothesis that the anatomical changes underlying morphological transformation are shaped by constraints that are shared with closely related lineages. In labyrinth fishes (Anabantoidei), we identified rapid evolution from a relatively deep-bodied ancestor to a torpedo-shaped body in the pikehead (*Luciocephalus pulcher* and *L. aura*). We then developed a novel method to compare the combination of anatomical changes leading to the pikehead with the major axis of anatomical diversification in other anabantoids. We found that the pikehead form results from exaggerated changes in the same anatomical features that drive shape variability across all anabantoid fishes. These results reveal a common anatomical basis for body shape diversity that is taken to the extreme in the evolution of the pikehead form.

GEN2-1 11:30 am

Morphology of the ovarian germinal epithelium in bony fishes: Centropomidae *Centropomus undecimalis*, Goodeidae *Xenotoca eiseni* and Chlorophthalmidae *Chlorophthalmus agassizi*.

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Abstract: The female germinal epithelium was examined in three species of distantly related teleosts. In *C. undecimalis*, *X. eiseni* and *C. agassizi*, the germinal epithelium lines the ovarian lumen and is composed of epithelial cells within which are scattered, and widely separated oogonia and cell nests. The process of folliculogenesis is precisely the same in all three species. The germinal epithelium is supported by a basement membrane that separates it from stroma. In similar fashion, during folliculogenesis, the germinal epithelium basement membrane is extended to surround individual follicles, separating them from stroma from which the theca forms. Therefore, the theca is not part of the follicle. Rather, the follicle and its encompassing theca, represent cells derived from two different tissue compartments that comprise a follicle complex. An ovarian follicle is simply the oocyte and its encompassing follicular cells. In all three species, epithelial cells from the germinal epithelium become prefollicle cells during folliculogenesis and then follicle cells when the forming follicle is completely surrounded by a basement membrane, marking the completion of folliculogenesis. After ovulation, a postovulatory follicle (POF) remains within the ovarian lamellae and is composed of just the former follicle cells. The postovulatory follicle is encompassed by a basement membrane and a postovulatory theca (POT). Together, POF and POT compose a postovulatory follicle complex (POC).

GEN2-2 11:45 am

Comparison of cranial development of Siberian sturgeon, *Acipenser baerii*, and Russian sturgeon, *Acipenser gueldenstaedtii* (Acipenseriformes: Acipenseridae).

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Abstract: The development and evolution of the vertebrate head has been studied a great deal throughout the history of morphology. Still, there are gaps in our fundamental knowledge that can be filled through renewed study of exemplar taxa using modern approaches to morphology. Here we study the morphogenesis of the cranial and pectoral girdle skeleton in two species of sturgeons, *Acipenser baerii* and *A. gueldenstaedtii*, which both show a generalized sturgeon phenotype and are readily available through hatcheries. Closely staged ontogenetic series of these species showing the development of the neuro-, viscer- and dermatocranium were analysed and compared. Sturgeons (Acipenseridae), together with the paddlefishes (Polyodontidae), belong to the order Acipenseriformes and have a phylogenetic position close to the base of the Actinopterygii. This makes them a valuable group to study in the large-scale evolutionary context of osteichthyan vertebrates. Furthermore, resolving the phylogeny within Acipenseridae calls for additional molecular as well as morphological data. Ontogeny is a rich source of information for phylogenetic analyses and in this study we provide a baseline for future comparative phylogenetic studies. Our results show an early development of neurocranial elements, starting with the trabeculae cranii and the parachordal cartilages, followed by the otic capsule and the mandibular arch elements. The elements of the hyoid arch appear simultaneously with elements of the first branchial arch. The posterior branchial arches follow subsequently. The branchial arches are patterned in a ventral to dorsal direction. The first bony elements appear in the mandibular arch. Teeth are formed and later reduced in an antero-posterior direction, on the dentary, dermopalatine, palatopterygoid and on tooth plates in the buccal cavity. Closure of dorsal fenestrae of the neurocranium and ossification of overlying dermatocranial elements occur relatively late.

GEN2-3 12:00 pm

Comparative beak morphology of two subspecies of Australian Red-tailed Black-Cockatoos: Small changes with significant functional effects as a model for macroevolutionary processes.

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Abstract: A comparison of the beak morphology and feeding behavior of two Red-tailed Black-Cockatoos served as

a natural experiment to model evolutionary changes in adaptation to particular environments and foods. The eastern population of *Calyptorhynchus banksii samueli* feeds mainly on seeds in hard woody fruits of forbs in arid open woodlands of northwestern New South Wales. Its psittacid beak is characterized by an upper bill tip that overhangs the lower beak and whose internal surface is rough with a transverse step, in which the transverse cutting edge of the lower beak fits. It cracks open fruits between the transverse step of the upper beak and the cutting edge of the lower beak. *C. b. graptogyne* feeds mainly on seeds in complex fibrous-woody eucalypt capsules in Gondwanan forest refugia in southeastern South Australia and northwestern Victoria. Its calyptorhynchid beak is characterized by (1) a short upper bill tip that is apposed to the gonys of the lower beak and whose internal surface is smooth without a step, and (2) an emarginated v-shaped transverse edge of the lower beak. It tears apart fruits with the upper bill tip while the tongue and lower beak move sideways and back-and-forth to position the fruit for the upper beak's actions. This multi-step feeding mechanism requires dexterity that must be learned and practiced by fledglings for months. It also depends on the exceptionally dense touch receptors in the beak and tongue of Psittaciformes in general. During the drying of Australia separating from Gondwana, the selection of minor changes in surface structures of the calyptorhynchid bill resulted in a psittacid bill with a fundamentally different feeding mechanism to exploit changed food sources. This scenario exemplifies how minor structural changes can have fundamental effects that set the stage for further modifications leading to what are perceived as macroevolutionary events. Supported by NSF and LSU Foundation "Morphology of Birds"

GEN2-4 12:15 pm

Evolution of cornification in amniotes: the case of Sauropsids.

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Abstract: During the adaptation of the integument to terrestrial conditions in amniotes an efficient stratum corneum was originated through the evolution of numerous corneous proteins in addition to the framework of (alpha-)keratins forming the intermediate filaments of keratinocytes. The new genes for corneous proteins such as involucrin, loricrin and filaggrin evolved in a chromosome region indicated as Epidermal Differentiation Complex (EDC), a locus with no relationship to keratin genes. The addition of EDC proteins to alpha-keratins transformed the prevalent epidermal keratinization of anamniotes into a widespread new process of terminal differentiation known as cornification in the epidermis but more accentuated in appendages such as hard scales, claws, hairs and feathers in amniotes. In Sauropsid amniotes among other EDC proteins a unique type of small proteins of 10-24 kDa evolved a central region of 34 amino acids conformed as beta-sheets that, differently from the other EDC proteins, allowed the formation of long polymers of filamentous proteins customarily termed beta-keratins. To the initial beta-sheet core of these new Corneous Beta Proteins specific N- and C-regions were later added in different lineages of sauropsids in relation to the evolution of specific epidermal adaptations and appendages, such as claws, shell in turtles, adhesive pads in some lizards, and feathers in birds. The presentation stresses the evolution of the process of cornification as an extension of the general process of keratinization.

GEN2-5 12:30 pm

Comparative morphology of the quadrate bone within Gekkota (Squamata): Phylogenetic and functional implications.

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Abstract: The functional components of the reptile skull are divided into the chondrocranium, dermatocranium, and lower jaw. These regions are interconnected and become operational through the quadrate: a bone vital for cranial biomechanics and support of the auditory system. The quadrate is a very complex and variable structure in squamates; however, the comparative anatomy of this element has never been studied in detail. We investigated the diversity of quadrate morphology within geckos (117 of 125 genera examined) using high-resolution x-ray micro-computed tomography and cleared and double-stained specimens. Our objectives were to 1) quantify quadrate shape using three-dimensional geometric morphometrics and 2) investigate the interactions of phylogeny, function, and allometry influencing quadrate morphology using comparative methods. Our results demonstrate substantial variation in quadrate morphology across gecko species. Carphodactylids and pygopodids each possess uniquely derived quadrate morphologies, while the remaining gecko families retain extensive overlap in quadrate shape. All carphodactylid taxa, as well as one gekkonid and diplodactylid, possess broad and laterally expanded quadrates, and we hypothesize this is a functional modification that has evolved to support enlarged adductor mandibulae musculature. Three miniaturized pygopodid genera have reduced or lost the external auditory meatus and tympanic membrane, and this modification has resulted in the reduction of the posterior concavity and tympanic crest of the quadrate. Lastly, miniaturized taxa in four families possess elongate, slender quadrates, suggesting a strong influence of allometric scaling. Therefore, our study has identified the disparity of quadrate morphology within geckos and has highlighted the importance of considering multiple processes that may influence the diversification of phenotypic characters.

GEN2-6 12:45 pm

Musculoskeletal systems simplified to 2D and 3D biomechanical models: the potentials and limitations of modeling bite forces.

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Abstract: In case the bite force of an organism can't be measured *in vivo*, it can be estimated mathematically using static-state equilibrium models. Although this approach will always simplify reality, several models presently exist that exhibit different levels of simplifications of the musculoskeletal topography and the parameters describing muscle physiology. To investigate the impact of such simplifications, three frequently used models are compared in this study. The first model calculates bite forces by projecting all lever arms and the muscle's line-of-action onto the mid-sagittal plane of the specimen. Muscle force is based on the muscle's PCSA and therefore remains constant throughout the simulation of different gape angles in this model. The second model is comparable to the previous model, but describes the specimen's musculoskeletal topography using 3D-coordinates of the muscles and levers. The third model again uses these 3D-coordinates, but calculates muscle contraction force based on a series of parameters (including fiber and tendon lengths and pennation angle) and physiological characteristics (including F-L and F-V relationships, activation rise time and passive elasticity). As the lower jaw becomes depressed, this model accounts for changes in muscle parameters according to this movement. Input-data for these models is obtained from a European yellow eel specimen (*Anguilla Anguilla*). Several allometric-scaled morphs, testing the effects of changes in skull width, lever arms and muscle-length, are implemented in the models as well. Model results visualize the effects of different muscle orientations on the same lever, of 2D versus 3D (2D overestimates forces), of constant versus variable muscle contraction force (changing output profile), and of increasing the head width. Therefore, these comparisons allow defining constraints on the predictive power of different models generally used to calculate bite forces.

GEN3-1 2:30 pm

Primates hearing: ear morphology, functions and ecology.

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Abstract: The morphology of the basi-cranial elements and especially the ear structures shape have been essentially studied for taxonomic and phylogenetic purposes. Due to the development of new acquisition techniques such as micro-computed tomography, new morphological data are available. Since the ear is the center of auditory capacity, new ear studies also provide additional information on hearing, allowing the identification of adaptations to specific environments. Previous works have already study the relationships between ear morphology and functions. The order Primates is the third most diverse order (number of species) of mammals, but also one whose life history traits, lifestyles, behaviors and social interactions are the more diverse. Hearing sensitivity is variable among primate's species, suggesting an adaptive selection on this function related to socio-ecological parameters. However, intraspecific variation is almost never quantified. In this study, we measured 8 morphological variables of the middle and inner ear for 80 extant and extinct strepsirrhines of 12 genera. Morphological and hearing parameters were quantitatively analyzed to compare intra- and inter-specific variations. Our morpho-functional results were compared to ecological and behavioral data, such as activity patterns and social organization. We also tested the effects of body size and phylogeny on ear morphology. The phylogenetic effect is not significant, however, our preliminary results show that the communication differs according to the population density. Thus, ear morphology is a relevant tool to assess ecological and behavioral characteristics. Assumptions are made on fossil species in order to estimate paleoecological and paleo behavioral parameters, directly from ear morphology.

GEN3-2 2:45 pm

Convergent Loss of Paranasal Sinuses in Mammals is explained by their Deleterious Effects on High-Frequency Communication.

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Abstract: Investigation of the evolutionary history of mammalian paranasal sinuses has generally focused on their origin and adaptive benefit. However, the pattern of convergent loss of these structures in a variety of mammalian species has been largely overlooked, or dismissed as a result of developmental effects that dominate after their presently non-adaptive role. Here, we test an alternative hypothesis for convergent loss of paranasal sinuses in mammals based on their potential effects on auditory communication. This draws upon previous work that has linked the evolution of paranasal sinuses with enhanced vocal communication in the low frequency range, where lower density structures in the cranium are suggested to act as amplifiers. In a complimentary way, paranasal sinuses may also negatively affect high frequency communication when the size of the cavity matches the wavelength, or corresponding whole wave number, of sounds resulting in destructive interference. Consequently, we suggest that convergent loss of paranasal sinuses may result from the selective pressure to eliminate these structures due to their deleterious effect in species that use high frequency communication. We collected data on optimal communication frequency range and presence/absence of paranasal sinuses in 62 mammalian species, and tested our hypothesis using phylogenetic least squares regression. Preliminary results support the hypothesis that destructive interference from paranasal sinuses in species that rely on high frequency communication created a selective pressure that led to their loss, but leaves room for alternative explanations for their loss in some taxa. Future studies should further refine our hypothesis by enhancing data on paranasal sinus size, location, and frequency range in a wider range of

mammalian species.

GEN3-3 3:00 pm

Evolution of the laterosensory canals of the snout in Osteognathostomata (Vertebrata: Pisces).

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Abstract: The snout region of basal osteognathostomates has been subjected to many studies, most focusing on the homologization of bone elements. The laterosensory system of that region is usually used only as landmark for bone identity, but not as source of phylogenetic information. In order to fill this knowledge gap, we carried out comparisons, under a phylogenetic perspective, on the pathways of laterosensory canals on the snout of basal actinopterygians and sarcopterygians, both fossil and living. In the putative ancestral condition, the nasal canal passes longitudinally between the contralateral nares; its terminal portion may fuse to the anterior transverse commissure. In the most basal Sarcopterygii, the canal does not fuse to the anterior transverse commissure, although a connection is probably present in the common ancestor of Onychodontidae, Actinistia and Dipnomorpha. In the non-monophyletic, basal actinopterygian 'palaeonisciforms', the terminal portion of the nasal canal passes between the anterior and posterior nares. This condition may be interpreted as a synapomorphy of Actinopterygii, as is also present in Acipenseriformes. In Polypteriformes and Holostei, the nasal canal passes also between the anterior and posterior nasal openings but it has a lateroposteriorly directed curvature at its anterior portion. In Teleostei, a condition similar to the ancestral condition is present, but it is likely as a secondary acquisition, since the curvature is also present in larval stages of *Salmo*. Therefore, we concluded that the curvature at the anterior portion of the nasal canal was present on the common ancestor of Polypteriformes+Actinopteri but it has been reversed in Acipenseriformes and lost in adult teleosts. A plate-like nasal bone is absent in Acipenseriformes, inasmuch as its nasal canal is entirely reduced to tubular ossicles, possibly a new synapomorphy for the order. This work was funded by FAPESP (#2015/10849-6) and CNPq (# 312067/2013-5).

GEN3-4 3:15 pm

Coos, booms, and hoots: the evolution of closed-mouth vocal behavior in birds.

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Abstract: Most birds vocalize with an open beak, but vocalization with a closed beak into an inflating cavity occurs in territorial or courtship displays in disparate species throughout birds. Closed-mouth vocalizations generate resonance conditions that favor low-frequency sounds. By contrast, open-mouth vocalizations cover a wider frequency range. Here we describe closed-mouth vocalizations of birds from functional and morphological perspectives and assess the distribution of closed-mouth vocalizations in birds and related outgroups. Ancestral-state optimization suggests that closed-mouth vocalizations are unlikely to be ancestral to birds and evolved independently at least 16 times within Aves. Origin of the trait is always preceded by an increase in body size. Closed-mouth vocalizations are also rare in the small-bodied passerines, further supporting a relationship of closed-mouth vocalization to body size. In light of the large body sizes of non-avian dinosaurs and conserved motor patterns associated with vocal behavior across tetrapods regardless of vocal organ, closed-mouth vocalizations were likely represented among extinct non-avian dinosaurs. As in birds, this behavior likely was limited to sexually selected vocal displays, and not used in all contexts in which vocalizations occur, and therefore would have co-occurred with open-mouthed vocalizations. It may have originated in response to selective pressures favoring low-frequency sounds.

GEN3-5 3:30 pm

The head suspension apparatus of cats and the shoulder suspension apparatus of humans: Modeling a macroevolutionary transformation with extant organisms.

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Abstract: The macroevolutionary processes that result in the origin of supraspecific taxa are commonly assumed to have resulted from an accumulation of minor morphological changes. To test whether small structural changes may have fundamental functional effects, we modeled the morphological and biomechanical changes necessary to transform the head-neck-shoulder apparatus of a quadrupedal mammal into that of the bipedal human. For our comparative analysis, we selected a cat as the representative quadruped because cats and humans are surprisingly similar in some aspects of their head-neck-shoulder morphology and postures. In both species, the head-neck-shoulder apparatus comprises the mastoid processes and nuchal region of the skull, the clavicles, a *de facto* nuchal ligament, and the sternocleidomastoid-trapezius muscle complex and its related fascias. The postures and force regimes of the head-neck-shoulder apparatus of a ready-to-pounce cat and a slumped-forward human are also similar in that the head is suspended from the cervical vertebral column by the nuchal ligament. As postures change to various extents, so do the musculo-fascio-skeletal configurations and, as a result, their force regimes. For example, the head-neck-shoulder apparatus in an upright human with freely hanging arms suspends the shoulders from the skull and does the same in a cat that is capable of sitting on its haunches with freely hanging forelimbs. Thus, minor morphological variations in skeletal proportions, joint morphology and attachments of ligaments and muscles, which together have significant biomechanical effects, result in the fundamental change of the head-neck-

shoulder apparatus from a head suspension to a shoulder suspension in the same manner that can be assumed to have happened during the evolutionary transition from a quadruped to a biped.

GEN3-6 3:45 pm

Unique turbinal morphology in echolocation specialists (Chiroptera: Rhinolophidae).

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Abstract: The mammalian nasal fossa contains a set of delicate and often structurally complex bones called turbinates. Turbinates and the epithelia they support function in regulating respiratory heat and water loss, as well as increasing surface area for olfactory tissue. Here, we used high-resolution microCT scanning to investigate a unique and previously undescribed turbinal morphology in 29 species from the bat family Rhinolophidae, which we compared with those of closely related hipposiderid and megadermatid bats, as well as with *Pteropus lylei*. Rhinolophids have one of the most highly derived echolocation systems known among bats, and exhibit numerous morphological characteristics associated with emission of high duty cycle echolocation calls via the nasal chamber. In these bats, we found that the maxilloturbinates and a portion of one of the ethmoturbinates contribute to form a pair of strand-like bony structures on each side of the nasal chamber. These structures project anteriorly from the transverse lamina and complete a hairpin turn to project posteriorly down the nasopharyngeal duct, and varied in length among the species in our sample. We hypothesize that these structures may play a role in sound transmission of echolocation calls since they are located directly along the path that sound travels between the vocal chords and external nares during call emission. The strand-like turbinates may additionally – or alternatively – play a role in reducing respiratory heat and water loss without greatly impacting echolocation behavior since cylindrical structures take up little space within the nasal fossa, but still have high surface area to volume ratios. The strand-like structure of the turbinates in Rhinolophidae are unique and represent a new diagnostic character for this family.

GEN4-1 4:30 pm

Ventilatory rib kinematics in the savannah monitor, *Varanus exanthematicus*: an XROMM study.

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Abstract: Squamates use aspiration breathing, driving air into their lungs mainly by using costal expansion to generate negative internal pressures. Because squamates use lateral undulations to locomote, rib motions are thus responsible for both ventilation and locomotion in these animals. The vertebral ribs are single headed, permitting three degrees of rotation between the ribs and vertebral column. In this study, X-ray Reconstruction of Moving Morphology (XROMM) was used to quantify the three dimensional rib rotations in 3 individuals of *Varanus exanthematicus*, which are typically described as bucket-handle rotation about a dorsoventral axis, pump-handle rotation about a mediolateral axis, and caliper motion about a rostrocaudal axis. During deep breathing in standing and prone lizards, we found rib motion to include a mixture of bucket and pump handle motions. Although the vertebral ribs did not deform during ventilation or translate substantially relative to the sternal ribs, a thin segment of the sternal ribs deformed during each breath. Compared to standing breaths, the sternum and vertebral column move around a more acute angle during prone breaths, and the vertebral ribs exhibit a greater degree of bucket handle rotation in prone breaths compared to standing. These differences in kinematics between breaths during different postures may help to explain the evolution of unrestrictive costal joint anatomies in Squamata, as the joint design must permit variations in ventilatory and locomotor motions under different conditions and postures. We found most of the ribs of *V. exanthematicus* to move during ventilation, unlike in iguanas. This difference in ventilatory strategy may reflect differences in endurance, locomotor strategies, or lung designs between *Iguana* and *Varanus*.

GEN4-2 4:45 pm

Grow bigger, dig deeper? Allometric effects of size on forelimb muscle architecture in the southern brown bandicoot (*Isodon obesulus*; Marsupialia: Peramelidae).

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Abstract: Physiological cross-sectional area (PCSA), which is proportional measure of the maximum force-generating capacity of a muscle, is often used in studies of animal ecomorphology. In such studies, sample sizes is minimal and intraspecific variation is rarely considered, although is important where either potential ecological function changes with age, or where sexual dimorphism is correlated with behavioural differences or some degree of niche separation between the sexes. The southern brown bandicoot (*Isodon obesulus*) is a medium-sized, omnivorous scratch-digging marsupial that utilises subterranean food items. Males (0.89kg) are significantly heavier than females (0.62kg). *Isodon obesulus fusciventer* is commonly found across Western Australia, and reasonable numbers of ethically-sourced specimens are available, enabling a comprehensive comparison of the morphology of both sexes. We investigated intraspecific variation in forelimb muscle architecture during growth (for individuals ranging in body mass from 0.2-2kg). Larger animals (heavier than 1kg) have increased PCSA scores in 78% of muscles measured, with the extrinsic muscles, m. triceps brachii, muscles on the scapula and the m. flexor digitorum profundus muscles having the highest PCSA scores. Larger animals had greater investment in muscles involved in elbow extension, carpal flexion and digit flexion, while smaller animals had increased muscles involved in humeral

retraction – the muscle actions emphasised in fossorial mammals where they generate large out-forces to act against the soil during fossorial behaviour. The intraspecific variations suggests likely differences in feeding ecology between animals of different sizes.

GEN4-3 5:00 pm

Big cat, weak cat? The scaling of postcranial myology within Felidae.

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Abstract: Felids (cats) span a wide range of body masses, from around 1kg in the smallest extant species around 500kg in the largest extinct species. Across this range of sizes, they remain remarkably conservative with regards to the maintenance of a crouched posture, despite major biomechanical tradeoffs for the largest felids. Understanding the scaling of the locomotor musculature is important to see if and how felids compensate for their postural limitations. Using dissection, we collected data for vertebral and limb muscle architecture from nine species of felids spanning from 1.1kg to 133kg covering a wide range of extant body sizes. Data from the forelimbs show that many of the muscles involved in support functions scale with positive allometry, as do muscles linked to claw protraction and forearm flexion involved in the tackling of larger prey by the biggest felid species. In the hindlimb, only a few muscle metrics scale with positive allometry, and of those most are linked to hip and thigh movements. In the vertebral column, nearly all muscle metrics scale indistinguishably from isometry, despite there being osteological allometry across the vertebrae. When phylogeny is accounted for, nearly all significant allometries across the muscles of the postcranium become indistinguishable from isometry. Considering that cross-sectional area (a metric of force production) scales by mass^{2/3}, and most muscles scale near-isometrically, unlike allometric trends that seem to apply to other mammals, the result is that large felids become relatively weaker than their smaller relatives. Using the scaling equations calculated from the modern species, and CT scans of fairly complete specimens for both the extinct North American lion (*Panthera atrox*) and the sabre-toothed cat *Smilodon fatalis*, we were able to reconstruct digital skeletons, and upon those the myology of these taxa, more accurately than previously possible.

GEN4-4 5:15 pm

Transforming tails into tools: syngnathid fishes used as bio-inspiration.

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Abstract: The development and innovation of products can be compared to thousands of years of natural selection, where only those morphologies that had an adaptive advantage compared to others were retained. In our study, we have been looking for serially articulated systems that are characterized by an unlikely combination of strength, flexibility and the potential for miniaturization. A biological system that meets all these needs can be found in the tail of syngnathid fishes. Within this family, four different morphotypes can be distinguished, being pipefishes, pipehorses, seahorses and seadragons. The natural variation among the tails of these different morphotypes goes from very solid and rigid system (as seen in pipefishes and seadragons) to very flexible, but less rigid systems (as seen in some pipehorses) but also systems that combine flexibility and rigidity (as seen in seahorses). The first part of this study focused on the different morphological patterns observed within and between the tails of the different morphotypes. For this part, virtual 3D reconstructions of complete tails were made based on μ CT-scans. In the second part, a 3D surface based morphometric analysis was performed to determine the skeletal shape characteristics that can be linked to prehensile tailed species. In the third and last part, these characteristics were mimicked by using a virtual, dynamic model to determine what the implications are on the flexibility of the tail and which specific morphological adaptations could lead to the observed differences in tail flexibility and rigidity.

GEN4-5 5:30 pm

On the whole-anatomy of the murine hepatobiliary system by using the transparency method.

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Abstract: The biliary tract, including the gallbladder, is a well-branched ductal structure that exhibits great variation in morphology among vertebrates. Because of its variety, the biliary tract has been a major enigmatic body part in the field of comparative anatomy. However, the whole-anatomy of the biliary tract with related blood vessels, nerves, and smooth muscle has been not fully documented in many species especially in small animals, mostly because they surrounded by the opaque liver tissue. To reconcile this, at the outset, we described the whole-anatomy of the biliary system of mouse (*Mus musculus*) by the combination of the classical technique of the color injection in blood vessel and biliary tract, immunohistochemistry, and recently invented transparency method CUBIC. Although some rodents have highly derived morphology, in the result, the topographical relationships of the murine biliary system were very similar to those of human, dogs and opossums. Phylogenetically, the murine hepatobiliary system should represent at least the ancestral state of eutherians, and is also useful as an experimental model for studying the human hepatobiliary system. We also report the recent advances in the comparative anatomy with transgenic mice, and other vertebrate species.

Contributed Session — General Morphology 5: Climate Change, Environmental Drivers, & Morphological Change (GEN5)

Organizers: Blair Bentley, Jeanette Wyneken

GEN5-1 2:30 pm

Predicting the effect of climate change sea turtle embryos in North West Australia.

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Abstract: Increasing ambient temperatures associated with anthropogenic climate change are anticipated to have wide-scale adverse effects on all ecosystems, ecological processes and taxa across the globe. Sea turtle populations are particularly vulnerable to these changes, with higher temperatures expected to lead to female-biased primary sex-ratios, increased embryonic mortality, and the production of smaller hatchlings. Six of the seven extant species of sea turtle are found in the waters off the Kimberley coast in Western Australia, with globally significant rookeries of three species of sea turtle. While many studies have assessed the impacts of climate change on sea turtle sex-ratios, the Kimberley region is largely unstudied. Additionally, few studies have also investigated the genetic response of developing sea turtle embryos to thermal stress. Here, we predict the effects of climate change on sex-ratios and embryonic mortality at three rookeries in the Kimberley, and present a transcriptome-wide analysis of the response of developing embryos to simulated climate change. Using constant and cycling incubation experiments to resolve baseline thermal biology data, coupled with predictions of future regional temperatures, we show primary sex-ratios skewing towards female bias and increases in mortality while identifying genes associated with thermal stress. We also show a decrease in hatchling weight, but not carapace, head or flipper measurements as temperature increases. Our study explores the effects of climate change on globally significant rookeries of sea turtles in the Kimberley and shows the underlying genetic response to climate change, with 299 genes differentially expressed as a consequence of thermal stress, including decreases in a number of genes associated with development and morphogenesis. Initial results suggest that Kimberley populations may be more resilient to the effects of climate change than first anticipated, at least for the near future.

GEN5-2 2:45 pm

Environmental impacts on reptilian nests and offspring: differential embryonic success and neonate growth.

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Abstract: Because sex in many reptiles is environmentally determined, thermal effects associated with climate change have been postulated to have profound sex ratio effects, almost to the exclusion of consideration other developmental and morphological consequences. Large-scale modeling approaches infer thermal effects on reptiles, particularly on marine species; these use historic weather data or sea surface temperatures as proxies for incubation conditions that are rarely verified for the eggs, the hatchlings or estimates of the primary sex ratios. In the context of climate change, turtles are particularly interesting because their long evolutionary history includes surviving changing climates. This presentation provides a critical review of the existing approaches to assessing weather and climate-scale impacts on marine turtle eggs, their developmental success and neonate morphology. We present a case study in which *in situ* results are verified. Experimental laboratory studies aid our understanding of previously under-appreciated impacts. Comparisons among species show that outcomes from nests vary with nest depth. These findings also suggest that most large-scale models disregard important biological effects upon the incubation environment and fail to consider the impact of embryonic death and sublethal effects on neonate growth and survival. Eggs that experience hyperthermia during development experience stage-related mortality; surviving embryos tend to incubate rapidly and hatch at small size, many with scute anomalies. Some show delayed post-hatching growth, which can increase predation risk. Hyperthermia after hatching and during nest emergence can result in bleeding into the aqueous humor of the eye, which can compromise seafinding orientation. Hatchlings from nests that experience heavy rainfall with high incubation temperatures tend to produce hatchlings that emerge larger, grow more uniformly, and experience lower levels of delayed mortality.

GEN5-3 3:00 pm

Virtual fish gills: Computational modeling of gills to quantify hydrodynamic trade-offs in actinopterygian fishes from diverse habitats.

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Abstract: When compared with air, water is a poor respiratory fluid, with a high viscosity and low dissolved oxygen concentration. Therefore, fluid dynamics likely play a large role in the evolution of respiratory morphology of vertebrates that rely on aquatic respiration. While the mechanism of aquatic ventilation in non-tetrapod vertebrates is relatively conserved, there is tremendous diversity in the morphology of this system, particularly in the microstructures of gill tissues. Vertebrate gill tissue consists of long filaments (primary lamellae), which are covered with small folds of tissue (secondary lamellae) that are the main site of gas exchange. These secondary lamellae vary considerably in shape, size, and spacing among species. In this study, I quantify hydrodynamics of secondary

lamellae morphology in species of actinopterygian fishes representing six ecological categories: open-ocean pelagic, benthic-pelagic, deep sea, benthic, freshwater pelagic, and diel vertical migrators. Using a 3D computational model of the secondary lamellae that I have developed in COMSOL Multiphysics, I model the hydrodynamics of the gills of each species based on measurements from scanning electron microscopy. By measuring flow rate through and around the secondary lamellae over a range of pressures, I examine the trade-off between the total volume of fluid passing over the lamellar surface and the ability of water to pass through the gills.

GEN5-4 3:15 pm

Pattern of habitat use of the parasitic nematode *Crassicauda* within its host, the pygmy sperm whale (*Kogia breviceps*).

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Abstract: Giant nematodes (>3m) of the Genus *Crassicauda* infect kogiid whales. Only three studies to date have provided detailed descriptions of these *Crassicauda* worms, which were based upon fragmented specimens (Johnston and Mawson 1939, Dollfus 1966, Jabbar *et al.* 2014). These studies described worms within the neck region of kogiids, an unusual anatomic site for this parasite. Keenan-Bateman *et al.* (2015) demonstrated crassicaudids to be a species-specific parasite among kogiids, infecting only *Kogia breviceps*, and confirmed its primarily cervico-thoracic distribution. To date, though, the pattern of habitat use within the host, and transmission path of this parasite are unknown. This study utilized necropsy reports (n=32), detailed gross and micro-dissections (n=12), histological examination of host tissues (n=5), and scanning electron microscopy of excised worms (n=7) to enhance our understanding of this host-parasite relationship. Results reveal a critical habitat for the worm is a previously undescribed compound tubuloalveolar exocrine gland, which opens at the terminus of the "false gill slit" pigmentation pattern in the whale's neck. *Crassicauda* male and female tails were found hanging freely in the glandular central lumen, and eggs have been observed in its presumed secretion, indicating the likely transmission path out of the host body. The cephalic ends of these worms were found, often meters away (curvilinearly), embedded deeply within the host's epaxial muscle. A single worm's complete, tortuous 312cm course from the gland to its termination in the contralateral epaxial muscle of its definitive host, *K. breviceps*, is described for the first time. The species-specific nature of *Crassicauda* infection, the exocrine gland, and the distinct features of the false gill slit pigmentation pattern associated with the gland, suggest that they are all useful characters to identify kogiid species in the field.

GEN5-5 3:30 pm

Identification and characterization of ionocytes in branchial epithelium of Catfish *Heteropneustes fossilis* and the effect of salinity on their morphometry.

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Abstract: The identification and characterisation of ionocytes in the branchial epithelium of the catfish *Heteropneustes fossilis* was done employing light microscopy and immunohistochemistry. Among successful stains, the acid haematein (AH) and osmium zinc iodide (OZI) selectively stained ionocytes which were round or ovoid, located singly or in clusters of 2-4 cells mainly in the interlamellar area and at the tip region and only occasionally at the lamellae. The ionocytes stained black with OZI and blue with AH exhibiting granulation in the latter. The ionocytes were also localized immunohistochemically using monoclonal antibody specific to α subunit of chicken Na⁺/K⁺-ATPase. Transmission electron microscopy (TEM) revealed ionocytes, pavement cells, accessory cells, pillar cells and undifferentiated cells. The ionocytes were characterized by high mitochondrial density, extensively amplified basolateral membrane and narrow apical pit which was either flat or slightly convex without microvilli. Two subtypes of ionocytes, designated as Ccl and CclI, were differentiated on the basis of round mitochondria and electron dense cytoplasm in Ccl and round and elongated mitochondria and electron lucent cytoplasm in CclI. Under scanning electron microscopy (SEM), pavement cells were characterized by concentrically arranged microridges, the mucous cells had flocculent mucus near their openings and the ionocytes appeared as swollen structures with faint concentric rings. In 25‰ sea water adapted catfish, the number of ionocytes, visualized under light microscopy, was significantly decreased but their size remained unchanged. Similarly, an increase in the number of mucous cells openings under SEM and an increase in the number of lamellar accessory cells under TEM were observed in 25‰ SW catfish. The identification of ionocytes in this study may help to elucidate the role of these cell types in stenohaline FW teleosts in higher salinities.

Contributed Session — Geometric Morphometrics (GMM)

GMM1-1 9:30 am

Morphological responses of the scapula and os coxae to selection for high voluntary locomotor activity in laboratory mice (*Mus musculus domesticus*, Rodentia: Muridae).

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Abstract: In mammals, the major girdle elements (scapula and os coxae) serve as attachment sites for muscles powering locomotion and in females, the os coxae also forms much of the bony birth canal. Previous comparative work shows that scapular and coxal morphology reflect variation in locomotor function. However, few studies differential responses in these elements similar locomotor variation. Additionally, sexual dimorphism of the os coxae is common in mammals and numerous studies suggest that this dimorphism results from an evolutionary trade-off between reproduction and locomotion but the potential performance trade-offs are difficult to demonstrate. Given the importance of their functional roles, the scapula and os coxae can greatly inform our understanding of both morphological responses to changes in locomotor behavior and potential trade-offs between different functions, yet much of the work done to understand these questions is comparative in nature, presenting some limitations. To add to the existing knowledge of these patterns of scapular and coxal morphology, we employ an experimental evolutionary approach by using laboratory mice bred for high voluntary wheel running (HR) and from non-selected control (C) lines to investigate how selection for high locomotor activity differentially affects the morphologies of the scapula and os coxae as well as variation in the magnitude of sexual dimorphism in the os coxae. Specifically we used geometric morphometric analyses of the os coxae and scapula in a sample of male mice. We then used both geometric morphometrics and X-ray micro computed tomography to measure differences in the shape and in bone mineral density and bone volume of the os coxae in a sample of male and female mice. Our results indicate that the scapula and os coxae differ in the magnitude of their response to selection and that dimorphism of the os coxae differs with selection, but the trajectories of those differences were not as predicted.

GMM1-2 9:45 am

Using 3D geometric morphometrics to study interspecific variation in the forelimb of modern tapirs (Perissodactyla: *Tapirus*).

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Abstract: Forelimb morphology is an indicator for terrestrial locomotor ecology. The limb morphology of the enigmatic tapir (Perissodactyla: *Tapirus*) has often been compared to that of basal perissodactyls, despite no quantitative studies comparing forelimb variation in modern tapirs. Here, we present a quantitative assessment of tapir forelimb osteology using three-dimensional geometric morphometrics to test whether the four modern tapir species are monomorphic in their forelimb skeleton. The shape of the scapula, humerus, radius and ulna of 24 individuals across the four species (*T. indicus*; *T. bairdii*; *T. terrestris*; *T. pinchaque*) was investigated. Bones were laser scanned to capture surface shape. 3D landmark analysis was used to quantify bone shape. Discriminant function analyses were performed to reveal landmarks which can be used in interspecific discriminations. Overall our results show that the appendicular skeleton contains notable interspecific differences. Our results demonstrate that upper forelimb bones can be used to discriminate between species (>91% accuracy), with the scapula proving the most diagnostic bone (100% accuracy). Features that most successfully discriminate between the four species include the placement of the cranial angle of the scapula, depth of the *condylus humeri*, and the lateral *fovea capitis radii*. Overall, the mountain tapir *T. pinchaque* most consistently exhibits the greatest divergence in morphology from the other three species. Despite previous studies describing all tapirs as functionally mediportal in their locomotor style, we find osteological evidence of a spectrum of locomotor morphology in the genus *Tapirus*. We conclude that the four extant tapir species differ in upper forelimb osteology; they are neither monomorphic, nor are they as conserved in their locomotor habits as previously described.

GMM1-3 10:00 am

3-D geometric morphometric exploration of pelvic girdle configuration in four ecomorphs of Greater Antillean anoles (Squamata: Dactyloidae).

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Abstract: Anoline lizards of the Greater Antillean islands have featured prominently in studies of convergent evolution, and have become a focal taxon for the study of ecomorphology. External morphological traits vary in association with exploitation of different portions of the structural habitat, and much of this variation is associated with the locomotor system. Previous morphological studies of the shoulder girdle of island anoles revealed that the 3-D form of isolated girdle elements differs markedly between anoline ecomorphs from Hispaniola and Puerto Rico, although girdle structure is relatively conservative in Jamaican anoles. Here we apply 3-D geometric morphometric approaches to the analysis of the in situ pelvic girdle of twenty-six species of anoles, belonging to the only four ecomorphs common to Jamaica, Puerto Rico and Hispaniola. Our investigations reveal subtle differences in the morphology of the pelvic girdle between anole ecomorphs. The structural differentiation of the pelvic girdle is less prominent than predicted based upon an earlier study of the pectoral girdle. Structural differences in the pelvic girdle are evident consistently, however, in anoles from all three islands. Twig anoles, in particular, are characterised by a relatively elongated ilium, an anteroposteriorly shortened pubis, and a greater anteroventral inclination of the pubic

apron, when compared to the other ecomorphs. Trunk-crown anoles show a more posteriorly positioned ilium, with a greater anteroventral inclination. This differentiation in form likely relates to changes in the direction of muscle vectors, thus representing skeletal-morphological adaptations associated with differences in locomotor style and habitat use.

GMM1-4 10:15 am

How good is the tarsometatarsus for species identification? 3D Geometric Morphometrics in living and extinct foot-propelled diving birds.

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Abstract: Hesperornithiformes (Aves: Ornithurae) were flightless foot-propelled diving birds that lived during the Late Cretaceous and have an excellent fossil record compared to most Mesozoic birds. Extinct bird taxa are often identified from fragmentary or isolated specimens, and several species of *Hesperornis* have been named on the basis of the tarsometatarsus alone. Size has often been the criterion for taxonomic differentiation, but little has been done to examine intraspecific factors that determine the form of this bone. To test for intraspecific and interspecific variation in the tarsometatarsus of hesperornithiforms, I examined variation in extant members of the foot-propelled diving Gaviidae (loons) and Podicipedidae (grebes). Loons and grebes are morphologically similar to extinct hesperornithiforms, making them appropriate analogues, even if we cannot assume homologous levels of variability in the two groups. Only adult female specimens were chosen for analysis, to reduce the possibility of sexual dimorphism or ontogenetic differences. I used landmark-based Geometric Morphometrics to analyze 3D scans of specimens from three species per family, totaling 22 extant specimens. Thirteen individuals from five named species of *Hesperornis* were also used. Separate analyses were performed on the shape of the full bone, the shape of the distal end, and the shape of the proximal end for each clade (Gaviidae, Podicipedidae, and *Hesperornis*). In nearly every Principal Component Analysis of extant and extinct groups, individuals did not group by species, and any "taxonomic" grouping recovered was poorly defined. These results indicate that intraspecific variation swamps interspecific variation in foot-propelled divers, and so the tarsometatarsus alone is not a reliable taxonomic guide. Therefore published taxonomic schemes of named hesperornithiforms based solely or mainly on tarsometatarsi should not be used in studies of diversity.

GMM1-5 10:30 am

Femoral neck bone density and morpho-functional feature in chimpanzees.

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Abstract: Morphology of bone well reflects daily behavior of animals. In the past studies, it is known that the cortical thicknesses of the femoral neck inferior regions are larger than the superior region in chimpanzees, but not so conspicuous in humans (Matsumura et al., 2010, *Int. J. Primatol.*). In order to confirm the mechanical effects of daily locomotion on the femoral neck of chimpanzees (*Pan troglodytes*), we examined the relationships between the density and thickness of cortical bone along the circumference in a cross-section of femoral neck. Femora from captive chimpanzees (specimens of Dokkyo Medical University; n=8) were used in this study. We obtained serial scans of 5 parts along the femoral neck, perpendicular to its long axis by using pQCT (XCT Research SA+, Stratec Medizintechnik GmbH). In each cross-section, data of cortical thickness were measured in 8 parts at every 45 degrees around the circumference. Data of cortical density were measured in 8 regions of ROI corresponding to the measurement parts of cortical thickness. Cortical density of femoral neck around mid-region showed lower values in the superior parts of every individual. The average density tended to show the smallest value in the superior part where cortical thickness was the smallest, and showed relatively small tendency in antero-superior region where cortical thickness was the second largest. In contrast, the density around anterior, inferior, and posterior regions showed relatively higher and almost constant values compared to the superior region while the values of density in the superior region had large dispersion. These results confirmed that the burdening of femoral neck of chimpanzees borne in daily locomotion is smaller in the superior parts compared to other parts. The results of the present study also indicate that cortical area and thickness reflect the strengthening of femoral neck rather than the cortical density against various loads.

GMM1-6 10:45 am

Ontogenetic changes in muscle architectural properties in the Eastern cottontail rabbit (*Sylvilagus floridanus*).

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Abstract: Rabbits have fast-contracting muscles that allow them to accelerate rapidly. Moreover, juveniles may have performance advantages relative to adults that could increase their chances of escaping predation. We predicted that force and power capacity of the extensor musculature would be optimized in juvenile rabbits, allowing them to achieve levels of locomotor performance similar to, or even greater than, that of adults. To test this hypothesis, we quantified muscle architectural properties across ontogeny in Eastern cottontail rabbits (*Sylvilagus floridanus*). Measurements of muscle mass (MM), belly length (ML), fascicle length (LF), pennation angle, and physiological

cross-sectional area (PSCA) were taken from each muscle, and these metrics were used to calculate functional estimates of maximum isometric force, joint torque, and instantaneous power. The scaling results did not support our hypothesis. Relative to body mass, extensor group MM and estimates of instantaneous power scale with positive allometry. However, juvenile rabbits may have several compensatory features that may allow for increased performance (and fitness) including higher LF/ML ratios, and greater effective mechanical advantage at the hindlimb joints. Therefore, development of their musculoskeletal system appears to provide juvenile rabbits with some advantages to evade predation by rapid acceleration. By contrast, adult rabbits may require positive allometry of muscle power in order to cope with greater absolute body size and associated limits on acceleration capacity. Supported by NSF IOS-1147044 and NEOMED.

GMM2-1 11:30 am

Quantitative morphological convergence and divergence of carnivorous rodents from the Indo-Pacific.

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Abstract: Convergence – the independent acquisition of similar characters across different lineages that did not share a common biological background – is a prime example to demonstrate the strength of extrinsic factors that might deterministically shape phenotypic evolution. Natural selection factors have often drive exceptional morphological convergences among unrelated organisms. Several placentals are famous to have independently evolved herbivorans, nectarivorans, insectivorans or carnivorans convergent adaptations highlighting the dietary constraint on their cranio-dental morphologies. Among the most spectacular dietary change of ecology and morphology are the shift toward termitophagy and vermivory found several independent lineages. Rodents of the family Muridae (rats and mice) have migrated from Asia to the major landmasses of the Indo-Pacific archipelago (IPA) multiple times since the Miocene. Their ecological diversity is facilitated by a remarkable array of morphologies, including some associated with unique niche shifts toward an animalivorous diet. Our study focus on four independent acquisitions of animalivory in the Indo-Pacific using an exhaustive murine sampling for this region and provide what is to date the most thorough examination of a mammal adaptive radiation involving a spectacular change of morphology and ecology. We obtained a new integrative framework on morphology, molecules, ecology and phylogeny from animalivoran rodents from all the Indo-Pacific area, comprising two thousand specimens from 221 murine species for jaw and skull. Demonstrating quantitative convergence among independent lineages is challenging. Morphological similarities among unrelated lineages may be qualitatively apparent but not reflect quantitative convergence of traits. Using recent comparative methods and a large dataset containing both ecomorphological and phylogenetical data we were able to infer the quantitative convergence among these animalivoran IPA murines.

GMM2-2 11:45 am

Morphometric models for estimating bite force in murid rodents: empirical versus analytical models.

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Abstract: Bite force is an ecologically significant performance trait that can be readily measured using an ad hoc device. However, it may also be derived from bone morphology either with simple models using muscular levers or more complex ones relying on geometric morphometrics. We quantified morphologies and measured bite force in different rodent species (Muridae), in the wild and in the lab, to better understand the relationship between performance and morphology. Using geometric morphometric data, we produced several predictive models uniting bite force with morphology at different evolutionary scales. These empirical models were compared with an analytical one, based on muscular lever and mechanical advantage. We first looked at how bite force and mandible morphology change throughout ontogeny in lab-reared pups of *Mus musculus domesticus* at different stages from 15 (just after incisor eruption) to 68 days (maturity). Then, we analysed mandible shape and bite force variation/covariation in four wild species of Muridae: *Rattus exulans*, *Rattus tanezumii*, *Mus cervicolor*, and *Mus cookii*. This allowed us to estimate the divergence among intraspecific and interspecific patterns of covariation of mandible shape with bite force. Finally, in order to estimate the best approach, we applied our predictive models to other individuals and species and interpreted the deviations between observed bite force and predicted bite force with regard to ecological and behavioural factors (e.g. differences in aggressiveness, commensalism...).

GMM2-3 12:00 pm

Darwin's Niata - an anatomical, morphometric, and genetic study of an extinct cattle breed: expanding morphological boundaries through selective breeding.

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Abstract: Domestication can produce phenotypes that expand the morphospace occupied by wild forms, providing case studies of rapid evolution and morphological transformation. An example is the now extinct Niata cattle form, its peculiar features having been the subject of discussion and argumentation in the writings on evolution by Charles Darwin. The Niata cattle form has been considered an achondroplastic dwarf, an oddity of selective breeding, and, owing to its atypical jaw shape, a non-viable variation of cattle. We explored the validity of these hypotheses, and the proposed unique features of the Niata cattle, by combining morphological, geometric morphometric, and genetic approaches. Using a sample of 87 breeds as comparison, we analyzed landmark data of 340 skulls, cranial suture closure data of 27 sutures, applied Finite Element Analysis (FEA) to 3D virtual models of the skull to evaluate feeding biomechanics, and extracted genetic data using SNiP sequencing methods. Our results reveal that the Niata cattle have very distinctive anatomical features that are unique to this taurine breed. Niata cattle occupy a very distinct position in morphospace owing to their short snout and high forehead, features that are much less pronounced in other classical brachycephalic cattle breeds. Although the Niata was described by some as an achondroplastic dwarf, it does not fit the morphological characteristics of this congenital disease. The size, postcranial skeleton, and external suture obliteration in diagnostic parts of the skull contradict this hypothesis. In conclusion, the Niata was a viable variation of cattle that is as much part of the potential morphospace of cattle as is the bulldog for dogs. The rarity of the morphological traits of the Niata in cattle seems to be the result of human preference and a misinformed interpretation of skull features that are reminiscent of the "snorter dwarf" condition, which is the general term for a lethal form of achondroplasia in cattle.

GMM2-4 12:15 pm

Physical media influence the rate and pattern of turtle carapace shape evolution.

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Abstract: Aquatic and terrestrial environments subject organisms to considerably different selective pressures because water is about 800 denser and 50 times more viscous than air. Therefore, it is not surprising that even remotely related aquatic animals resemble each other in form and function as the morphological solutions to the functional requirements are limited by mechanical constraints. However, how the physical environment influences the rate of morphological evolution is largely unknown. Here we tackle this question by comparing the rate and pattern of the carapace shape evolution between aquatic, semi-aquatic and terrestrial turtles. Shell shape was quantified by 3D geometric morphometrics, and rates of shape evolution were compared using a time-calibrated molecular phylogeny. Patterns of shape evolution were examined by comparing evolutionary rates for upper- (vertebral and costal plates) and lower-carapace (marginal plates) relative to the physical environment. The first phylogenetic principal component showed a gradient from terrestrial to aquatic turtles highlighting the correlated evolution of morphology with the physical environment. Whole shell shape showed a greater evolutionary rate for terrestrial turtles compared to aquatic ones. Although terrestrial turtles exhibited greater rates for both carapace parts compared to aquatic turtles, statistical significance was obtained only for the lower-carapace. While the terrestrial environment favors a tall, well developed lower-carapace, this part of the shell is unfavorable in aquatic media. As a consequence, aquatic turtles exhibited a greater evolutionary rate for the upper carapace compared to the lower part, while the opposite pattern was observed for terrestrial turtles. Semi-aquatic turtles showed same evolutionary rates for both parts. Results suggest that biomechanical constraint of two physical media influence rate and pattern of turtle carapace shape evolution.

GMM2-5 12:30 pm

Patterns of morphological and mechanical evolution in the turtle shell.

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Abstract: Turtles provide an excellent opportunity to study the interplay between morphology, functional performance, and diversification. Here turtle shells are used to test hypotheses regarding the influence of functional demands on morphological diversification. The traditional view suggests that structures which perform a greater number of functions will show lower rates of evolution and lower levels of diversification than those which perform fewer functions. More recent hypotheses propose that diversification may be greater in structures which have many functions, where performance cannot be simultaneously optimized on all functions. We test these hypotheses by comparing the diversification patterns of aquatic turtle shells (whose shells must be strong, hydrodynamically efficient, and allow efficient self-righting if overturned) and terrestrial turtle shells (for which hydrodynamic performance is not relevant). We find broad support for the traditional hypothesis: terrestrial shells show greater levels of morphological disparity within and among clades than aquatic shells. However, this is despite higher rates of morphological evolution in aquatic shells. Separate tests on the carapace and plastron on shells further complicate this picture. Analyses of shape-performance relationships in mechanical strength, hydrodynamic efficiency, and righting ability, provides a resolution: functional influences on diversification appear to be strongly influenced by the shapes of performance surfaces. Neither the presence of a single optimum (or even any optimum) morphology, nor the presence of one-to-one mapping of morphology onto performance, can be assumed when examining even modestly complex structures. However, it may be possible to use patterns of evolution to make testable hypotheses about the complex shapes of performance or selective surfaces. This research was funded by NSF-RUI grant IOS-

1257142.

GMM2-6 12:45 pm

A look at measurement error in geometric morphometrics.

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Abstract: Geometric morphometrics – once considered revolutionary – has now reached maturity and is routinely used in ecological and evolutionary studies. However, the presence and the extent of measurement error is often overlooked in empirical studies. Here, using empirical data, we analyse measurement error and bias from different sources (preservation, presentation, digitization, multiple operators). We then apply multiple methods to reduce measurement error. Our results suggest that measurement error is pervasive and often subtle (and for this reason, easy to overlook). We suggest that often multiple approaches should be used to test and account for different sources of measurement error.

GMM3-1 2:30 pm

Morphospace occupation and subclade disparity through time in monitor lizards.

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Abstract: Understanding the influences of morphological variation relative to other forms of diversity is a long-standing question in biology. To understand how phylogeny can affect measures of morphological variation, I quantified and compared levels of diversity regionally and temporally using a phylogenetic and non-phylogenetic framework in a morphologically conservative group, the monitor lizards. Monitor lizards are useful because they are morphologically conservative, but vary in size and regional diversity. I digitized a recent time calibrated molecular phylogeny of 39 species and ran a 2D geometric morphometric analysis on the snout of 313 skulls representing 29 species. All analyses were run in R, and morphological disparity through time was measured using both morphospace occupation (Procrustes variation) and average squared distance disparity-through-time (DTT) on size and shape (*geomorph* and *geiger* packages in R). Results indicate that monitor lizards may have explored large amounts of shape space early in their evolution. Discrepancies on patterns of morphospace size and DTT occurred when the shape of newly originating taxa fell within already occupied morphospace. Increased metrics of morphospace and DTT correlate with originations of clades like the dwarf monitors and the large *Varanus komodoensis*. Interestingly, regions of low taxic diversity show high morphological disparity and phylogenetic diversity. These results suggest that in order to understand the evolutionary consequences and causes of diversity shifts, we cannot just look at diversity with one metric alone. Origination, like extinction, can have disparate effects on measured morphological, taxic, and phylogenetic diversity. Trying to understand modern and past diversity without the power of a phylogenetic framework, in this case by accounting for when and where originations occurred across a phylogeny, may result in the loss of a wealth of information on underlying mechanisms.

GMM3-2 2:45 pm

Interspecific and intersexual morphometric variation in *Darevskia* lizards based on anal scale shape.

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Abstract: *Darevskia* lizards are a highly diverse genus mostly found in the Greater and the Lesser Caucasus. Most of them are morphologically similar with variable but strongly overlapping scalation patterns across the species. They occupy the same type of habitats and their distribution often overlaps. We tried to identify sex and species specific morphological traits and test if the habitat is related to anal scale shape. Six species of *Darevskia* lizards have been studied throughout their range in Georgia. Phylogenetically *D. mixta* and *D. derjugini* belong to the same matrilineal (phylogeny based on mtDNA) clade ('mixta clade'), whereas *D. valentini*, *D. rudis* and *D. portschinskii* belong to another one ('rudis clade'). The phylogenetic position of *D. parvula* remains ambiguous. They have a very limited range, except for *D. rudis* and *D. derjugini*. All of them are rock dwelling, except for *D. derjugini* which is a ground dwelling species. In order to test if anal scale shape differed across the species, sex, and populations, a MANOVA was applied on the outline shape data. The analysis showed significant differences only between species that belong to different clades. *D. derjugini*, the only ground-dwelling species, has the most dissimilar shape from all the other species. At the intersexual level, anal scales of females have, on average, more circular scales compared to conspecific males, though are only sexually dimorphic in *D. portschinskii* and *D. rudis*. At the species level, scale shape variation is highest in *D. rudis*, which is also the species with the wider distributional range. At the population level, there are no significant differences in scale shape of specimens from different areas. As such, we did not find habitat related differences in anal scale shape.

GMM3-3 3:00 pm

Assessing levels of variation among parthenogenetic and bisexual whiptail lizard using geometric morphometrics.

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Abstract: Determining baseline levels of morphological variation, within and among species, is difficult because of

the influence of genetic, ontogenetic, environmental, and sexual differences. Parthenogenetic organisms are an ideal study system because new genetic variation is solely introduced through mutation. It might be expected that bisexual species should have a higher potential to produce genetic variation, resulting in higher levels of morphological variation. Using geometric morphometrics, we analyzed 121 skulls of 8 species of *Aspidoscelis*, a genus of whiptail lizard. Our study includes 7 bisexual and 1 parthenogenetic (*A. velox*) species from three regions in North and Central America, with sampling design to allow parsing of factors and controlling for habitat differences within regions. All skulls were measured and photographed in dorsal and lateral views. We statistically quantified variation across 67 landmarked points using Procrustes superimposition. Specimens were grouped according to species, sex, locality, and field-assessed age based on diagnostic characteristics. PCA, CVA, MANOVA, and disparity analyses were conducted using the geomorph and Morpho packages in R. Size had negligible impact on skull shape. *A. velox* significantly differed in shape to *A. sexlineata* ($p < 2e-16$) a closely related bisexual species, but overall disparity between adult females was similar (respectively: 0.0012, 0.0014). Including males and juveniles created a negligible increase in disparity. Species from Mexico, New Mexico, and Florida significantly differ in shape ($p < 2e-16$) with Mexico occupying a larger area of morphospace (M: 0.0028, F: 0.0017, NM: 0.0012). *A. velox* overlaps in shape space with its parental taxon, *A. inornata*. There is a strong influence of environment and phylogenetic factors on morphological variation, and lower genetic diversity does not directly correspond to lower levels of morphological diversity.

GMM3-4 3:15 pm

The relationship between feeding ecology and phylogeny for Weberian ossicle and otolith morphology in the piranha and pacu family (Actinopterygii: Serrasalminidae).

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Abstract: The Weberian apparatus is a synapomorphy for otophysan fishes, a diverse clade of approximately 7,900 species. This feature involves a chain of three bilateral vertebral elements (Weberian ossicles) that transduce sound pressure from the swim bladder to the ear. The Weberian apparatus and associated inner ear modifications provide increased sensitivity to sound pressure and a wider auditory bandwidth that are hypothesized to have facilitated the radiation of otophysans. Otophysans may use acute hearing to assess their environment, find prey, and detect feeding conspecifics. This hypothesis, however, remains speculative. In this context, we examined morphology of the Weberian apparatus, swim bladder, vertebrae 1-4, and ears within a Neotropical otophysan family (Serrasalminidae) with diverse feeding ecologies. We used μ CT scans from 50 specimens (MNHN) from 19 species with broad ecologies: fruit and seed eaters, aquatic plant eating species associated with river rapids (rheophilic), and species that eat fish (parts or whole). 3D Geometric morphometrics with traditional and sliding landmarks were used to characterize shapes of Weberian ossicles (tripus, intercalarium, scaphium) and the lagenar otolith (asteriscus). Preliminary results indicate that Weberian apparatus and otolith morphologies are correlated with both phylogenetic association and ecology. Tripus and scaphium shapes were both found to be associated with ecology after accounting for phylogenetic history. In addition, after considering phylogeny, Lagenar otolith morphology differed between fish-eating taxa and plant-eating rheophilic taxa. In addition, some evidence of morphological integration was observed: tripus shape correlated with scaphium shape and scaphium shape correlated with lagenar shape. Tripus shape, however, was not found to correlate with lagenar shape. Future studies should examine how auditory sensitivity is associated with different morphologies and how sound influences feeding behaviors.

GMM3-5 3:30 pm

Probing the third dimension: are morphospaces of 2D and 3D fossil fish crania congruent?

Close R A*, University of Birmingham; Friedman M, University of Oxford roger.close@gmail.com

Abstract: Landmark-based geometric morphometric (GMM) studies of fossil fishes have overwhelmingly focused on 2D compression fossils. In addition to being less abundant, three-dimensionally preserved material presents technical challenges, and to date 3D GMM techniques have rarely been applied. Two-dimensional morphometric analyses of 3D biological structures are a common procedure in biology, using photographs taken in standardised orientations to record the features of interest in a two-dimensional coordinate plane. By contrast, researchers studying compression fossils are constrained to landmark specimens in their preserved orientations, and it remains unclear how faithfully compression fossils capture shape information present in specimens prior to taphonomic flattening. To assess potential discrepancies between shape information preserved in 2D and 3D fossils, we quantified shape variation in the skulls of Late Cretaceous to Paleogene teleost taxa that are known from both inflated specimens (drawn primarily from the English Chalk and London Clay) and compressed specimens (drawn from sites in Lebanon, Italy, USA and the former USSR). We find a significant but weak correlation between the relative positions of taxa within morphospaces derived from flattened and fully inflated skulls. This covariation appears to be driven almost exclusively by the second shape axis, corresponding to variation in skull elongation. However, differences in skull proportions associated with the third dimension (e.g., broad versus laterally compressed skulls) dominate over more subtle forms of morphological variation in 3D morphospace. This aspect of shape variation is lost or obscured in compression fossils preserved in lateral view. Thus, while some major axes of cranial variation are comparable in

morphospaces derived from flattened and inflated fossils, three-dimensional landmark constellations capture substantial shape information that cannot otherwise be extracted from flattened specimens.

GMM3-6 3:45 pm

Diversification of the avian bill revealed with crowdsourced 3D geometric morphometrics.

Bright JA, University of Sheffield; Cooney CR, University of Sheffield; Capp EJR, University of Sheffield; Hughes EC, University of Sheffield; Moody CJA, University of Sheffield; Nouri LO, University of Sheffield; Varley ZK, University of Sheffield; Thomas GH, University of Sheffield* jen.bright@sheffield.ac.uk

Abstract: With nearly 10,000 species, birds represent a hugely diverse and disparate class within the Tetrapoda. How birds achieved this diversity has been of interest to biologists for centuries. Of particular interest is how phenotypic trait variation corresponds to changes in the rate of speciation. For instance, do rapid bursts of diversity necessarily entail rapid increases in morphological disparity? Crucial to this is understanding how phenotypes vary within and between lineages on a broad phylogenetic scale. We took 3D surface scans of beaks representing every bird genus, and landmarks for Geometric Morphometric analysis were then gathered using a specifically developed crowdsourcing website (www.markmybird.org), allowing for extremely rapid collection of beak shape data. Principal Components (PC) Analysis reveals that alterations in overall beak dimensions (length, width, and depth) account for approximately 90% of variation in shape, with specific clades or ecomorphs usually identified on lower ranking PCs. Analysis of evolutionary rates shows increased rates in several interesting parts of the tree, including the ducks and geese, and the split between swifts and hummingbirds. In particular, we note that several clades often identified as classic examples of adaptive island radiations (Madagascan vangas, Hawaiian honeycreepers, and the estrildid finches) display rapid rates of both phenotypic evolution and speciation. Despite accounting for half of avian diversity, passerines have more conservative beak morphologies than non-passerine birds. Non-passerines explored extremes of morphospace early in their evolutionary history revealing a pattern that is consistent with adaptive radiation playing out at a global scale. Our results highlight how the diversity of modern birds derives from a process of gradual phenotypic divergence interspersed with dramatic evolutionary bursts and slowdowns, affecting both clades and single lineages right across the avian phylogeny.

Symposium — The many faces of the skeleton: a tribute to the achievements of Brian K. Hall (HAL)
Organizers: Eckhard Witten, Matthew Vickaryous

HAL1-1 9:30 am

Facing plasticity in the skeleton of teleosts.

Witten PE, Ghent University, Department of Biology; Huysseune A, Ghent University, Department of Biology* peckhardwitten@aol.com

Abstract: Black and white thinking or digitalising nature by assigning characters to zero or one, is not the way that Brian K. Hall understands evolution and development. A prominent example is how Brian Hall explains us the many gradients that exist between homology and convergence (1). Darwin took a similar approach when he addressed the species problem (2): "Species are merely artificial combinations made for convenience. This may not be a cheering prospect; but we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species". Perhaps one can say, in a very Darwinian way Brian teaches us to look at the nature of skeletal tissues. We assign skeletal tissues and cells to distinctive categories, but nature is full of intermediate skeletal tissues. Grading of tissue types and the transition of skeletal cells into other cell types are common processes, not exceptions. They are required for development, adaptation and regeneration. Teleost skeletal and dental development provides us with numerous examples of plasticity, in terms of how skeletal structures are patterned, as well as of how they achieve their morphological end product. We will provide examples taken from our studies on dental patterning and on development of dermal and endoskeletal elements in teleosts. Clearly, our research would not be possible without the Brian Hall's understanding of the skeleton (3). (1) Hall BK (2003) Descent with modification: the unity underlying homology and homoplasy as seen through an analysis of development and evolution. *Biol. Rev* 78:409 -433 (2) Darwin C (1859) The origin of species. 552 pages (3) Hall BK (2015) Bone and Cartilage. *Evolutionary Developmental Skeletal Biology*. Academic Press. 892pages

HAL1-2 10:00 am

Dermal skeletal plasticity and evolution of the chondrichthyan dentition.

Meredith Smith Moya, Kings College London; Johanson Z, Natural History Museum London; Underwood, Birkbeck College London*

Abstract: Adaptive structure of the dermal skeleton during its evolution depends on plasticity of developmental mechanisms for skeletogenesis to form bone, separately and coupled with dentine. Dentine forms within a morphogenetic unit, the odontode, and requires neural crest cells to interact with epithelium; in skin and oropharyngeal mucosa odontodes are serial homologues by shared regulatory genes. Major divergences occur through developmental plasticity for adaptive function as odontodes transform through evolution. This diversity of odontodes in different morphogenetic fields occurs within as yet uncharacterised developmental boundaries. Dentitions are uniquely patterned in an oral morphogenetic field that may arise in evolution by co-opting modules

from serially ordered, enlarged dermal denticles, as in axially aligned tail scales, or axial and paraxial dorsal rows. One such pre-patterned field, exemplified by extended rostra equipped with "saw-teeth", is present in the sawsharks, the sawfish and fossil Sclerorhynchoidea. We examined both adults, and embryos to determine the developmental plasticity of chondrichthyan dermal denticles and whether or not, they could have been co-opted to provide a module for the dentition. In the chondrichthyan dentition, toothed fields are restricted to a continuous dental lamina, where from the jaw symphysis teeth form as left right mirror images. This oral field regulates the pattern (in time and space) of tooth addition along the jaw (distal to proximal) and in each developmental set of lingual successor teeth. These comprise a sequence addition model of two adjacent replacement sets formed in alternate time and space, proposed to explain alternate tooth pattern in many chondrichthyan jaws. Alternatively, in the single file tooth pattern, each is iterative, as disto-proximal tooth files spaced out along the jaw, where all file teeth are central cusp aligned, an arrangement that may be ancestral for crown gnathostomes.

HAL1-3 10:30 am

A neural crest origin of trunk dermal denticles in the little skate, *Leucoraja erinacea*.

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Abstract: Although many stem-gnathostomes possessed an extensive dentinous trunk exoskeleton, this feature is present only in relatively few extant taxa (e.g. in the form of dermal denticles in cartilaginous fishes, and in the scales of *Polypterus* and *Latimeria*). The embryonic origin of the dentine producing cells (odontoblasts) of the vertebrate trunk exoskeleton is a longstanding unresolved question in vertebrate evolutionary-developmental biology. The odontoblasts of vertebrate teeth derive exclusively from cranial neural crest cells. However, trunk neural crest cells are generally regarded as non-skeletogenic/odontogenic, leading to suggestions that trunk odontoblasts may derive from cranial neural crest cells that undergo an exceptionally long caudal migration, or from mesodermally derived progenitors. We have experimentally tested the odontogenic fate of trunk neural crest cells in embryos of a cartilaginous fish, the little skate (*Leucoraja erinacea*). Using histology and mRNA in situ hybridisation, we have characterised the emigration of trunk neural crest cells in the early skate embryo, and by labelling the trunk neural tube with CM-Dil prior to neural crest cell emigration, we demonstrate that the odontoblasts of skate trunk dermal denticles are, in fact, neural crest-derived. Our findings highlight the odontogenic potential of trunk neural crest cells in cartilaginous fishes, and point to the neural crest as the primitive source of dentinous tissues in the vertebrate exoskeleton.

HAL1-4 10:45 am

Evolution and development of scleral ossicles.

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Abstract: My research into the evolution and development of scleral ossicles was begun in Dr BK Hall's laboratory while I was a post-doctoral fellow. Over the last decade, scleral ossicles have remained a key focus of my ongoing research program. Scleral ossicles are flat bony plates present in the sclera of most vertebrate eyes. They have a long evolutionary history but remain poorly understood. Through gross morphological and experimental developmental biology studies, we have shown that while ossicles vary in shape and size within different reptilian lineages, they are highly constrained during development. In contrast, the morphology of the scleral ossicles is highly conserved amongst teleosts. From a developmental perspective, scleral ossicles develop via different modes of ossification in reptiles and teleosts, and therefore they are not homologous. Using a variety of approaches that include analysing vasculature, surgically over expressing inhibitors for major signaling pathways in development (e.g. the Hedgehog and TGF β families), gene expression, and cell tracking, we have gained significant insight into how the sclerotic ring develops, how it is constrained in development, and how variation arises. This multi-faceted approach has led to major advances in our understanding of the evo-devo of this intriguing skeletal element. This research was funded by the Natural Sciences and Engineering Research Council of Canada.

HAL2-1 11:30 am

Ontogeny and homology of the vertebrate skull.

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Abstract: Embryological and other developmental data have been used for well over a century to infer the homology of morphological structures and substantiate claims of evolutionary relatedness. Darwin, for example, relied heavily on embryological development as evidence for his claims of common ancestry among disparate adult forms. A growing body of empirical data, however, demonstrates divergent patterns of development of otherwise homologous structures in independent lineages. Moreover, such divergence frequently occurs with little or no concomitant change in adult phenotype, a phenomenon termed "developmental system drift." These findings caution against the use of ontogenetic data as an infallible let alone exclusive criterion for evaluating homology. Instead, they reinforce recent claims that routine application of a so-called ontogenetic criterion of homology may be unjustified, if not downright misleading in specific instances, and thereby obscure, rather than reveal, important trends in comparative and evolutionary biology. Examples will be provided from recent comparative studies of the development of the vertebrate skull. These studies employ sophisticated cell-labeling techniques, which show that the embryonic derivation of individual bones may vary according to lineage and is thus subject to evolutionary change. According to these data,

longstanding homologies for at least some bones of the cranial vault may be incorrect and should be reevaluated.

HAL2-2 12:00 pm

Cranial morphology in the earliest shark-like fishes (Chondrichthyes).

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Abstract: The head skeleton (splanchnocranium, viscerocranium) of modern sharks has been widely used as a model for the generalized condition in jawed vertebrates. But how reliable is this "primitive" vertebrate paradigm? New information gleaned from the fossil record suggests that splanchnocranial and viscerocranial morphology in modern elasmobranchs is highly derived, whereas early/basal chondrichthyans resemble osteichthyans more closely in their basicranial, labyrinth, and visceral arch morphology. Additionally, the "boneless" condition is almost certainly derived, considering (1) the widespread presence of site-specific ossifications in the dermal and chondral skeletons of non-chondrichthyan gnathostomes, and (2) recent phylogenetic resolution of acanthodians as stem chondrichthyans, basal to "euchondrichthyans" (forms possessing tessellated calcified cartilage). Cranial morphology is now known in two Early Devonian euchondrichthyans, *Doliodus* and *Pucapampella*. However, these taxa present profoundly different morphologies, creating a dilemma for phylogenetic analysis. *Doliodus* is essentially a "conventional" Paleozoic chondrichthyan bearing acanthodian-like dermal spines. *Pucapampella* combines extreme autapomorphies with ontogenetically primitive features that may be neotenic, obfuscating its phylogenetic position within the euchondrichthyan total group. Either taxon is thus a candidate for "most primitive euchondrichthyan" status.

HAL2-3 12:30 pm

Cartilage regeneration and diversity in lizards.

Subramaniam N, University of Guelph; McDonald RP, University of Guelph; Jacyniak K, University of Guelph; Vickaryous MK*, University of Guelph mrvickary@uoguelph.ca

Abstract: Cartilage is an avascular skeletal tissue that not only acts as a transient model during bone development, but is also retained as a permanent tissue type contributing to the skull and the surface structure of joints. In lizards, cartilage is also found in the regenerated tail. Regenerated tail cartilage is unusual in several respects. It replaces an original tail skeleton made of bony vertebrae with an unsegmented hollow cone, and not an articulating series of block-like elements. In addition, the cartilage is distinctly cell-rich and extracellular matrix poor. To better understand regeneration-mediated cartilage formation, and the diversity of lizard cartilages, we conducted a spatiotemporal characterization of chondrogenesis using the leopard gecko (*Eublepharis macularius*). Our data reveals that regeneration-mediated cartilage formation is distinct from the embryonic process of chondrogenesis. Prior to tail loss, cartilage in the tail is restricted to articular surfaces of joints, intervertebral discs, and segments of the persistent notochord. Loss of the tail initiates a wound healing process that leads to the formation of a blastema—an aggregation of proliferating cells. The earliest sign of cartilage formation is a cone-like condensation of cells encircling the regenerating spinal cord that begins to secrete type II collagen and glycosaminoglycans. Cartilage cells activate the transforming growth factor beta signaling pathway, and express the principal regulator of chondrogenesis, the transcription factor Sox9. However, compared to embryonic chondrogenesis Sox9 expression appears to be relatively delayed. These findings reveal that regeneration-mediated cartilage formation is a unique process, and demonstrates an unexpected skeletal diversity in lizards. Funding source: Natural Sciences and Engineering Research Council (NSERC) Discovery Grant 400358 (MKV).

HAL2-4 12:45 pm

Integrative biology, evo-devo, and Brian Hall.

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Abstract: Brian Hall's research, his primary literature papers, and his several books present a progression in the development of new ways of doing science. The work, focused on the biology of the vertebrate skeleton, has spanned the hierarchy of biological organization, from molecules and cells to evolution over time. The presentation of the research reflects Hall's detailed knowledge at several levels of that hierarchy, and of a diversity of taxa. In part because of his breadth, and also his energy, Hall has been a major leader in the development of new syntheses that mesh several of the sub-disciplines of biology. His integrative scope has resulted in foundations for "evo-devo", the inclusion of development in the study of extinct vertebrates, and new ways of looking at life history strategies. Selected examples illustrate these advances, and Hall's role in them.

Contributed Session — Hard-Tissue Biology (HRD)

HRD1-1 9:30 am

Development of the basal chondrocranial elements in lizards.

Yaryhin O*, I. I. Schmalhausen institute of zoology NAS of Ukraine; Werneburg I, Senckenberg Center for Human Evolution and Palaeoenvironment (HEP) at Eberhard Karls Universität alex.yarigin@gmail.com

Abstract: The neurocranium of vertebrates is mainly derived from early cartilaginous anlagen, the so-called chondrocranium. In general, two initial bar-shaped and paired chondrifications flank the notochord, the more rostral trabecles and the more caudal parachordals. In most reptiles, there is an additional component, the transverse

acrochordal cartilage, which is placed between trabecles and parachordals. All these elements compose the base of the future chondrocranium. There are several theories concerning the development and interrelationship of these elements; i.e., the development of the basal plate, the formation of the basicranial fenestra, and the role of the acrochordal cartilage in the formation of crista sellaris. In the present study, we reexamined the basicranial development in one of the previously well-described skink species *Chalcides ocellatus* and compare it with that of *Lacerta agilis*. We found that *C. ocellatus* shows very similar conditions of early chondrocranial development when compared to *L. agilis*. The anterior most part of the notochord is not embedded into the basal plate as it was previously reported. It remains free. The medial edges of the parachordals form the lateral walls of the basicranial fenestra. Only the posterior portions of the parachordals fuse and form the basal plate. The space in-between the parachordals is fulfilled with a thin layer of cells, which, however, never chondrifies. The anterior most tips of the parachordals later fuse with the posterior edge of the acrochordal cartilage, which finally delimitates the basicranial fenestra anteriorly. Thus, crista sellaris does not form from the most anterior part of the basal plate, as it was previously thought, but from the acrochordal cartilage. We consider the observed processes a common development at least in lizards and discuss a variety of methodological approaches and differences in data interpretation as reasons for the anatomical differences reported in the literature.

HRD1-2 9:45 am

Body size and parafrontal bones in the Sphaerodactylidae (Reptilia: Squamata: Gekkota).

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Abstract: Well-resolved phylogenetic hypotheses and ontogenetic data are often necessary to investigate the evolution of structural novelty. With recent increased resolution of gecko phylogenies, questions of homology and convergence can now be investigated. The gecko family Sphaerodactylidae comprises several genera of miniaturized geckos, including the smallest known amniote. The genera *Aristelliger* and *Teratoscincus* are exceptions, with taxa reaching snout-to-vent lengths of up to 150 mm. These genera possess enigmatic, supraorbital ossifications, parafrontal bones, which are not found in any other squamates. Originally believed to be a product of evolutionary convergence, these structures have remained uninvestigated since their discovery. Though relationships between other Old World sphaerodactylids remain unresolved, recent molecular and morphological data has supported a close relationship between *Aristelliger* and *Teratoscincus*. We investigated the ontogeny of these bones in both *Aristelliger* and *Teratoscincus* to better understand the relationship between body size and the presence of parafrontal bones in sphaerodactylids. We hypothesized that there is a threshold body size in sphaerodactylids, below which parafrontals do not develop, thus explaining their absence in miniaturized taxa. Cleared and stained, radiographed, and skeletonized adult and juvenile specimens were used to verify the presence of parafrontals, and if present, measure the total surface area they occupied in seven species of *Aristelliger*, six species of *Teratoscincus*, and their respective sister taxa. The relative surface area of parafrontal bones increases with increasing body size. However, body size in relation to the onset of parafrontal development, differs between species of *Aristelliger* and *Teratoscincus*. Our data suggest that the onset of parafrontal development is dependent on the ontogenetic stage, not a threshold size.

HRD1-3 10:00 am

Evolution, development, and function of the elaborate frontal sinuses of porcupines.

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Abstract: Fronto-nasal sinuses are common features in the skulls of many mammals, although their function is unclear. We used micro-CT scanning to analyze the 3D internal anatomy of fronto-nasal sinuses in 12 species across the two independent lineages of Old and New World porcupines (Hystricidae and Erethizontidae). Both lineages have convergently evolved large fronto-nasal sinuses that create a prominent dome shape to the skull, with the sinuses sometimes being comparable in volume to the rest of the cranium. The integuments of these domes are covered in anteriorly projecting quills in erethizontids and highly elongated display quills that form a "crest" in hystricids. The sinuses in most erethizontids are small and maintain a flat shape to the dorsal skull roof. Within this family, two independent evolutions of domed sinuses have occurred in the largest taxa. We found that the hystricid *Trichys* completely lacks a frontonasal sinus, but the more derived *Atherurus* contains a small but well defined sinus. Ontogenetic data demonstrates that the sinus in *Hystrix africae australis* invades the maxilla, parietals, and squamosal bones, creating near full coverage of the dorsolateral cranium with sinuses. Both families demonstrate an evolutionary relationship between fronto-nasal sinus volume and body size, as seen in other mammals. The data herein provide some support for the hypothesis that mammals utilize fronto-nasal sinuses to maintain cranial shape when evolving larger body size, and their existence allows for co-option into novel structural roles. The absence of a sinus in *Trichys* and the close association between sinus size and quill elaboration on the head argue against a necessary physiological role for the fronto-nasal sinuses in porcupines.

HRD1-4 10:15 am

Predicting calvarial growth in normal and craniosynostotic mice using finite element analysis.

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Abstract: At birth, the cranium consists of multiple bones joining at their edges by soft tissues called sutures. Early fusion of sutures is a medical condition, known as craniosynostosis. The mutant (*Fgfr2C342Y/+*) Crouzon mouse is a well-established animal model displaying premature bicoronal suture fusion and an invaluable model to understand the biomechanics of skull growth and craniosynostosis. The aim of this study was to develop a computer model that can predict calvarial growth in both wild type (WT) and mutant (MT) mice. Two ontogenetic series of WT and MT mice were scanned using micro-CT. A 3D finite element model of a WT mouse skull at day 3 postnatal development age (P3) was created and used to predict WT and MT calvarial growth at P7, P10 and P20 where intracranial volume in mouse plateaus. Input parameters to the model were estimated based on a series of parallel experimental studies, and sensitivity studies carried out to determine their effect on the model predictions through comparison of overall calvarial shape and suture ossification to *ex vivo* specimens. By appropriate selection of the input and remodelling parameters the model could predict the radial expansion of the calvarial bones and bone formation at sutures at P7 and P10 in the WT mouse. For example, the difference of calvarial length between the *ex vivo* and FE prediction was 5%. Further, the model predicted the overall shape of the MT skull at P10, which has a slightly taller, wider and shorter profile compared to the equivalent WT skull at P10. The developed models are the first models of mouse calvarial growth. The close match between the predicted shape of models and *ex vivo* data build confidence in the modelling approach. However, further studies are required to refine the models. The aim is to use such models in the long term for human individual-specific modelling of craniosynostosis.

HRD1-5 10:30 am

The developmental genetics of mammalian tooth and jaw morphological integration and evolution.

Boughner JC*, University of Saskatchewan; Raj MT, University of Saskatchewan; Phen A, University of Saskatchewan; Uppal J, University of Saskatchewan; Greer J, University of Saskatchewan; Paradis MR, University of Saskatchewan Julia.Boughner@gmail.com

Abstract: Phenotypic diversity of vertebrate mouths is nothing if not impressive. Yet the developmental genetic mechanisms that allow dental and jaw morphologies to evolve, sometimes dramatically, but still fit and function together properly, remain enigmatic. Using an edentulous p63 mouse mutant with normal mandible morphogenesis despite the early and complete arrest of tooth development, we tested the hypothesis that a tooth-specific gene regulatory network (GRN) exists that has no significant impact on jaw formation. Using microarray and RT-QPCR analyses of p63^{-/-} and wildtype mice aged embryonic days (E) 10-13, in complement with micro-CT scanning and 3D geometric morphometric studies of prenatal mouse heads, we identified for the first time in tooth organs a subset of genes (e.g., *Fermt1*, *Cbln1*, *Krt8*) acting in a putative GRN that regulates the development of the mandibular dentition with virtually no impact on mandible morphogenesis. This GRN thus provides a mechanism via which dental phenotype can vary and evolve without deleteriously affecting the lower face. Conversely, our findings suggest that this GRN is important to tooth and bone morphogenesis of the upper jaw. Thus our work aligns with the current consensus that different sets of genes pattern and drive upper jaw vs. lower jaw skeletal formation; however, for the first time, our work extends this framework to apply to the integration of upper and lower dentitions with their respective jaw skeletons. Further, our results suggest that functional integration in the absence of pleiotropy is the mechanism enforcing coordinated evolutionary change between the jaw and its dentition. This work was funded by an NSERC Discovery Grant to JCB, and supported by a CIHR-THRUST MSc Fellowship to MTR and College of Medicine Summer Research Scholarships to JG, JU and MRP.

HRD1-6 10:45 am

Aberrant amelogenesis and osteogenesis in DSPP mutant mice.

Cusack BJ, University of Pittsburgh; Kang R, University of Pittsburgh; Chong R, University of Pittsburgh; Yang Xu, University of Pittsburgh; Beniash E, University of Pittsburgh; Verdelis K, University of Pittsburgh; Szabo-Rogers HL*, University of Pittsburgh hsrogers@pitt.edu

Abstract: Dentin sialophosphoprotein (DSPP) is one of the major non-collagenous proteins present in dentin, cementum and alveolar bone; it is also transiently expressed by ameloblasts. In humans, many mutations have been found in DSPP, and are associated with two autosomal-dominant genetic diseases - dentinogenesis imperfecta II (DGI-II) and dentin dysplasia. Both disorders result in the development of hypomineralized and mechanically compromised teeth. Since dentin and enamel formation are interdependent, we decided to investigate the process of the onset of enamel mineralization in young *Dspp*^{-/-} animals. We focused our analysis on the constantly erupting mouse incisor to capture all of the stages of odontogenesis in one place. Using high-resolution Micro-CT, we revealed that the onset of enamel matrix deposition occurs closer to the cervical loop and both secretion and maturation of enamel are accelerated in *Dspp*^{-/-} incisors compared to the *Dspp*^{+/+} control. Finally, for the first time we demonstrate expression of *Dspp* mRNA in secretory ameloblasts from embryonic day 16.5 in the mouse. These data led to the hypothesis that *Dspp* protein is required for normal development of the alveolar bone and tooth even earlier during embryogenesis. To test this hypothesis, we have initiated the analysis of the fetal stages of development and have found that the alveolar bone is defective in the *Dspp*^{-/-} animals. We are currently testing if Hedgehog (HH) signaling, fibroblast growth factor (FGF) and bone morphogenetic protein (BMP) signaling pathways are changed in the *Dspp*^{-/-}

animals. We will determine if the loss of Dspp protein has an effect on cell physiology or the extracellular matrix during embryogenesis. In summary, our data show that DSPP is required for craniofacial development.

HRD2-1 11:30 am

Environmental change, resource availability and the evolution of dental eruption patterns in artiodactyls (Mammalia: Artiodactyla).

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Abstract: Environmental change, habitat structure and resource availability have been influential in the evolution of craniodental morphology in mammals. Our work explores variation in dental eruption patterns across Artiodactyla and investigates the ecological and environmental factors driving these patterns. Terrestrial artiodactyls are globally distributed, almost exclusively herbivorous, and play significant roles in their local ecosystems. Additionally, many species are habitat specialists that respond strongly to environmental change. We examined postcanine eruption patterns in 80 genera spanning 10 families of Artiodactyla. We visually examined specimens across ontogenetic stages using earlier and/or more complete eruption of either the fourth premolar or the third molar to classify dental eruption patterns. Our ancestral state reconstruction supports that the third molar erupted last in the ancestor of Artiodactyla with a 93.5% likelihood, and that the fourth premolar erupted last in the ancestor of ruminants with 100% likelihood. Eruption of the third molar last evolved secondarily in Subfamily Caprinae, likely sometime in the Miocene. The ruminants are characterized by an unfused lower jaw and forward placement of the masseter muscle, and the ruminant dental eruption pattern may be associated with diet, jaw morphology and/or the biomechanics of chewing. The derived dental eruption pattern of the caprines is not correlated with lifespan, litter size, or body size, but is significantly associated with the habitation of mountainous ecosystems. Caprines occupy such high-elevation habitats, fairly uniquely among artiodactyls. We hypothesize that evolution of the unique dental eruption pattern in caprines is associated with limited resource availability in high-elevation mountain systems and the necessity to process a wide range of vegetation types. *This work was funded by the Museum of Vertebrate Zoology and the Department of Integrative Biology at UC Berkeley.*

HRD2-2 11:45 am

Convergent dental dynamics between extinct rodent-like mammals and rodents.

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Abstract: Understanding the ontogenetic dynamics of the dentition in extinct and extant mammal species is crucial to better understand the evolutionary mechanisms driving dental diversification patterns. The recently extinct group of South American notoungulates precociously (i.e. 35 Ma) acquired a range of cranio-dental innovations, some of which strikingly resemble the masticatory apparatus of rodents. For instance, they repeatedly acquired enlarged and ever-growing incisors and cheek teeth combined with a reduction of the number of teeth. Questions concerning the exact sequence of ontogenetic and morphological changes that guided the evolution toward these convergent specializations remain, however. This is difficult to assess due to the rapid and extreme simplification of mesial cheek teeth and the lack of data concerning dental generations for the most specialized taxa. The study of undescribed juvenile specimens coupled with X-Ray microtomographic data on dental replacement in diverse groups of notoungulates allowed a more accurate definition of their dental homologies. Interestingly, rodent-like notoungulates (e.g. Mesotheriidae) show dental ontogenetic dynamics convergent with some rodents in having a strong reduction of the dentition related to the gradual enlargement of distal teeth during growth, leading to mesial drift and loss of mesial teeth. Such a dental drift also occurs in some other mammals, including the closest extant relatives of notoungulates, the Perissodactyla, but to a lesser extent. These results on the dental dynamics of notoungulates combined with recent data on enamel microstructure stress the interest of studying and comparing the masticatory apparatus of notoungulates with extant rodents to provide more robust functional and paleoecological inferences. This study benefited from LabEx BCDiv fundings.

HRD2-3 12:00 pm

The effects of dental wear on hard object food breakdown.

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Abstract: Tooth occlusal morphology is important in food breakdown as it typically forms the initial point of contact between forces generated by the masticatory muscles and a food item. Differences in dental topography have previously been associated with differences in mechanical performance, therefore changes in dental form due to wear during an individual's lifetime may affect function. *Cercocebus atys* a specialist hard object feeding primate, erupts molar teeth with high sharp cusps that wear down to form an enamel ridge surrounding a dentine pool. Individuals of all ages have been observed feeding habitually on the stress resistant seed casing of *Sacoglottis gabonensis*, as such it is predicted that differences in dental topography due to tooth wear are functionally neutral. In order to test this, stainless steel M1 dental models representing hypothetical wear stages in *C. atys* were compressed onto 3D printed hard brittle hemispheres (hollow and solid domes, representing a seed case and seed respectively)

using a universal tester, and force required to initiate fracture was recorded. For the hollow dome force at initial fracture was comparable across all dental wear stages, with the exception of a decrease in force in the intermediate wear stages. For the solid dome the results were similar to the hollow but the enamel ridge model had an increase in force required (thus a decreased performance). Results suggest adult *C. atys* teeth with extreme wear are functionally neutral for feeding on hollow hard food items. This is beneficial given their diet but also suggests that dental wear in *C. atys* is not producing a dental 'secondary morphology' as is found in many terrestrial herbivores. Interestingly results also suggest that the dental topography at intermediate wear stages may compensate for reduced overall muscle capabilities of younger *C. atys* by decreasing the force required to initiate failure.

HRD2-4 12:15 pm

A biomechanical explanation for the ampullae of tyrannosaurid teeth based upon fracture mechanics.

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Abstract: The teeth of tyrannosaurid dinosaurs possess ampullae, rounded or circular structures found in the dentin of serration interdentine sulci. The function of these structures has been a mystery. Hypotheses include: devices to 1) anchor serrations or 2) maintain the structural integrity of the tooth during feeding. Considering engineering fracture mechanics, presumably they function to decrease stress concentrations at interdentine sulci that would cause cracking. To test this hypothesis, we conducted a combined histological and FEM analysis of ampullae in tyrannosaur teeth. Longitudinal sections of serrations were described using comparative dental histology. Additionally, a finite element model of a tyrannosaur tooth was made. This incorporated our findings on tissue distribution and their inferred material properties. Meshes with and without ampullae were loaded along the distal carina. To evaluate crack resistance, the inhomogeneous J-integral was computed for a propagating crack. Histological analysis revealed that the ampullae are composed of globular mantle dentin surrounded by sclerotic dentin. FEM results revealed stress concentrations at each interdentine sulcus as hypothesized, predisposing the tooth to cracking. Additionally, fractures within the sections do originate between serrations, propagating through the enamel and terminating within the ampullae. By plotting the J-integral, we find that computed values decrease at the globular mantle dentin-sclerotic dentin junction, facilitating crack arrest. Additionally, pores within the globular mantle dentin act to increase the radius of the crack tip, decreasing stress concentration. Lastly, multiple fractures in the globular mantle dentine cause shielding at neighboring crack tips, causing further toughening. However, these toughening mechanisms have only been evaluated numerically and we propose material property testing will be needed to further evaluate the likelihood of any of these mechanisms.

HRD2-5 12:30 pm

Microanatomical diversity of amniote ribs.

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Abstract: Bone microanatomical diversity in extant and extinct tetrapods has been extensively studied with increasingly sophisticated quantitative methods in order to assess its ecological, biomechanical and phylogenetic significance. The majority of previous works was conducted on the appendicular skeleton, and a strong relationship has been found between limb bone microanatomy and lifestyle (e.g., aquatic, amphibious, terrestrial). This relationship has been used for paleoecological reconstructions. Few comparative studies focused on the microanatomy of the axial skeleton and its ecological signal. Here, we propose the first exploratory study of the microanatomical diversity of amniote ribs. Our comparative sample comprises 155 species of extant amniotes and encompasses the taxonomic, ecological, and body size diversity of this group. We standardized our sampling location to the midshaft of mid-dorsal ribs. Transverse sections were obtained from classical petrographic methods, as well as from X-ray microtomography. Most of the microanatomical and size parameters of the ribs display a phylogenetic signal, an expected result also observed in amniote limb bones and vertebrae. We found a significant relationship between rib cortical thickness, global compactness and lifestyle. As for the vertebrae, the development of the spongiosa in the medullary region seems to be strongly correlated with size. Even though an ecological signal was found in the inner structure of the ribs sampled, additional work is needed to document the intra-individual variability of the rib microanatomy along the rib cage and within a single element.

HRD2-6 12:45 pm

Mechanical loading and lifestyle adaption response in secondary bone tissue: A quantitative assessment of secondary osteon geometry.

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Abstract: Fatigue and micro-crack damage in bones has been shown in studies on a few species to be a major contributor to bone remodeling, stimulating secondary osteon formation along the main loading direction in compact bone. Secondary osteons have also been observed to be associated with muscle attachment sites, further indicating

a response to mechanical loading. Although secondary osteons can be found in numerous taxa, both extinct and extant, very few quantitative comparative analyses have been performed to test the relationship of Haversian tissue to factors such as mechanical loading across different species. This study investigates whether secondary osteon geometry (area and aspect ratio) of long bones and ribs of several taxa within Aves, Dinosauria, Mammalia and Testudines can be quantitatively correlated with mass as well as lifestyle adaptation (e.g., terrestrial versus aquatic adaptation) in a phylogenetic framework. Results indicate that secondary osteon area increases with mass, whereas more semi-aquatic species have less round secondary osteons compared to terrestrial species. Moreover, the variance in area and aspect ratio is correlated with mass and lifestyle adaptation, respectively. The larger and more varied aspect ratios in semi-aquatic to aquatic species indicate secondary osteons form at different angles to the plane of section, whereas secondary osteons of terrestrial species are more constrained to one direction. This may result from reduced loading in aquatic environments, supporting the idea that the mechanical stress on bones is a controlling factor in secondary osteon formation.

HRD3-1 2:30 pm

Walking with giants: is the cortical bone structure and vascularization adapted to load bearing in large terrestrial vertebrates?

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Abstract: The cortical bone of long bones is perforated by vascular canals. This interconnected network is an integral component of the bone microstructure and undergoes continual change throughout life. Bone remodeling will affect the vascular organization, i.e. its size, volume and orientation. The external loads experienced by the long bones will shape the cortical microarchitecture. Sauropods are an ideal group to study this question because of their great body mass and late ontogenetic remodelling. We used propagation phase-contrast synchrotron microtomography to precisely characterize and quantify the vascular cortex organization of the long bones of sauropods in 3D. We compare the results to those obtained for extant and extinct large mammals. The vascular volume, orientation, and connectivity were used to understand the impact of growth and bone remodeling on bone integrity. Sauropods present in their early stages of development, a peculiar laminar vascular organization made of longitudinal “plates”. This organization is kept in periphery at the adult stage where a decrease of the cortical porosity goes along with a narrowing of the longitudinal plate and a consecutive enlargement of the radial canals. The late bone remodeling observed in adult sauropods results in a reduction of the canal size and generates a more tubular longitudinal architecture, similar to large mammals’ long bone. These vascular organizations are discussed in developmental and mechanical perspectives.

HRD3-2 2:45 pm

Patelloid and patellar sulcus: clues to kneecap evolution?

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Abstract: The patella (kneecap) is a large sesamoid bone found within the patellar tendon. It has evolved independently at least three times: in mammals, birds, and lepidosaurs (lizards and kin). The presence of a fibrocartilaginous ‘patelloid’ in lieu of an ossified patella in many marsupials suggests a stepwise evolution; from tendon to cartilaginous ‘patelloid’ to ossified patella. It remains uncertain, however, whether other animals lacking an ossified patella might have a similar ‘patelloid’ soft tissue structure. Some older literature refers to a possible patelloid in the turtle *Terrapene carolina* and in an unspecified crocodilian, but these are isolated anecdotes. We have therefore sought to investigate how common such a structure might be – if widespread, it could infer that the patella is not truly independently evolved but commonly inherited in the form of the patelloid. Our studies also explore the relationship between the patella and intercondylar (patellar) sulcus of the femur. The sulcus is sometimes taken to infer presence of a patella/patelloid in incomplete fossils, providing valuable missing data with implications for the reconstruction of patellar evolution. We have dissected and sampled patellar tendons from several animals without ossified patellae, representing extant outgroups of those with patellae (turtles, e.g. *Caretta caretta*, *Agrionemys horsfieldii*; crocodylians, e.g. *Osteolaemus*, *Melanosuchus*, *Caiman*; lissamphibians, e.g. *Salamandra salamandra*, *Ambystoma tigrinum*). To date we have found no clear evidence of a soft tissue patelloid or cartilaginous modifications to the tendon in these other animals. Furthermore, we observed that several species with an ossified patella have a shallow sulcus, and conversely, some without the patella/patelloid have a relatively pronounced sulcus. Our data show that presence and depth of the patellar sulcus is not necessarily linked to patellar (or patelloid) presence.

HRD3-3 3:00 pm

The micro-structure, composition and mechanical properties of bones of the Olm (*Proteus anguinus*).

Haggag L, The Hebrew University of Jerusalem; Jelic D, Croatian Institute of Biodiversity, Croatia; Shahar R*, The Hebrew University of Jerusalem ron.shahar1@mail.huji.ac.il

Abstract: The olm is an aquatic salamander that lives in dark, under-water caves in the limestone-rich areas of central Europe. The adult olm is fully adapted to total darkness, exhibits neoteny (retains larval features into adulthood) and impressive longevity (over 60 years). Not much is known about the material properties and micro-architecture of the olm skeleton. We present here results of our studies of the jaw bones, vertebrae and long bones of mature olms by micro-CT, light microscopy and electron microscopy, micro-indentation and thermo-gravimetric analysis.

HRD3-4 3:15 pm

Variation in limb bone stiffness between aquatic and terrestrial salamanders.

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Abstract: Salamanders have a generalized tetrapod *Bauplan* that has served as a popular model to study locomotion in context to the water-to-land transition in tetrapod evolution. Recent analyses have demonstrated that a terrestrial salamander, *Ambystoma tigrinum*, exhibited differential limb function that was associated with different biomechanical properties in the humerus and femur. Given that many basal tetrapods may have been largely or even exclusively aquatic, additional studies are needed to determine whether the material properties of bone also differ between the forelimb and hind limb in salamanders with different lifestyles. We explored whether the stiffness of the humerus and femur vary among aquatic versus terrestrial salamanders in the same genus. The axolotl, *Ambystoma mexicanum*, is exclusively aquatic throughout its life. Eastern tiger salamanders, *Ambystoma tigrinum*, are aquatic as juveniles but terrestrial as adults. In this analysis, we compared the stiffness of the femur and humerus among three groups: adult aquatic axolotls, large sub-adult aquatic tiger salamanders and adult terrestrial tiger salamanders. We used three point bending tests to measure the tangent Young's modulus of elasticity, or bone stiffness, among these groups. The limbs of the terrestrial tiger salamanders had greater stiffness than the limb bones of both the aquatic axolotls and aquatic phase tiger salamanders, and the humeri were stiffer than the femurs across the three groups of salamanders. These results supported previous research that the humerus of the terrestrial tiger salamander had greater hardness values and higher safety factor against skeletal failure than the femur in this species. These results demonstrate how the stiffness of bones may correlate with the terrestrial capabilities of salamanders, potentially contributing new insights into the role of the forelimb and hind limb during the water-to-land transition in basal tetrapods.

HRD3-5 3:30 pm

Fiber courses of the Achilles tendon enthesis in the mouse (*Mus musculus*) as test for biomechanical hypotheses.

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Abstract: As a transition zone between the compliant tendon and the stiff bone an enthesis could be expected to be the weakest link in the force transmission chain between muscle and bone. At such an interface peak stresses can emerge from several phenomena: (1) forces due to tensile load and the resulting transversal contraction can sum up at the transition's margins. (2) Loads may concentrate in a part of the enthesis area, leaving another part of the tendon fibres relaxed due to an oblique orientation of the transition relative to the force vector. However, clinical evidence shows that entheses rather rarely cause failure of the muscle-tendon-bone chain. One explanation for their robustness is the "stretching brake model": Fibers, which loop over cartilage chondrons, deform the chondrons, whenever the structure is stretched under tension. In this scenario the chondrons' material properties influence the stiffness of the transition zone – and could create a stiffness gradient by an increase in sphericity towards the bone. We scanned cell-macerated, demineralized and dried specimens of the mouse [C57BL/6J] Achilles enthesis in order to examine the fiber courses, and to test whether they fulfill the geometric requirements of this model. In the unmineralized fibrocartilage parallel fiber courses prevailed, their curvatures were mainly corresponding to the curvature of the complete tendon. Therefore we conclude that this macroscopic curvature of fibers in the unmineralized fibrocartilage is a major parameter for the recruitment of chondrons as stretching brake elements.

HRD3-6 3:45 pm

The remarkable armor of poachers.

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Abstract: Poachers (Agonidae) are small, cold water fishes. They have no swim bladder, armor, and an unusual pit at the posterior margin of the skull. We have micro CT-scanned every genus of poacher with the aim of understanding the selective pressures that have led to the diversity of armor forms. In some species the armor is quite flat and unornamented, very much in line with medieval scale mail. In others the armor is ornate, with sharp spines, ridges and crenellations reminiscent of the baroque ceremonial armor. The armor serves at least two

purposes in these fishes - it is protection from predation and also a source of sound production. There are constraints on the armor in that the fish must be able to swim, and therefore the armor must have some flexibility. Poachers swim primarily through pectoral fin oscillation, so this constraint may not be particularly strong, though there are other reasons it might be important to bend the body. Of particular interest is the amount of mineral in the armor versus the internal skeleton of the fish. In some species more than half the total mineral content is in the armor. The tubenose poacher (*Pallasina barbata*) is particularly interesting because this fish is the only poacher that swims up in the water column. It mixes with schools of tubesnouts (*Aulorhynchus flavidus*) and may be a useful model for how to lighten armor while maintaining effectiveness.

Contributed Session — Locomotion (LOC)

LOC1-1 9:30 am

Comparing rodent species of different sizes for ecomorphological analyses.

Verde Arregoitia L.D.*, *Natural History Museum Bern* luisd@ciencias.unam.mx

Abstract: Multispecies comparative analyses can identify the functional relationships between morphology and ecology. In comparisons across multiple species, two methodological issues are controversial because they can alter a study's results and interpretation: size correction and relative measurements. First, we are usually interested in the interspecific trait differences that remain once differences in overall size have been controlled for. Second, ecologically-relevant characters are often relative measures. For example: in mammals jumping locomotion is associated with increased hind foot length relative to the length of the body. Relative measures (ratios) can lead to data with poor distributional properties and the potential for spurious correlations with ecological data. Combining size correction and relative measures becomes problematic, because the calculation of ratios is not effective for statistical control but is essential for evaluating proportionality. This work explores how the choice of size-related statistical procedures affects ecomorphological analyses. I test the effects of various methods on a set of craniodental, external, and ecological characters for 200 species of rodents from five biogeographic realms, representing all the ecotypes in the order. Relative measurements relate to locomotion mode and feeding strategy better than individual size-corrected traits, but their use requires careful testing of how the variance components behave in a comparative framework. Additionally, comparative analyses across species need to control for the non-independence of species data that arises through patterns of shared common ancestry.

LOC1-2 9:45 am

Coevolution between forelimb shape and loading regime in strepsirrhines.

Fabre A-C*, *MNHN*; Granatosky M C, *Duke University*; Hanna J, *West Virginia School of Osteopathic Medicine*; Schmitt D, *Duke University* fabreac@gmail.com

Abstract: Animals can move in similar environments using different locomotor strategies that can be difficult to define using only strict qualitative categories. Despite the interesting results that have come forth from this approach, analyses remain hampered by a lack of quantitative data linking kinematics or kinetics of locomotion to bone shape. Few studies have considered the effect of limb loading on anatomical form directly. In this study we quantify 1) the shape of the forelimb, 2) the loading regime of the forelimb during arboreal locomotion, and 3) the relationship between the shape of the forelimb and the loading regime. Eight species showing substantial variation in the use and morphology of the forelimb, ranging from quadrupedal terrestrial (ring-tailed lemur) to quadrupedal arboreal (Aye Aye) to vertical leaping (Sifaka) were examined. The morphology of the bones of the forelimb was quantified using geometric morphometric approaches and peak loads on the forelimb were recorded as animals walked on an instrumented horizontal pole at the Duke Lemur Center. These data were then used to quantitatively link locomotor behavior, morphology, body mass and mechanics using covariation analyses in a phylogenetic comparative framework (2B-PLS and phylogenetic 2B-PLS). Our results show strong anatomical differences between slow quadrupedal climbers, vertical leapers and quadrupedal species in the shape of the long bones of the forelimb. Loading regimes were also different between animals with different locomotor strategies. A strong covariation between long bone shape and loading regime was detected even when taking into account the phylogeny. The covariation between shape and mechanical demands was stronger in bones involved in load transfer (humerus and ulna) compared to the radius. This project was supported by an NSF BCS 0749314 grant, the Leakey and Force and Motion Foundation, Fondation Fyssen and the Marie-Skodowska Curie fellowship (EU project 655694 - GETAGRIP)

LOC1-3 10:00 am

Limb specializations and adaptive diversification in Mustelidae.

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Abstract: Mustelidae, a carnivore clade of ~60 species consisting of weasels, otters, badgers, and martens, exhibit a diversity of locomotor habits, including climbing, digging, and swimming. The combined functional diversity and species richness of Mustelidae make this clade an ideal group in which to test whether primary locomotor habit constitutes a selective regime acting upon limb morphology. To quantify limb skeletal morphology, I performed a principal component analysis on 28 variables reflecting bone robustness and muscle moment arms for a sample of 36 mustelid species. The scores for each taxon along PC axes 1 to 3 were then fitted to models of trait diversification.

Using Ornstein-Uhlenbeck models, I tested whether single and multi-optima models of adaptive diversification best describe the variation in limb skeletal morphology, with multi-optima models reflecting selective regimes for locomotor habit and differences in body size. Additionally, single and multi-rate models of Brownian motion were also tested. PC-1, which represents 95% of the variance, is a measure of taxon size. PC-2 and PC-3 respectively represent 2 and 1% of the variance yet distinguish climbing, digging, and swimming specialists. Notably PC-2 represents a trade-off between bone gracility and robustness, whereas PC-3 represents an elongation of the deltoid tuberosity, olecranon process, and greater trochanter. The variance in PC-1 is best fit by a model of selective regime based upon differences in body size, whereas PC-2 and PC-3 are best fit by selective regimes based upon locomotor habit. Though differences in body size appear to have the greatest bearing upon the overall diversification of limb skeletal morphology in mustelids, locomotor habit remains an influential selective regime for the relative mass and proportions of the limb bones, as well as the moment arms of limb muscles.

LOC1-4 10:15 am

Variation of the felid (Mammalia: Felidae) scapula and implications for felid biology.

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Abstract: The forelimb of felids is vital for understanding how these carnivorans move and capture prey. In turn, felid forelimbs are important for understanding the biology of these hypercarnivores. The scapula is pivotal in the anatomy of the forelimb as it is a key area of attachment for both extrinsic and intrinsic muscles. While cats are considered conservative in their bodyplans, differences are present in the morphology of the scapula and the corresponding forelimb myology. Although felids are generally similar, extant taxa fill different ecological niches, including cursoriality, piscivory, semi-arboreality, and scansoriality. Members of all major modern felid clades and predatory types were investigated. Eighty-five scapulae from 12 modern genera and 21 modern species of felids were utilized. Some features of the felid scapula are common to the entire family (e.g., enlarged caudal angle for pronounced large m. teres major and enlarged supraglenoid tubercle for a pronounced and large m. biceps brachii). However, key areas for understanding differences within the family include differences in the morphology of the cranial border, and of the acromion and suprahamate processes. Based on several variables, maximum variation occurs in medium-sized felids. By using geometric morphometrics and investigating the principal component analyses, the region of highest variation is the suprahamate process. Laterally, most felid clades form distinct groups, although the *Prionailurus* clade tend to group with or near the *Lynx* clade. On the medial scapular surface, the cursorial *Acinonyx* is distinct from all other felids. Additionally, some felid clades show a high degree of variation on the medial surface (e.g., *Leopardus* and *Lynx*), with the majority of variation present around the scapular head and neck. The inclusion of fossil felids with the data set should allow for interpretations of their possible behavior, biomechanics, and paleobiology.

LOC1-5 10:30 am

Hand skeleton and wingtip shape in coraciiform and piciform birds.

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Abstract: Differences in avian wingtip shape have well-characterized relationships to flight performance, migratory behavior, and feeding ecology. Kingfishers, woodpeckers, and their kin (Coraciimorphae) display a broad range of wingtip shapes, as well as a range of flight behaviors (including intermittent flight and flexed-wing upstroke) that cannot, as of yet, be clearly identified as adaptive responses to flight performance demands. These taxa also possess an unusual suite of morphologies in the forelimb skeleton at sites of flight feather attachment and articulation. This study examines the relationships between feeding and migration ecology, forelimb musculoskeletal characters, and distal primary feather lengths. Initial exploration of these relationships was conducted using phylogenetic co-inertia analysis on matrices of feeding and migratory behaviors (13 binary characters) and musculoskeletal morphology (79 categorical characters) for 65 coraciimorph taxa. Co-inertia between ecological characters and musculoskeletal characters points to several hot-spots of morphological variation, most notably the joint surfaces and muscle attachments of the carpometacarpus and digits II – III. A more fine-grained co-inertia analysis using skeletal GM semi-landmarks and distal primary feather lengths for 26 coraciimorph taxa recovers links between rounded wingtips and an elongate carpometacarpal-ulnar articular surface, increased area for the origin of flexor digiti minimi, and the presence of a pronounced dentiform process of the carpometacarpus that guides the tendon of extensor digitorum communis. The skeletal variability seen in coraciimorph taxa highlights potential mechanical constraints on flight stroke kinematics in these taxa.

LOC1-6 10:45 am

Is variation in vertebral spine morphology associated with variation in myomere morphology in the killifishes?

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Abstract: In fishes, the axial musculature is characterized by W-shaped muscles termed myomeres. However, little is known about the evolutionary factors that influence axial muscle morphology or how morphology affects locomotor performance. Our goal is to quantify variation in axial morphology in the caudal peduncle and, ultimately, determine how morphology influences locomotion in the killifishes (Cyprinodontiformes). We begin by surveying peduncle

anatomy in three killifish species to test the hypothesis that muscle morphology and vertebral spine morphology co-vary. We predicted that if neural/hemal spines form a shallow angle relative to the vertebral column in a given species, then the myomeres would also inscribe shallow angles and form a compressed W shape; alternately, vertebral spine and myomere angles could demonstrate distinct patterns. Alizarin-red-stained and partially-cleared specimens of *Gambusia affinis*, *Poecilia mexicana*, and *Kryptolebias marmoratus* were dissected to expose myomeres in the peduncle. We quantified myomere and vertebral spine morphology (angles and lengths) to test the hypothesis that these two morphological parameters co-vary across species. We found that myomere morphology does vary significantly across species, and this variation is associated with parallel variation in spine angle: in species where the neural and hemal spines are more "sloped" toward the posterior vertebral centra to form a shallow angle, the anterior and posterior cones also form shallow angles, both relative to the vertebral column and to one another. In addition, when muscle length is normalized to body size, species with "deeper" (dorso-ventrally larger) caudal peduncles are formed by longer myomeres. Because vertebral elements and axial musculature are both derived from somites, these elements may be linked developmentally; however, the functional consequence of variation in peduncle depth and muscle/spine orientation remains unclear.

LOC2-1 11:30 am

The transition to adhesion in geckos: evidence from *Gonatodes* (Gekkota: Sphaerodactylidae).

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Abstract: The adhesive system originated in at least 11 separate gekkotan lineages, but taxa representing transitional phases are poorly known. Comparative studies led us to the "padless" sphaerodactyline genus *Gonatodes* to investigate this transition. We examined the macroscopic and microscopic digital anatomy of *Gonatodes* (about 27 species displaying considerable variety in digit form and locomotor substrate preferences). One species, *Gonatodes humeralis*, bears enlarged proximal subdigital scales that are candidate incipient pads. We investigated digit proportions, shape, scalation and skeletal form throughout the genus, and correlated these with the patterns of micro-ornamentation encountered on the subdigital surfaces. We then measured the ability to generate adhesive force in key taxa, and examined locomotor capabilities on low-friction surfaces. We found that *G. humeralis* generates adhesive force that is only slightly less than that for *Anolis* (when normalized for body mass). It thus has feet that are functionally adhesive, even though it lacks the manifold anatomical modifications typical of pad-bearing geckos. Indeed, its digital anatomy is even more basic than that of *Anolis*. Despite this it can scale vertical Plexiglas® sheets. As in *Anolis*, release of adhesion is achieved through passive digital hyperextension, with the digits rolling off the substratum at the end of pedal plantarflexion (rather than being actively disengaged by muscular action prior to raising the heel, as is typical of geckos with a more derived adhesive system). *G. humeralis* thus exhibits a very basic rendition of the gekkotan adhesive system. Field observations provide evidence of circumstances in which adhesive capabilities are selectively advantageous, and which are unavailable to species of *Gonatodes* lacking adhesive capabilities. The enormous geographic range of *G. humeralis* relative to its congeners suggests that its adhesive capabilities are associated with ecological release.

LOC2-2 11:45 am

The coordinated motion control model of tetrapod limbs with mono- and bi-articular muscles: Model, application, and evolutionary origin.

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Abstract: The presence of bi-articular muscles in tetrapod limbs has created an enigmatic paradox. When the rectus femoris acts alone, the knee is extended but the hip is flexed. When the hamstring acts alone, the knee is flexed but the hip is extended. When both muscles act together, however, they act as a braking against each other for one joint whereas they act coordinately for another joint. To solve this paradox and examine functional roles of and motion control over mono- and bi-articular muscles in human limbs, the coordinated motion control model has been established based on human biomechanics and robotics. The model has demonstrated that three antagonistic pairs of six mono- and bi-articular muscles control coordinated output force and force direction at the wrist or ankle, perform weight-bearing motion, and maintain stable posture. These antagonistic muscles are defined as functionally different effective muscular system (FEMS) of the two-joint link mechanism. Using robotics, the model has also been shown to achieve the contact task without slippage. Recently, some of the results have led to practical applications for automotive engineering and robotics, i.e., Twin Lever Steering (TLS) system and an amphioxus robot, respectively. Since the model was proposed for biomechanics of human limbs, we have investigated morphology, evolutionary origin, and biomechanics of FEMS in vertebrates by examining the pectoral fin musculature of extant sarcopterygians, the African coelacanth *Latimeria chalumane* and two lungfish

species, *Neoceratodus forsteri* and *Protopterus aethiopicus*. Since terrestrial locomotion necessitates solving contact tasks and achieving weight-bearing motions and stable posture on the ground against gravity, we will discuss the model and present our results, particularly by focusing our discussions on the fin-to-limb transition and the subsequent evolution of tetrapods.

LOC2-3 12:00 pm

Rachis morphology cannot accurately predict the mechanical performance of primary feathers in extant (and therefore fossil) birds.

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Abstract: It was previously suggested that the flight ability of feathered fossils could be hypothesized from the diameter of their feather rachises. Central to the idea is the unvalidated assumption that the strength of a primary flight feather (i.e., its material and structural properties) may be consistently calculated from the external diameter of the feather rachis, which is the only dimension that is likely to relate to structural properties available from fossils. Here, using three-point bending tests, the relationship between feather structural properties (maximum bending moment, M_{\max} and Young's modulus, E_{bend}) and external morphological parameters (primary feather rachis length, diameter and second moment of area at the calamus) in 180 primary feathers from 4 species of bird of differing flight style was investigated. Intraspecifically, both E_{bend} and M_{\max} were strongly correlated with morphology, decreasing and increasing, respectively, with all three morphological measures. Without accounting for species, however, external morphology was a poor predictor of rachis structural properties, meaning that precise determination of aerial performance in extinct, feathered species from external rachis dimensions alone is not possible. Even if you could calculate the second moment of area of the rachis, our data suggest that you could still not reliably estimate feather strength.

LOC2-4 12:15 pm

Estimating scapular positions in extant quadrupedal tetrapods by using two different approaches: implications to forelimb posture reconstructions in extinct taxa.

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Abstract: The scapulae have no direct skeletal connection to the rib cage, but are connected to the rib cage via thoracic (e.g., serratus and rhomboideus) muscles. Therefore, the scapular position remains one of the most difficult hurdles in reconstruction of the extinct tetrapod skeletons. In a quadrupedal stance of tetrapods, the presacral portions of the body are lifted upward by pitching torque about the acetabular joint produced by the thoracic muscles, and avoid collapsing on the ground during the locomotion. The thoracic muscles produce roll and yaw torques as well, which disturb stable stance; and compress the rib cage dorsoventrally against the downward body weight, which may cause the bone fracture. Assuming a stance phase supported by left hind- and right forelimbs, 3D musculoskeletal models of *Mus*, *Felis*, and *Chamaeleo* were constructed based on CT-scanned images and dissection to find the 3D scapular positions (1) where the roll and yaw moments of the presacral body produced by the thoracic muscles are minimized, and (2) where the strength against the vertical compression of the rib cage beneath the scapula is maximized. According to the moment analyses model by using SIMM software (Musculographics, Inc.), the distribution of the scapular positions where the muscles minimize yaw and roll torques of the trunk was limited near the median plane and above the cranial-most portion of the rib cage. According to the strength analyses model by using Voxecon software (Quint), the strength of the rib cage against the vertical compression was maximized at above the cranial-most portion of the rib cage. The scapular positions estimated by these two different approaches are consistent with the scapular positions during the stance phase *in vivo* not only in the studied taxa, but also in most of the extant quadrupedal tetrapods. The scapular positions in extinct quadrupedal tetrapods are expected to be reliably reconstructed by using these two different approaches.

LOC2-5 12:30 pm

Computational and experimental analysis of terrestrial locomotion in fire salamanders: insights into the evolution of walking and running in tetrapods.

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Abstract: The water to land transition in stem tetrapods is a key evolutionary event in Earth's history. However, difficulties arise when using static fossil morphology to rigorously determine how adapted early tetrapods were to dynamically moving through a terrestrial environment. Salamanders are the most commonly used postural model to provide a basis for inferring stem tetrapod movement capacity due to their presumed plesiomorphic morphology and to their specialized life cycle that involves an ontogenetic transition from water to land. Here we present a novel approach that combines experimental data, computational models, and forward dynamics simulations to estimate the maximum terrestrial movement capability of a direct-developing salamander, the fire salamander (*Salamandra salamandra*). Hindlimb muscle (e.g., mass, pennation angle and musculotendon paths) and segment data (e.g., mass, geometry) were obtained via dissection and microCT scans to create a detailed hindlimb musculoskeletal model. The maximum torque that each hindlimb joint could sustain at each point in its range of motion was then

estimated from muscle properties and segment geometry. Torque-driven forward dynamic simulations were then generated to validate the simulation framework and estimate walking capacity. First, a simulation was generated that reproduced collected experimental kinematics (collected using biplanar radiography; XROMM) and ground reaction forces to validate the model. Additional simulations were then generated using different theoretical goals (e.g., maximize forward velocity) to estimate movement capabilities of the fire salamander. We show how we are using this information as a basis for constructing torque-driven models of individual stem tetrapods, thereby inferring their locomotor capabilities in a quantitative way for the first time, without relying on the assumption that they moved just like salamanders.

LOC2-6 12:45 pm

A novel joint-based approach for studying skeletal evolution and motion.

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Abstract: Understanding skeletal and locomotor evolution – especially across major transitions – is currently hindered by fundamental obstacles to measuring, comparing, and transferring motion between disparate animals. In particular, representations of anatomy and kinematics are often poorly integrated with one another, and lack an evolutionary perspective. This is especially problematic for reconstructing motions in extinct organisms. Here we establish a methodology for representing both bone morphology and motion, based upon the surfaces of articular joints. The anatomical utility of this joint-based approach is illustrated by comparative analysis of humeri from various archosaurs and mammals. Results enabled the discovery of new evolutionary patterns, through the three-dimensional quantification of joint transformations (e.g., humeral torsion, reorientations of individual articular surfaces). The kinematic utility of this approach was also demonstrated, through integration with *in vivo* kinematics (XROMM) and high-resolution imaging of fossil anatomy, in order to analyze and reconstruct the shoulder motions of extant and extinct archosaur representatives. Compared to current methods, the joint-based approach resulted in greater intra- and interspecific similarity of humeral motion paths, enabling more valid comparisons of alligator and avian locomotion. These kinematic benefits, along with the standardization and repeatability of the joint-based approach, provide a framework for "scientific motion transfer." This in turn provides a testable method for predicting motion in extinct forms, and ultimately a more empirical understanding of locomotor evolution. Additionally, the ability to standardize and compare disparate skeletal systems may also have applications for other disciplines, such as orthopedics, computer animation, and robotics.

LOC3-1 2:30 pm

The gibbon's Achilles tendon revisited.

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Abstract: Among great apes (Hominidae), only humans have a well-developed Achilles tendon. This is generally interpreted as an adaptation for energy storage and recoil during cyclic locomotion. The premised basic condition, a short external tendon in favour of long fibered triceps surae muscles, is found in all extant non-human great apes, and therefore probably precedes the last common ancestor of Hominidae. Providing a large Range of Motion, this morphology is thought to be beneficial for locomotion in a complex arboreal habitat. Lesser apes (Hylobatidae), however, also have well-developed long Achilles tendons. Despite their arboreal lifestyle, these species frequently perform bipedal 'grounded running'. As such, it's tempting to suggest that the gibbon's Achilles tendon represents an adaptation for an economical bouncing gait, too. Several aspects of the functional anatomy of the triceps surae seem to support this view, but the compiled evidence is not entirely convincing. We revisit and integrate all our data on hylobatids (anatomy, kinematics, inverse dynamics, material properties) and conclude that the percentage energy return from the Achilles tendon is limited, and may even come at an extra cost. Inertial reduction or catapult action may be forwarded as alternative adaptive explanations. However, we want to offer a new perspective. Based on the available information, cercopithecids, sister group of the apes, also seem to possess well developed Achilles tendons. It is therefore not improbable that this represents the basic condition also present in the last common 'Cercopithecoidea-Hominoidea' ancestor. The Achilles tendon would thus be retained as a relict ('no harm – no benefit') in the brachiating gibbon, whereas its energy saving potential could have further been exploited in the evolutionary lineage towards human terrestrial bipedalism. If true, the common non-human great ape triceps surae anatomy should represent convergent evolution.

LOC3-2 2:45 pm

Loading distribution over the four fingers of the tapir during locomotion.

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Abstract: The tetradactyl equid ancestor has evolved into a monodactyl modern horse (*Equus*). In order to create realistic models simulating equid ancestor locomotion, a reliable model that would predict how the ground reaction forces would be distributed over the fingers is necessary. We chose the tapir (Perissodactyla: *Tapirus*), which has retained the tetradactyl state in its forelimb, as a model species. We used a pressure mat to measure plantar pressures during walk in four species of tapir, with 3 to 5 representatives of each species. A Matlab program

calculated the total load on each finger for each trial based on total pressure and total area underneath each finger. The load underneath the foot pad was also determined. Speed was taken into account by digitizing the stride length and duration on the corresponding videos. Surface scans for the appropriate species were made for the four metacarpals from museum specimens. Maximal stress was calculated in a FEBio v2.4. Four hypotheses on load distribution were tested. Loads were expected to either be proportional to metacarpal length or inversely proportional to the stress caused by a constant load. A third hypothesis was based on a possible prevention of sinking in the compliant substrate by testing whether the mean and maximal pressure differed between the four toes. Finally, the last hypothesis correlated the distances from the center of the pressure for each finger to the total center of pressure path based on the summed pressures over time to test whether finger configuration determined load distribution. The first three hypotheses on the load distribution over the fingers were rejected. With increasing speed, the load was shifted more towards the foot pad, hereby avoiding overloading the fingers. The last hypothesis was partially confirmed. These results will be discussed with respect to general rules regarding predicted load distributions in animals for which only osteology is available i.e. fossil taxa.

LOC3-3 3:00 pm

Walking with giraffes – joint angles, moments and effective mechanical advantage.

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Abstract: Giraffes (*Giraffa camelopardalis*) are ruminant artiodactyls that possess extreme body proportions, whilst maintaining a large body mass. This morphology (for example long limbs), is expected to have functional consequences on aspects of locomotion, such as joint angles in the limb, joint moments and effective mechanical advantage. We measured ground reaction forces and synchronized kinematics of over 100 walking strides from three adult reticulated giraffes in a zoological park. The giraffes walked at a preferred speed of 0.96 m/s, with a mean stride length of 2 metres, and mean stride frequency of 0.5 Hz. We documented musculoskeletal geometry and measured muscle architecture from the dissection of a different, but similar sized adult male giraffe, weighing 880 kg. The muscles with the largest physiological cross-sectional areas in the forelimb and hindlimb were M. triceps brachii (0.042 m²) and M. vastus lateralis (0.022 m²), respectively. The longest musculotendon unit in the forelimb was the common digital extensor (1.75 m), and in the hindlimb the lateral digital extensor (1.5 m). We combined these data to create a dynamic 3D musculoskeletal simulation of locomotion, using this model to estimate muscular moment arms and effective mechanical advantage of individual joints across the stride, and compare this with other animals of extreme size.

LOC3-4 3:15 pm

Impacts of stream velocity and prey morphology on predator-prey interactions in Hawaiian stream fishes.

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Abstract: There are five amphidromous gobiid fishes endemic to the Hawaiian Islands. The only piscivorous species among the five, *Eleotris sandwicensis*, resides in estuaries where it preys on juveniles of the other four species as they migrate upstream. However, the strength of stream flow through which juveniles migrate can vary substantially, and the impact of such flow variation on aquatic predator-prey interactions has had limited study in any system. Using a combination of flow tank experiments and in-stream video collection, we collected data to address the following questions: (1) Does ambient flow inhibit the detection of predators? (2) For fish that respond to attack stimuli in flow, does body shape impact escape behavior? (3) Do predators take advantage of potential masking of stimuli that they impose on prey? We found that juveniles from the prey species showed a reduced frequency of response to attack stimuli that came from the same direction as ambient flow. However, fish that did generate an escape response when attacked in line with stream flow escaped at higher angles compared to fish attacked perpendicular or opposite to the direction of stream flow. Body shape did not impact escape angle but, contrary to expectations, peak accelerations were higher for fish with more streamlined bodies rather than deeper bodies under certain flow conditions. Preliminary results of in-stream video observation suggest a trend that matches our flow tank trial results, with juvenile gobies that were attacked cranially (as they migrate upstream) exhibiting larger escape angles than fish attacked more caudally. Understanding how flow impacts predator prey interactions is important for many aquatic systems, particularly those that are prone to frequent changes in flow speed. This system exemplifies how environmental selection pressures can interact with biotic selection pressures to impact behavior and survival during predator-prey interactions.

LOC3-5 3:30 pm

Waterfall-climbing performance of gobiid fishes from La Réunion: how conservative are novel functional behaviors?

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Abstract: Several species of gobiid fishes from oceanic islands have evolved the ability to climb tall waterfalls. This behavior is most common among juveniles that are returning to adult stream habitats after completing a marine larval

phase, and is facilitated by the fusion of the pelvic fins (in all gobies) into a ventral sucker. Previous observations identified two distinct modes of climbing. "Powerbursting" is found in many species and is likely the ancestral mode, with climbing powered by brief bouts of axial undulation between periods of attachment to the substrate. In contrast, "inching" is known only in the genus *Sicyopterus*, and is executed through alternating attachment of the pelvic sucker and a novel oral sucker. Comparisons among powerbursting species from Hawai'i and the Caribbean have shown a wide range of performance within this climbing mode; however, inching performance has only been measured in one species, *S. stimpsoni* from Hawai'i. To evaluate whether inching species might show less diversity in performance than powerburst climbers due to the more recent evolution of inching, or the demands of oral-pelvic coordination, we filmed climbing by two additional species from the Indian Ocean island of La Réunion: the inching climber *S. lagocephalus*, and the powerburst climber *Cotylopus acutipinnis*. For inching *S. lagocephalus*, climbing speed and the percentage of time spent moving closely matched previous results from *S. stimpsoni*; however, *C. acutipinnis* showed reduced climbing performance that differed from that measured in other powerburst species. Thus, the novel evolution of inching may restrict gobies to a more conservative range of climbing performance than powerburst mechanics.

LOC3-6 3:45 pm

Tetrapod-like pelvic girdle in a walking cavefish.

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Abstract: Fishes have adapted a number of different behaviors to move out of the water, but none have been described as being able to walk on land with a tetrapod like gait. Here we show that the blind cavefish *Cryptotora thamicola* walks and climbs waterfalls with a salamander-like lateral sequence gait and has evolved a robust pelvic girdle that shares morphological features associated with terrestrial vertebrates. In all other fishes, the pelvic bones are suspended in a muscular sling or loosely attached to the pectoral girdle anteriorly. In contrast, the pelvic girdle of *Cryptotora* is a large, broad puboischiadic plate that articulates with a hypertrophied sacral rib; fusion of these bones in tetrapods creates an acetabulum. The vertebral column in the sacral area has large anterior and posterior zygapophyses, transverse processes, and broad neural spines, all of which are associated with terrestrial organisms. The gait kinematics of *Cryptotora* walking up 45 and 90 degree inclines are described as a lateral sequence gait with the axial body following a standing wave. These findings are significant because they represent the first example of behavioural and morphological adaptation in an extant fish that converges on the tetrapodal walking behaviour and morphology.

LOC4-1 4:30 pm

Functional pelvic anatomy of the red-legged running frog (Anura: Hyperoliidae, *Kassina maculata*).

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Abstract: While all frogs share a generalised body plan typified by a short body, elongate hindlimbs and reduced forelimbs, their pelvic anatomy is variable. Differences in muscle and ligament position, sacrum shape, and joint morphology are thought to allow different movements at the ilio-sacral joint to enable locomotor diversity among species. However, the biomechanical consequences of the various pelvic morphotypes and their associated motions remain unexplored. Specifically, morphotype 2A is associated with lateral rotation of the pelvis during walking. Although careful anatomical inspection and muscle activation data have led to inferences of pelvic function, we lack direct evidence regarding how the pelvic musculature causes lateral rotation. We combine gross dissection, I_2Kl enhanced microCT, and 3D kinematics data to model the propulsive roles of pelvic muscles of *Kassina maculata*, a walking specialist. Kinematic models based on data collected from N=3 frogs suggest the pelvis undergoes a mean peak to peak lateral excursion of 11.5 degrees throughout a stride. Additionally, we found bony and soft tissue anatomy consistent with the 2A pelvic type. The coccygeo-iliacus (CI) and coccygeo-sacralis both originate along the majority of the urostyle, inserting on the anterior two thirds of the iliac shaft and the bow-shaped sacrum respectively. The iliolumbaris (IL) also inserts onto the iliac shaft (lateral surface) anteriorly, having originated from five pre-sacral vertebrae. Both CI and IL thus act on the ilia, likely producing the lateral rotation of the pelvis when activated bilaterally. Deeper analysis of microCT images will reveal muscle architectural details that, when combined with a biomechanical model, will allow estimation of muscle length changes. Further, this model can then be used to investigate how pelvic muscles contribute to walking by transmitting propulsive force to the limb and by modulating the actions of the femur.

LOC4-2 4:45 pm

The importance of good posture: clinging in climbing and non-climbing salamanders.

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Abstract: Scansoriality has evolved multiple times in plethodontid salamanders. In the absence of claws or specialized toe pads common in other scansorial organisms, clinging and climbing on rough and smooth surfaces is likely achieved through gripping via the toes, adhesion of the skin surface, and in some species, by suction. In order to explore whether behavioral or morphological convergence enables access to vertical habitats, clinging performance was examined in multiple climbing and non-climbing species from nine genera within the

Plethodontidae. Maximum cling angle, ranging from 0 through 180 degrees from horizontal, and functional adhesive surface area were quantified with a smooth, edge-illuminated acrylic sheet using frustrated total internal reflection. Significant variation in maximum cling angle was found among species, with some climbing and non-climbing species able to cling to 180 degrees from horizontal (i.e., upside down), and some species, including one arboreal species, unable to maintain clinging performance over 90 degrees. Variation in clinging performance on smooth surfaces could be accounted for by behavioral (i.e., postural) or morphological adaptations to increase functional adhesive surface area in relation to body mass, or by species-specific attachment mechanisms, such as increased skin stickiness or suction. Maintenance of cling performance over a wide range of body masses was observed in both the climbing *Bolitoglossa* and non-climbing species of *Desmognathus*; in many non-climbing species, clinging ability was strongly limited by functional surface area in relation to body mass. Variation in the minimum relative surface area necessary to maintain attachment suggested species-specific attachment mechanisms benefit climbing species and increase cling performance.

LOC4-3 5:00 pm

Scaling of morphology and performance in elastically powered systems.

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Abstract: Individuals of a species may face the same selective pressures across a range of body sizes, so small and large individuals should be capable of similar absolute performance. Scaling of underlying morphology and physiology can determine scaling of locomotor performance. All else being equal, if limb muscle mass scales isometrically with body mass, then kinetic energy of a jump should be similar for individuals of all masses. Studies of frog muscles have found positive allometry of muscle velocity and power output with respect to body mass, leading to predictions of greater jump performance in more massive individuals. However, some frog species use stored elastic energy to power their jumps and often these systems amplify power beyond the capabilities of muscle alone. When using stored elastic energy, the velocity and power of muscle contraction do not influence performance thus performance should be the same for frogs of all sizes if all else scales geometrically. We tested this prediction in Cuban treefrogs using a 3D motion-capture system to quantify takeoff velocity and kinetic energy. We found that these measures of performance scale with positive allometry to body mass and snout-vent length despite the hypothesized unimportance of muscle velocity and power in an elastically powered system. These results suggest positive allometry in underlying muscle properties, particularly muscle mass and maximum force. Preliminary results from in vitro muscle experiments indicate positive allometry in mass and peak force of jumping muscles, suggesting that larger frogs are capable of doing relatively more muscle work and thus can achieve jumps of higher absolute performance compared to smaller frogs. Future experiments will test the prediction that the energy storage capacity of elastic tendons also scales with positive allometry to body mass to accommodate the relatively greater work done by larger individuals.

LOC4-4 5:15 pm

Hind limb muscle function in turtles: is novel skeletal design correlated with novel muscle function?

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Abstract: Most vertebrates move extensively through their environment in order to find food, shelter, and mates. The capacity to perform such movements depends on a variety of factors, including the arrangements of the muscles that enable locomotion. Changes in muscle arrangement can have significant implications for locomotor performance, as a change in origination or insertion of a muscle can impact its line of action, and how well it performs a given movement. In pleurodire turtles, hind limb muscles that primitively originated on the pelvis have shifted to an origin on the shell, due to the derived fusion of the of pelvic girdle to the shell in this lineage. To test if the function of these muscles has also changed in relation to these positional rearrangements, we measured hind limb kinematics, muscle activity (EMGs), moment arms, and physiological cross sectional areas for aquatic generalist species of both pleurodire (*Emydura subglobosa*) and cryptodire (*Trachemys scripta*) turtles. We found not only that some hip muscles with differing attachments between taxa showed different patterns of activity, but also that some muscles with different attachments show similarities in muscle use. In cryptodires, puboischiofemoralis internus (PIFI) protracts the hip during swimming and walking, but in pleurodires it exhibits an additional burst during stance. Because the origin of PIFI has shifted ventrally to the shell in pleurodires, this additional burst could function in limb adduction or stabilization. In contrast, muscles such as the flexor tibialis internus retain similar muscle use profiles in both lineages, despite their changed origination in pleurodires. Our results suggest that, at least in turtles, a change in muscle origination can result in shifts in muscle function, but need not necessarily do so.

LOC4-5 5:30 pm

One foot out the door: limb function during swimming in a recently evolved, terrestrial lineage of turtles.

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Abstract: Although aquatic lifestyles are considered ancestral among extant turtles, multiple lineages have become independently specialized for nearly exclusive use of terrestrial habitats, including the tortoises (Testudinidae) and the

emydid box turtles (genus *Terrapene*). The extent to which swimming performance is retained in such lineages, despite terrestrial specialization, is unknown. Given that tortoises diverged from other turtles over 50 million years ago, but box turtles diverged from aquatic emydids only approximately 5 million years ago, we predicted that the swimming patterns of box turtles would more closely resemble those of their more aquatic relatives than those of tortoises. To test this prediction, we used high-speed video to compare limb kinematics during swimming in a flow tank across Russian tortoises (*Testudo horsfieldii*), eastern box turtles (*Terrapene carolina*), and two generalized aquatic emydid species: sliders (*Trachemys scripta*) and painted turtles (*Chrysemys picta*). Kinematic vector analyses indicated that the forelimb and hind limb showed different patterns of kinematic divergence across the species. For the forelimb, box turtles show kinematic profiles most similar to those of tortoises for four out of five variables; in contrast, for the hind limb, box turtles show kinematic profiles most similar to sliders or painted turtles for four out of five variables. These results suggest that terrestrial specialization may have impacted forelimb function more than hind limb function in box turtles, emphasizing the different roles that these limbs play in meeting locomotor demands.

LOC4-6 5:45 pm

The effects of differential function in the limbs of turtles on patterns of symmetry: an examination of fore- and hindlimb propelled species.

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Abstract: Understanding how selective forces influence patterns of symmetry remains an active area of research in evolutionary biology. One hypothesis, which has received relatively little attention, suggests that the functional importance of morphological characters could influence patterns of symmetry. Specifically, it posits that features with greater functional importance should be more symmetrical. The aim of my research was to examine the patterns of fluctuating asymmetry (FA) present in the limb bones of turtles, focusing on two specific groups: freshwater turtles (family Emydidae) and marine turtles (family Cheloniidae). Emydid turtles primarily employ a hindlimb-dominant swimming style, whereas cheloniid turtles employ a forelimb-dominant swimming style. This dichotomy in propulsive modes provides an excellent test of the biomechanical hypothesis of symmetry. I measured the length of the proximal limb bone of the left and right fore- and hindlimbs (humerus and femur) of several emydid species. I also collected data from the hindlimbs of multiple cheloniid species. These data were used to calculate asymmetry (FA) in each set of bones for each species. I then used these data to test two predictions. First, I tested whether within emydid turtles, the hindlimbs (primary propulsor) would display greater symmetry than the forelimbs (secondary propulsor). Second, I tested whether the hindlimbs of emydid turtles (hindlimb dominant) were more symmetrical than the hindlimbs of cheloniid turtles (forelimb dominant). Preliminary data indicate that within emydid turtles, symmetry is always higher in hindlimbs. Thus, with the biomechanical hypothesis supported in emydid turtles, determining whether the major locomotor change found in cheloniids (reversal of the primary propulsor) is accompanied by decreased levels of hindlimb symmetry (relative to emydids) is an important second test of the ability of natural selection to drive evolutionary changes in symmetry.

LOC5-1 9:30 am Digital musculoskeletal modelling of an Australian sauropod dinosaur.

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Abstract: Since muscles are rarely fossilised, advanced computer modelling techniques are increasingly being used to reconstruct the musculature of extinct species to investigate muscle function and its role in locomotion. The gigantic size of sauropods posed many challenges for their musculoskeletal system in regards to supporting their body mass and moving on land. Three-dimensional models of the forelimbs and hind limbs and associated muscles of a well preserved Australian titanosaur from the Cretaceous, *Diamantinasaurus matildae*, were reconstructed to gather information on mobility, support and bipedal rearing ability. After digitising the fossil material, musculoskeletal modelling software (SIMM) was used to reconstruct the musculature of *D. matildae* using information from extant archosaurs (i.e. crocodiles and birds). Muscle moment arms and associated forces were analysed at multiple joint angles, as well as interactions between muscles to assess muscle activation during locomotion. Modelling musculoskeletal features of extinct taxa, like the appendicular skeleton of *D. matildae*, can provide insight into locomotor function and assist in developing our understanding of sauropod palaeobiology.

LOC5-2 9:45 am

How the largest known flying animal, the pterosaur *Quetzalcoatlus*, walked on land.

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Abstract: The giant pterosaur *Quetzalcoatlus northropi* (QN) lived at the very end of the Cretaceous Period, about 67 million years ago, in Texas. It was named on the basis of a few incomplete post-cranial bones that suggested a wingspan of 11-13 m; a morph about half this size is known from numerous bones and partial skeletons. In the air, like most large aerial animals, it mainly soared, but it could flap to some degree. We studied the functional morphology of the skeleton by manipulation of many dozens of bones and assessing range of movement, reconstructing posture and gait, and calculating the kinematics of walking and flying at each joint. On the ground, like all pterodactyloids, QN walked quadrupedally, but this was mainly because its metacarpals were so long that the

manus could not avoid touching the ground. Pterosaurs were originally bipedal, like their ancestors. Manipulation of QN's forelimb and hindlimb bones confirms that in a quadrupedal pose the humerus had limited rotation (about 25°) and the forearm and metacarpus could be slightly elevated and depressed at the elbow, but the forelimb had no significant retractor power. All joints of the hindlimb are hinges except the hip, a ball-and-socket offset by a neck oriented dorsally, medially, and posteriorly. The hindlimb thus had an erect stance and parasagittal gait, as in other ornithodirans. Pterodactyloids such as QN lifted their limbs unusually, because overstepping was not possible: the lift cycle was LM – LP – RM – RP, where M is manus and P is pes; however, the sequence of emplacement would have been LP – LM – RP – RM. The full step cycle was: LM lift – LP lift – LP place – LM place – RM lift – RP lift – RP place – RM place. Although technically quadrupedal, QN showed its bipedal heritage when it walked on land. Our analysis shows the importance of incorporating phylogenetic heritage into interpretations of functional morphology.

LOC5-3 10:00 am

Forelimb kinematics of rats using XROMM, with implications for small eutherians and their fossil relatives.

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Abstract: The earliest eutherian mammals were small-bodied locomotor generalists with a forelimb morphology that strongly resembles that of extant rats. Understanding forelimb bone kinematics in extant rats can inform and constrain hypotheses concerning typical posture and mobility in early eutherian forelimbs. The locomotion of *Rattus norvegicus* has been extensively studied, but the three-dimensional kinematics of the bones themselves remains under-explored. We used markerless XROMM (Scientific Rotoscoping) to explore three-dimensional long bone movements in *Rattus norvegicus* during walking. Our data show a basic kinematic profile that agrees with previous studies on rats and other small therians: a crouched forelimb posture is maintained throughout the step cycle, and the ulna is confined to flexion/extension in a parasagittal plane. However, our three-dimensional data illuminate long-axis rotation (LAR) movements for both the humerus and the radius. Medial LAR of the humerus throughout stance maintains an adducted elbow with a caudally-facing olecranon process, which in turn maintains a cranially-directed manus orientation (pronation). The radius also shows significant LAR correlated with manus pronation and supination. Moreover, we report that elbow flexion and manus orientation are correlated in *R. norvegicus*: as the elbow angle becomes more acute, manus supination increases. Our data also suggest that manus pronation and orientation in *R. norvegicus* rely on a divided system of labor between the ulna and radius, and radius LAR is necessary for manus pronation. We suggest that forelimb posture and kinematics in *Juramaia*, *Eomaia*, and other basal eutherians were grossly similar to those of rats, and that humerus and radius LAR may have always played a significant role in forelimb and manus posture in small eutherian mammals.

LOC5-4 10:15 am

Ontogenetic changes in effective mechanical advantage in the Eastern cottontail rabbit (*Sylvilagus floridanus*).

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Abstract: Juvenile animals must compete and survive in the same environment as adults, despite a smaller body size and musculoskeletal immaturity. One way to overcome these disadvantages is to increase effective mechanical advantage (EMA). EMA is defined as the quotient of extensor muscle lever arm length (r) and the length of the external load arm of the ground reaction force that those muscles must resist (R). This value is directly proportional to both the mass-specific muscle force needed to maintain posture as well as the magnitude of the output force resulting from a given muscle input force. Therefore, we predicted that to overcome absolutely lower muscle mass and muscle force capacity, juvenile animals should exhibit higher extensor muscle mechanical advantage either through growth-related changes in r or postural adjustments of R . We tested this hypothesis using a dataset on growth and locomotor development in Eastern cottontail rabbits (*Sylvilagus floridanus*) as a model system. We found that relative to body mass, hindlimb muscle lever arm length (r ; averaged across the hip, knee, and ankle joints) scales with negative allometry, whereas hindlimb load arm (R ; average across hindlimb joints) scales with positive allometry. Although the 95% confidence intervals of both variables overlapped the isometric expectation of proportional growth relative to body mass, predicted hindlimb EMA nevertheless decreases throughout ontogeny, likely giving juvenile rabbits an advantage in output force production. Given that ontogenetic declines in mechanical advantage appear to be common across mammals, these allometric patterns may represent a “pathway of least resistance” by which juveniles are able to overcome a deficit in muscle strength and still achieve adult-like levels of locomotor performance. Supported by NSF IOS-1146916 and NEOMED.

LOC5-5 10:30 am

Jumping performance in the Longshanks mouse. Bradley MM, University of Calgary; Hou L*, University of Calgary; Sparrow LM, University of Calgary; Rolian C madi.meta@gmail.com

Abstract: There is an evolutionary trend among jumping mammals to have long hind-limbs relative to body size. This convergence on long and gracile hind-limbs is hypothesized increase jumping performance by increasing the distance and time over which the limb muscles generate force, which, all else being equal, increases push-off velocity

and jumping distance. Here, we used Longshanks, a unique long-limbed mouse produced over 19 generations of selective breeding for increased tibia length relative to body mass, to test this hypothesis. Specifically, we tested the prediction that the Longshanks mice, whose hind limb length is on average ~15% greater, can produce larger push-off velocities and jump higher than weight- and age-matched random-bred controls with normal limb length. Mice were first trained to jump onto a raised platform in an enclosure, using a positive reinforcement training schedule (operant conditioning). Jumps were then recorded using high-speed video (250 fps) to obtain kinematic data (angular velocities and accelerations about hind-limb joints, push-off durations and linear velocities). Contrary to our prediction, maximal jump height in Longshanks mice was lower than in Controls: average maximal jump height of the Longshanks mice was 20cm (n=6), while in Control mice it was 22.5cm (n=6). In a preliminary kinematic analysis (n=4 LS, n=2 C), at lower jump heights (h<17cm), push-off duration is longer in the Longshanks line. They also exhibited higher average angular accelerations and velocities about the hind limb joints, and produced greater push-off velocities. At lower heights, the Longshanks mice can thus generate greater push-off velocities and are in theory able to achieve greater jump heights than controls. Our kinematic data lend support to the hypothesis that elongated hind limbs improve jumping performance, suggesting that the lower maximal jump height in Longshanks is due to other factors such as behavior (e.g., motivation).

LOC6-1 11:30 am

The biological role of carpal sinus hair sensing on the body posture during locomotion of rats (*Rattus norvegicus*, Rodentia).

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Abstract: While the facial (mystacial) sinus hairs are intensively studied regarding their structure, follicle anatomy and biological role in various mammals, less is known about the tactile hairs found on the palmar side of the rat's forelimbs near the wrist. These carpal sinus hairs are assumed to play an important role during locomotion in dark or narrow environments as well as for animals possessing a poor vision. In these cases, sensing substrate properties and diameters before touchdown of the forelimbs would facilitate the adjustment of body posture to maintain the dynamic stability of the trunk. So, a coupled sensorimotor control mechanism between the sinus hairs' sensory system as well as the proprioceptors of the body should exist. To explore the biological role of the carpal sinus hairs and their function during substrate contact, spatiotemporal speed-dependent and kinematic parameters of the limbs and spine were quantified. Measuring was done by x-ray fluoroscopy and normal-light high-speed cameras. A continuous and a discontinuous substrate in the form of a treadmill were used. Data were collected under the presence and absence of the sinus hairs during the preferred animals' speed. Our investigation shows a time window of approx. 30 ms from carpal sinus hairs' contact to the substrate until forelimb touchdown. Within this time, adjusting the body posture due to a changing surface takes place. While the sensory input of the carpal sinus hairs does not affect the failure rate on a perforated substrate, it affects the mystacial sinus hairs' motion (whisking) pattern and has a stabilizing effect on the trajectory of the center of mass, pointing to a connected sensorimotor control loop. Further the carpal sensors act as speedometer by influencing the speed dependence or speed-dependent adaptations of the limb and body kinematics.

LOC6-2 11:45 am

3D dynamics of burrowing in pocket gophers.

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Abstract: Using a self-designed force-sensitive tunnel tube inside an X-Ray, we have been able to measure burrowing in realistic and natural substrates. Here, we present the first full 3-D dynamic analysis of burrowing biomechanics in a vertebrate. The Tunnel-Tube 3.0 is comprised of two tubes arranged in series, with each half mounted on an ATI nano-17 6-axis load cell. The animal enters the first tube and begins digging at the second tube, which is filled with the substrate material. The substrate-filled tubes are uniformly packed and can be exchanged between trials, allowing for a more consistent substrate over time. The dual-tube design allows us to independently measure forces produced by the animal's fore- and hindlimbs. We tested our design in a representative digger: the Botta's pocket gopher (*Thomomys bottae*), which spend most of their lives underground. Pocket gophers burrowed through the Tunnel-Tube in four substrate conditions: Soft radiolucent substrate, hard radiolucent substrate, soft natural soil, and hard natural soil. In soft substrates, pocket gophers exhibited scratch-digging, using the forelimbs to loosen and remove the substrate. In harder substrates, pocket gophers exhibited both chisel-tooth and scratch-digging, typically using the teeth to penetrate the hard substrate and the forelimbs to remove loosened substrate. As substrate hardness increased, the pocket gophers produced more force in order to penetrate the substrate. During scratch digging, gophers produced a minimum mean force of 0.08 ± 0.03 body weights in soft radiolucent substrate and a maximum of 2.0 ± 0.81 BW force during chisel-tooth digging in the hardest substrate. The fact that force profiles spanned nearly two orders of magnitude between treatment conditions indicates that gophers are able to effectively modulate force production during digging in response to soil conditions.

LOC6-3 12:00 pm

The kinematics of grooming: How mammals clean their coat.

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Abstract: Non-locomotory movements in the behavioural context of grooming, social interaction or food acquisition, in sum referred to as idiomotion, play a major role in the daily activities of mammals. We are interested in their significance for the functional morphology of the motion system in order to better understand the evolutionary role of idiomotion in mammals. So far, studies into grooming, reaching, grasping and other idiomotory activities are mainly initiated by neurobiological questions. Our present studies focus on grooming and we studied the kinematics of grooming-associated movements of limbs and trunk in species with different locomotor adaptations (rats, rabbits, dogs and squirrels) using biplanar X-ray fluoroscopy. Our observations so far support the notion that idiomotion rather than locomotion explains the form and mobility of ball-and-socket joints. Idiomotion also involves repetitive and stereotypic motion cycles (e.g., during scratching or face washing), likely controlled by central rhythm-generating networks. However, grooming movements are less symmetrical than locomotory movements. Differences across species appear to be related to the mobility of the trunk. Rats are able to groom almost all of their body regions using mouth, tongue and teeth, and make use of a plenty of assisting and stabilising postures. Rabbits and dogs have in common a rather limited overall flexibility; they predominantly scratch their fur using the hindlimbs. For the future, we hope to further expand the base for interspecific comparison with respect to the biomechanics of idiomotion as the prerequisite for linking variations in structure and behaviour. This research project is funded by the budget of the institute.

LOC6-4 12:15 pm

Out on a limb: effects of substrate compliance on the gait mechanics of common marmosets

(Primates: *Callithrix jacchus*).

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Abstract: The arboreal "fine-branch niche" - the zone at the edge of canopies where supports are narrow and compliant - has been cited as fundamental in adaptive scenarios of primate locomotor evolution. However, though previous studies have evaluated the influence of substrate breadth on primate locomotor performance, the influence of substrate compliance has been mostly unexamined. We investigated how substrate compliance affects the gait kinematics of marmosets (*Callithrix jacchus*; n = 2 males) moving over simulated arboreal substrates. As small-bodied quadrupeds with limited grasping abilities, marmosets are a reasonable analogue for ancestral stem primates, and a good model for testing the performance demands of fine-branch locomotion. We used 3D-calibrated video to quantify marmoset locomotion over a 4m long trackway constructed of differently-sized poles (5, 2.5 and 1.25cm), analyzing a total of 120 strides. Depending on experimental condition, the central 0.6m of the trackway was either immobile or mounted on compliant foam blocks. Marmosets predominantly used asymmetrical gaits (i.e., gallops and half-bounds), using symmetrical gaits in only 8% and 15% of strides on the stable and compliant substrates, respectively. Marmosets responded to substrate compliance by increasing contact durations (i.e., greater forelimb and hindlimb duty factors) and more evenly distributing hindlimb contacts (i.e., relatively longer lead durations). Together, variation in duty factor and hindlimb lead spacing explained nearly 60% of the variation in compliant substrate displacement over a stride, suggesting a direct performance advantage to these kinematic changes. Overall, our results show that compliant substrates can exert a significant influence on primate arboreal locomotor performance. Substrate compliance, and not just substrate breadth, should be considered a critical environmental variable in models of primate locomotor evolution. Supported by NSF BCS-1126790 and NEOMED.

LOC6-5 12:30 pm

Quantifying trabecular bone density and anisotropy in the primate lower ilium with implications for reconstructing locomotor loading.

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Abstract: Understanding the relationship between bony pelvic morphology and locomotor behavior has long been of interest to evolutionary anthropologists seeking to use the fossil record to reconstruct our lineage's transition to bipedalism. While early work focused on morphological variation in the external anatomy of the innominate, recent technological advances have permitted the examination and quantification of the internal trabecular architecture of this skeletal element. As trabecular bone is understood to change during life in response to mechanical loading, it is first crucial to characterize the cancellous architecture of extant primates of known locomotor mode in order to build a comparative sample for later work on fossil primates. One of the issues here is that pelvic loading (particularly in non-human primates) is not well understood. Recent experimental work has suggested potential loading regimes for the primate lower ilium (e.g., axial compression, bending, and torsion), which may serve as hypotheses to be tested via trabecular bone analyses (i.e., each should produce different, predictable patterns of trabeculae). The aims of this study were to quantify bone volume fraction and degree of anisotropy (which together explain greater than 80% of mechanical properties of bone) in the lower ilium of 31 extant primates (six species) using high-resolution X-ray CT scans, and to test hypotheses about relationships between loading regime/locomotor mode and these trabecular

variables. These results will be novel, as primate iliac trabecular architecture has not previously been quantified at such a fine-grained resolution, and will have important implications for future work using cancellous bone in reconstructing locomotor behavior in fossil primates. This project was funded by a Wenner-Gren Foundation Dissertation Fieldwork Grant, a Bigel Endowment Grant, a Zelnick Research Award, and the Center for Human Evolutionary Studies at Rutgers University.

LOC6-6 12:45 pm

The stability-mobility conflict in the primate thumb.

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Abstract: Primates use their thumb both in manipulation and locomotion leading to conflicting mechanical demands. High thumb mobility is required for manipulative skills while stability and strength are important in locomotion. In this study, we want to investigate how the anatomy of the primate thumb is adapted to this stability-mobility conflict. We focus on two highly dexterous catarrhines, the bonobo (*Pan paniscus*) and the olive baboon (*Papio anubis*), with a distinct locomotor, postural and prehensile behavior leading to a different thumb use and load. We obtained fresh-frozen cadaveric hand and forearm specimens via collaboration with the Royal Zoological Society of Antwerp (RZSA), Belgium (5 bonobos; Bonobo Morphology Initiative) and the CNRS, France (3 baboons). A detailed dissection was performed of each specimen with quantification of soft-tissue parameters (e.g. muscle mass and length, fascicle length, ligament dimensions). Each specimen was CT scanned and 3D surface models were created for the trapezium and first metacarpal (MC1) using Mimics software to assess the geometry of the trapeziometacarpal (TMC) joint. Bonobos and olive baboons have a fully opposable thumb, which is reflected in the well-developed thumb musculature. Bonobos have a saddle-shaped TMC joint allowing a wide range of motion, while the prominent volar beak and high joint curvature provide stability. In addition, five ligaments surround the TMC joint, acting as passive stabilizers. We believe that this anatomical configuration offers the required stability for forceful gripping during climbing and suspensory locomotion. Thumb loading is relatively low in baboons, being restricted to occasional climbing and palmigrady. Despite the cylindrical-shaped TMC joint, opposability is maintained by the relatively long length of the thumb. We want to thank Drs. Nauwelaerts, Stevens, Pereboom (RZSA), and Berillon (CNRS) for giving us access to the primate specimens.

LOC7-1 2:30 pm

Does exaggerated morphology constrain locomotor performance in the peacock, *Pavo cristatus* (Aves: Galliformes).

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Abstract: The evolution of exaggerated sexually selected morphology is paradoxical, as although these traits are thought to enhance reproductive success, they are widely presumed to be costly to possess. The costs associated with sexually selected traits are suggested to handicap their possessors, causing a negative impact on survival and acting as an honest signal of quality to potential mates. Exaggerated traits such as the peacock train, represent an additional load that must be carried by the animal and therefore may influence locomotor performance, which in turn could influence predation risk. To examine the effect of the train morphology on the energetics and kinematics of locomotion, we conducted respirometry experiments on peacocks with and without their trains and on peahens, which do not produce a train. In addition, we performed jumping experiments on peacocks with and without trains to assess the traits effect on initial take-off performance. We demonstrate that peacocks with fully-grown trains had a lower absolute and mass specific metabolic cost of locomotion when compared to peacocks that had shed their trains. Furthermore, when controlling for size, peacocks had a lower mass specific metabolic rate during walking than peahens. Peacocks also had improved jump performance with trains than without. Our findings indicate that the sexually selected train does not compromise locomotor performance. We suggest that adaptations to mitigate any costs associated with exaggerated morphology are central in the evolution of sexually selected traits.

LOC7-2 2:45 pm

Fifty ways to measure a moment arm: cadaveric analysis of emu toe joints using XROMM.

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Abstract: The torque generated by a muscle is dependent upon the muscle's force-generating capacity and the leverage with which it acts about a joint – its moment arm. The moment arms of muscles spanning proximal hindlimb joints of terrestrial birds have been studied in detail. However, those of the toes, which interact directly with the substrate, have received less attention. Three prevailing approaches have been used to obtain measurements of moment arms (after Tsaopoulos et al. 2006; Clinical Biomechanics 21: 657–667): tendon excursion (the distance a tendon translates as a function of joint angle), 2D or 3D geometric measurement (the linear distance between the tendon and the axis of joint rotation), and by direct load (computed from static equilibrium equations based on variable known in- and out-forces). We used XROMM to obtain moment arm measurements of the deep digital flexor tendons about the tarsometatarso-phalangeal joints of emu feet based on all three methods. Because each of these

techniques assumes an axis of joint rotation, we calculated joint kinematics using two different approaches: an axis fit geometrically to the joint condyles, and an axis normal to the motion path of a distal marker. Despite variation within and among techniques, there was broad agreement among methodologies for digit III, which experiences little ab- or adduction during flexion and extension. Although similar to digit III in the overall magnitude of its moment arm, the greater complexity of joint motion in digit IV resulted in greater variation in moment arm length with joint angle, greater discordance among methods, and greater sensitivity to the axis of rotation used. We discuss how differences in the variability of moment arms between middle and side toes, yet similarity in their overall magnitudes, may be mediated by the interaction among the subarticular cartilages, condyles, and flexor tendons, despite observable differences in joint condyle diameters.

LOC7-3 3:00 pm

Patella mechanics in avian terrestrial locomotion.

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Abstract: Patellar sesamoid bones are found in the knee extensor tendons of a broad range of tetrapod vertebrates, yet their mechanics have only been studied in few of these taxa. Based on ex vivo study, the patellae of humans are thought to increase the leverage of the knee extensor muscles during walking and running (0-20° flexion from vertical), reducing the forces that they otherwise would need to generate. Due to lack of comparative data, it is currently unclear if the patellae of other taxa may perform a similar function. Inspired by this, we used dual x-ray video analysis and biomechanical modelling to estimate the effects of avian patellae on knee extensor leverage during terrestrial locomotion. We considered avian patellae as an ideal starting place for comparative study, for as obligate bipeds, they place similar locomotor demands on their hindlimbs to humans, but their similarly-positioned patellae (when present) are non-homologous with those of humans and other mammals. Our results indicate that avian patellae enhance the output force of the knee extensors muscles to a varying degree during the stance and swing phases of terrestrial locomotion. Because increasing leverage about a joint also decreases the speed of induced rotation, this indicates that avian patellae also variably retard the rate and extent of knee extension during locomotion. We find the patellae increase leverage considerably (~150%) during early-mid stance, when they may assist the knee extensors in controlling active knee flexion under high ground reaction force loads, and in late stance/early swing, when they may instead prevent excessive knee extension as the biarticular knee extensors/hip flexors flex the hip to protract the limb. When rapid knee extension is required in mid-stance and especially early-mid swing, we find that the leverage-enhancing effect of the patella (and so its retarding of extension rate), is minimised. Based on these findings we speculate that, as in humans, avian patellae perform important functions tuning knee extension mechanics during locomotion.

LOC7-4 3:15 pm

The locomotion of the Hoatzin chick.

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Abstract: The Hoatzin (*Opisthocomus hoatzin*) is a strange South-American bird that lives in bushes along the streams of the Amazonian Basin. This bird has a suite of unique features among which features most prominently their ability to digest leaves using foregut fermentation. This unique feature has important consequences on their anatomy: the crop is so large that the place available for the sternal keel is reduced which impacts its flight ability. However, the wings are strong enough to allow locomotion in both adults and the chicks. The juveniles uniquely have two functional claws on the wing. Young reported in 1888 that "as soon as the young escape from the egg, they creep about with the assistance of these hands, stretching out their wings and digging these claws into hooking on whatever the meet". Furthermore, they escape by jumping into the river under the nest, swim back to the vegetation and then climb back to the nest. This behaviour is well known, often reported, but has never been studied since the late 1880's. Here we present novel data obtained in the field in Venezuela on the locomotion of juvenile Hoatzin and discuss how these results may improve our understanding of the evolution of the birds.

LOC7-5 3:30 pm

Rapid growth backfires: Biomechanical simulations of broiler chicken gait reveal the effects of intrinsic pelvic limb muscle weakness on locomotion.

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Abstract: Estimates show that 2.52 million broiler chickens are affected by lameness or poor walking ability ('leg weakness') every year. Broilers have a unique anatomy and an extremely rapid growth rate, associated with muscle damage and metabolic stress. In addition, our previous work has shown that maximal isometric stresses of the pelvic limb muscles are low (15-80kNm⁻²), 5-35% of typical avian/vertebrate values. In broilers, low muscle forces may indicate a greater reliance on passive structures (ligaments and bony processes) during locomotion and may partly explain the high incidence of joint-related pathologies. In this study, we aim to determine the effects that weak

muscles (i.e., having low isometric stress) may have on passive tissue mechanical demands in broiler chickens. We developed a 3D musculoskeletal model (male broiler chicken, 42 days old) using anatomical data (muscle-tendon unit lengths and architectural measurements) obtained via dissection and CT scans. Experimental kinematic and kinetic data were then used with the model to generate a number of stance phase simulations and estimate muscle activity, force and passive tissue contributions to the movement. Comparisons between simulations using an upper limit for muscle force (predicted from muscle architecture data) and a lower limit (based on our muscle physiology data) were used to determine how muscle weakness influences passive force mechanical demand. Our results indicate that at extremely low muscle stress values the reliance on passive tissues increases by ~20%. Rapid growth has likely led to changes in pelvic limb muscle, which ultimately means the broiler must rely more on passive structures through locomotion resulting in detrimental effects for broiler chicken leg health.

LOC7-6 3:45 pm

Intraspecific scaling of the minimum metabolic cost of transport in leghorn chickens (*Gallus gallus domesticus*): links with limb kinematics, morphometrics and posture.

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Abstract: The minimum metabolic cost of transport (CoT_{\min} ; $\text{J kg}^{-1} \text{m}^{-1}$) scales negatively with increasing body mass ($M_b^{-1/3}$) across species from a wide range of taxa associated with marked differences in body plan. At the intraspecific level, or between closely related species, however, CoT_{\min} does not always scale with M_b . Similarity in physiology, dynamics of movement, skeletal geometry and posture between closely related individuals is thought to be responsible for this phenomenon, despite the fact that energetic, kinematic and morphometric data are rarely collected together. We examined the relationship between these integrated components of locomotion in leghorn chickens (*Gallus gallus domesticus*) selectively bred for large and bantam (miniature) varieties. Interspecific allometry predicts a CoT_{\min} 16% greater in bantams compared with the larger variety. However, despite 38% and 23% differences in M_b and leg length, respectively, the two varieties shared an identical walking CoT_{\min} , independent of speed and equal to the allometric prediction derived from interspecific data for the larger variety. Furthermore, the two varieties moved with dynamic similarity and shared geometrically similar appendicular and axial skeletons. Hip height, however, did not scale geometrically and the smaller variety had more erect limbs, contrary to interspecific scaling trends. The lower than predicted CoT_{\min} in bantams for their M_b was associated with both the more erect posture and a lower cost per stride ($\text{J kg}^{-1} \text{stride}^{-1}$). Therefore, our findings are consistent with the notion that a more erect limb is associated with a lower CoT_{\min} and with the previous assumption that similarity in skeletal shape, inherently linked to walking dynamics, is associated with similarity in CoT_{\min} .

Contributed Session —Lightning Talks (LTG)

LTG-1 2:30 pm

Exploring integument mass properties in extant archosaurs and implications for digital volumetric modelling of centre of mass.

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Abstract: Feathers account for up to 16% of a bird's total body mass, and play an essential role in flight for many avians. Despite this, integument data are yet to be rigorously incorporated into models exploring mass properties. Here, we report the first investigation and application of integument mass properties in sauropsids. In 29 specimens, sections of integument were excised encompassing key integument types (flight feathers, non-flight feathers and scaly skin), and major body segments. For each integument section, area, thickness and mass were measured, and density calculated. The density of all integument types correlated significantly with body mass, but our data also exhibit considerable scatter. When examined by body region, non-flight feather density showed non-significant differences. However, both scaly skin and flight feather density varied considerably. Some significant differences were found between feather types, likely a reflection of their different mechanical functions. Scaly skin density did not vary between birds, crocodilians and lizards. Flight feather density differed between major avian lineages, with hawks and moorhens at the extremes, potentially a result of distinct functional requirements (i.e. soaring vs. diving habits). Non-flight feather densities were similar across avian clades, with the exception of ostriches, the only flightless birds included here. Ostriches were also statistically distinct when density was assessed by locomotor type. Flight feather density showed differences between soaring birds and those favouring other flight modes. Application of our results to volumetric models of extant and extinct taxa enabled an examination of the effects of integument properties on whole-body mass properties. The consequences of this, and other common simplifications made around the application of densities to models are discussed, as well as their implications for the broader conclusions drawn from

models, such as flight capabilities.

LTG-2 2:35 pm

A survey of tooth character data amongst iguanian lizards reveals patterns related to size and taxonomy.

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Abstract: Tooth number, size, and shape vary amongst fossil lizards and therefore have the potential to be used as taxonomically informative characters in the study of both living and fossil species. But for many taxa, data concerning the teeth remains limited, with basic data such as tooth number unreported for many, and published data is often based on a small sample of adult specimens. This knowledge gap brings into question the value of tooth data for interpreting fossils, particularly when fossils may not represent adult animals. The aim of this research is to assess whether data collected from teeth can be useful for identifying reptile fossils. The family Agamidae is one of many squamate clades for which we have not yet developed sets of dental and other osteological characters that would allow species-level identification. Using a sample of 596 extant iguanian skull specimens, including 322 agamids, we compiled a dataset of tooth characteristics including tooth number, size of the largest tooth, tooth row length, and basal skull length. Snout-vent length, sex, and age data were also available for some specimens. We investigated whether the data could be used for fossil identification. Clear differences exist between families of iguanian lizards. Discrimination between genera and species tends to be less obvious, but meaningful variation is still apparent across the sample. Some genera (e.g. *Pogona*) showed little difference amongst species, however others (e.g. *Ctenophorus*), showed some clear patterns potentially useful for fossil identification. A pilot study based on material from two Late Pleistocene locations in Southern Australia, finds that, when used in combination with other data such as other features of the maxilla, tooth number can meaningfully contribute to a confident identification for some Pleistocene fossil species.

LTG-3 2:40 pm

Homologies in forelimb structure between moles and Early Paleogene insectivore mammals.

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Abstract: Fossil records of Didymoconida, the insectivore like mammals from Early Paleogene, are well known from the literature (Lopatin, 2006). Some scientists think they were good burrowers and that they lived in holes like moles. In our research we compared the forelimb structure of moles with that of Didymoconida and found some homologies in humerus morphology. In didymoconids as in moles humerus is widen, lateral and medial epicondyles are well developed. On the cranial side of the humerus in both forms there is a triangular fossa to which pectoral muscles attach. This space was supposed to be unique among moles for it corresponds to their empowered burrowing activity and is related with the transformation of ligamentum m. biceps brachii. In other mammals ligamentum m. biceps brachii lies in the intertubercular transverse, but in moles it changes direction. In semifossorial moles ligamentum m. biceps brachii runs along special ridge and in fossorial moles it is hidden inside the crest of lesser tubercle because the typical place for this ligament is filled by the increased pectoral muscles. In the humerus of Didymoconidae the similar patterns occur (in this group of mammals we can also find semifossorial and fossorial forms). Here we see a unique case of homology in forelimb structure between recent moles and extinct early Paleogene insectivore mammals. Special aspects of humerus structure can't be considered as phylogenetic relationship between these two groups of mammals but perhaps they are connected with the similar type of locomotion.

LTG-4 2:45 pm

Hunting in the Late Triassic: insights on the ambush strategy of the metoposaurs (Temnospondyli: Stereospondyli).

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Abstract: The fluvial ecosystems of the Late Triassic were mainly dominated by different groups of early amphibians as capitosaur and metoposaurs and archosaurs such as phytosaurs. The ecological niche of phytosaurs, with typical tubular-longirostral snout, clearly contrasts with the broad and flattened skulls found in capitosaur and metoposaurs (e.g. *Metoposaurus*, *Buettneria*, *Apachesaurus*). The paleoecology of these early amphibians is still debated, with capitosaur usually considered as active top predators with an amphibious mode of life. The paleoecology of metoposaurs is less understood. Some of its members presented a tendency to gigantism and characterized by huge thickness of skull bones. Metoposaurs were aquatic and potentially burrowing animals, with adaptations to burying during dry seasons. However, no study focused in the feeding ecology and biomechanical capabilities of these animals. Herein, we analyzed two metoposaur taxa—*Metoposaurus krasiejowsis* and *Apachesaurus gregorii*, from Europe and North America respectively—using Finite Element Analysis (FEA). Two adult skulls were CT-scanned and 3D models were analyzed under different biomechanical scenarios including bilateral, unilateral and lateral biting, as well as skull raising system, under different gapes. Stresses are specially found in posterior part of the skull, in agreement with higher thickness of the bones, providing support to stress constraints. Considering the palate, the results reflects the importance of the cultriform process, well developed in metoposaurs, in the functional stability of the skull. Our results confirm that these animals were ambusher predators, resting on the floor and waiting for preys

as previously suggested. Of particular interest, our results reveal that these animals were specialized feeders, using only a rapid bilateral biting, clearly avoiding other biomechanical behaviors such as rapid lateral strike of the head or unilateral biting.

LTG-5 2:50 pm

Genome assembly and annotation of *Mastomys coucha*, a murid with an extreme mammary phenotype.

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Abstract: Mammary glands are the latest in a series of derived ectodermal involutions that include teeth, hair and sweat glands. They are located on the surface of the body in a tightly regulated and repetitive manner. There is a large variation in mammary gland numbers between mammals in general and in rodents in particular with numbers ranging from two to twelve pairs. The Southern multimammate mouse, *Mastomys coucha*, has evolved a total of twelve pairs of mammary glands since the 8MYA divergence from *Mus* and can be used to contrast with the more typical five and six pairs present in *Mus* and *Rattus* respectively. To better understand the molecular determinants that lead to mammary gland number diversity, we sequenced and assembled a draft genome of *M. coucha*. Our genome is at an estimated depth of 75x with an N50 of over 100kb. We identified 67% of conserved eukaryotic genes and 83% of mouse genes in our assembly. Importantly, we identified homologs of 81% of mouse genes expressed in the E12.5 mammary bud. Further comparative genomic analyses and functional genomics will examine *M. coucha* for differential gene expression at key mammary gland developmental time points and diverged gene regulatory regions around these genes. Combined, our analyses show that the draft genome of *M. coucha* is a valuable resource for questions of rodent phenotypic diversity.

LTG-6 2:55 pm

Body shape vs. osteology in the fish superfamily Cottoidea.

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Abstract: Sculpins are a speciose and morphologically diverse group of fishes found in diverse habitats across the northern hemisphere. The morphological diversity of sculpins, especially of the North American species of the genus *Cottus*, is broad and has led to confusion. Within this widespread genus, there can be a confounding overlap in many commonly used morphological characters (i.e., fin rays, mandibular pores, etc.), and substantial morphological phenotypic plasticity within a given species. We are using X-ray micro-tomography (μ CT) to determine the extent to which changes in the morphology of specific bones correlate with changes in aspects of body shape across the diversity of sculpin species. We are finding differences in osteology that ultimately result in a superficially indistinguishable phenotype. This could lay the framework for a better understanding of not only the evolution and radiation of sculpins, but perhaps more practically, more concrete and precise delimitation of some of the sculpin species, particularly in the genus *Cottus*. The use of μ CT in this study allows us to reconstruct and quantitatively compare minute structures in three dimensions across large numbers of individuals with high precision. As we catalog morphological diversity and generate hypotheses of the evolutionary history of sculpins, we are making the μ CT data available as an open resource freely available via the Open Science Framework website (<https://osf.io/>) so any researcher can download and analyze scans as they are completed.

LTG-7 3:00 pm

Physical properties of the sub-dermal fibrous layers in cetacean tail flukes.

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Abstract: During swimming, cetaceans generate hydrodynamic thrust with dorso-ventral oscillations of flexible tail flukes. These flukes do not contain rigid skeletal structures. Instead, they are mainly comprised of densely packed collagenous fibers that are arranged into two distinct layers. Flukes from common dolphins (*Delphinus delphis*), bottlenose dolphins (*Tursiops truncatus*), harbour porpoises (*Phocoena phocoena*), and pygmy sperm whales (*Kogia breviceps*) were dissected out to compare the morphology of the two fibrous layers. In all species, the fibers of the ligamentous layer (outer layer) were angled with respect to the spanwise axis of the fluke. The core layer (inner layer) of all species was found to contain fibers angled with respect to the chordwise axis, while the core layer of the pygmy sperm whales was found to contain additional fibers embedded throughout the layer that were angled along the spanwise axis. Compression tests were performed on the core layer fibers of harbour porpoises and pygmy sperm whales at multiple locations along the span of each fluke. Greater compressibility was found along the chordwise axis than along the spanwise axis at all locations for both species. The two-dimensional orientation of the core layer fibers was determined using a stereomicroscope under polarized light. Fibers in the core layer in the parasagittal plane displayed a crisscrossing arrangement with fibers oriented at an average of either 66° or 115° in relation to the chord line. In all species, the arrangement and orientation of the fibers within the fibrous layers impart anisotropic properties to the flukes and help them to maintain their shape and flexibility during swimming.

LTG-8 3:05 pm

Seasonal skin anatomy changes in three sympatric anuran species from the Midwestern United States.

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Abstract: Vertebrates have evolved multiple strategies to cope with high seasonality and avoid unfavorable conditions (e.g., hibernation and migration). In some anuran species, skin anatomy has been observed to differ seasonally; for example thicker during dry or winter seasons, thinner in the wet or summer seasons. This suggests that anurans modify epidermal anatomy to acclimate to high seasonality. However, studies regarding this variation have only compared skin thickness between generalized seasons, so the timing and drivers of this anatomical change are unclear. I used museum collections to sample three sympatric anuran species native to the Midwestern United States, the American bullfrog, the Northern leopard frog, and the spring peeper, across multiple months to 1) confirm seasonal-related differences in skin anatomy and 2) elucidate the timing of these anatomical changes on a finer scale. Skin samples were taken from the dorsal, ventral, and thigh regions and prepared using standard histological techniques. Epidermis thickness was averaged from 10 measurements for each region. Snout-vent length (SVL) was used to account for body size. Epidermis thickness, standardized by SVL, was then plotted against the month the specimen was collected. The analyses found that spring peepers follow previously predicted patterns by having thinner skin in the summer months compared to the spring and fall. However, bullfrogs and leopard frogs increase skin thickness near the end of summer, reaching greatest skin thickness in September or October before then thinning the skin again. Together, these results suggest that seasonal changes in anuran skin anatomy are more complex than previously recognised and may be related to differential overwintering behavior or shared evolutionary history among these species.

Symposium — Interdisciplinary and evolutionary approaches to vertebrate biological materials (MAT)

Organizers: Mason Dean, Alfred Crosby, Duncan Irschick, Ling Li

MAT1-1 9:30 am

From physical to digital and back: How 3D modeling and additive manufacturing reveal nature's design rules.

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Abstract: The study of morphology is rapidly advancing, largely due to major technological improvements over the past 10 years. Enhancements in laboratory and synchrotron-based microCT techniques (including those in computational power and data storage), for example, have pushed digital, 3D, and high-resolution investigations of anatomy forward at remarkable speeds. Less explored, however, are 3D-parametric modeling and 3D-printing techniques in morphological studies, although these hold particular promise as tools for helping us understand the functional performance of biological systems. Whereas first generation 3D printers were exorbitantly expensive and relatively inaccessible, modern additive manufacturing options are far more available to researchers as desktop units and DIY kits. Here, we present various studies of vertebrate morphology and biomechanics that harness modern geometric modeling and 3D-printing techniques, drawing in particular on our labs' works investigating structure-function relationships in the scales, armors, teeth, and skeletons of fishes, while also including examples of paleontological and medical applications. The range of available printing techniques—from powder-bed to UV-curable options—offers the ability for detailed, non-destructive morphological analysis via the scaling-up and printing of microCT-scanned specimens. Combining 3D printing with direct mechanical testing allows the querying of performance effects of existing anatomies, as well as exploring hypothetical morphologies and evolutionary pathways, via modifiable parametric modeling, printing and characterization, followed by verification through computational/analytical models. Furthermore, high-resolution, multi-material printers, with the ability to precisely deposit both rigid and elastomeric phases in a single part, permit rendering of local gradients in both material and shape properties, and therefore analyses of more complex biological morphologies (e.g. structural interfaces and material modulus gradients).

MAT1-2 10:00 am

Additive manufacturing of composites inspired by vertebrates.

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Abstract: Composite materials made by vertebrates exhibit heterogeneous architectures that are tuned to fulfill the functional demands imposed by the surrounding environment. Examples range from the bilayer dentin-enamel structure of teeth to the complex, multiscale architecture of bone. Because they are often utilized to combine opposing properties such as strength and low-density or stiffness and wear resistance, the heterogeneous architecture of natural materials can potentially address several of the technical limitations of artificial homogeneous composites. However, current man-made manufacturing technologies do not allow for the level of composition and fiber orientation control found in natural heterogeneous systems. In this talk, I will show that additive manufacturing (AM) routes might offer a new exciting pathway for the fabrication of biologically-inspired composite materials with unprecedented heterogeneous architectures.

MAT1-3 10:30 am

Bioinspired design and mechanical characterizations: a case for soft/flexible systems and living tissues.

Li L, Harvard University; Crosby A.J.*, University of Massachusetts Amherst crosby@mail.pse.umass.edu

Abstract: Many natural materials conform to complex topology while maintaining extreme mechanical robustness, a rare combination for synthetic materials. Key to such properties in biological systems is structural hierarchy, with distinct interactions between flexible, yet stiff, components. We discuss two examples that demonstrate the importance of multi-level mechanics in bioinspired materials design, as well as new approaches to quantifying mechanics in living systems. The first example is the development of gecko-inspired adhesives. Revelations with regard to synthetic design, as well as how natural climbing systems work, were found through a simple scaling theory, which highlights the importance of sub-surface mechanics in determining interfacial properties. Another example is based on flexible biological armor from the dorsal girdle scales within chitons. This composite system consists of three main components: aragonite-based scales, a soft tissue, and an assembly of mineralized microrods. A full 3D parametric model describes the geometry of scales, from which a new bio-inspired armor is developed to achieve simultaneous protection and locomotion flexibility. Although morphological data often lead bioinspired materials design, it is equally important to understand mechanical properties within biological systems. Current methods for measuring such properties in vivo are limited. We discuss approaches to quantify properties for soft tissues across a wide range of length scales. One method, called cavitation rheology, measures the critical pressure for delivering a volume of fluid within a tissue. The second method introduces nanoribbons that can be fabricated into grids or helices and integrated into soft tissues to measure strains. Overall, this presentation aims to emphasize the importance of sub-surface mechanics in bio-inspired materials systems, and new testing strategies for gaining better fundamental insight into these mechanics in living systems.

MAT2-1 11:30 am

Material perspectives on the evolution of bone across fishes and tetrapods.

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Abstract: Bones are an iconic feature of vertebrates and form a load-bearing skeleton that supports, protects, and allows movement of the body. The osteocytes, bone cells entombed within the bone matrix, are thought to orchestrate bone building and repair as well as the ability to respond to changing loads, yet these hypotheses have primarily resulted from observations made in amniotes. Studies of a wider array of vertebrates have revealed new dimensions in bone biology. Fish bones are particularly enigmatic because while sharing many similarities with mammalian bones, they also have some remarkably different features. In particular, most extant fishes have skeletons composed entirely of anosteocytic bone (i.e. complete lack of osteocytes). While the existence of anosteocytic fish bones has been known for over 100 years, studies on the functional consequences of anosteocytic bone have only recently gained momentum through the integration of cutting-edge techniques in engineering and biomedical imaging to biomaterials. These studies have demonstrated that fish bones exhibit various unique traits, including being less stiff but considerably tougher than mammalian bones. Yet another example is the osteocytic bone of amphibians, whose mechanical properties can vary with the locomotor capabilities of the animal. Evaluations of salamanders indicated that loading mechanics during terrestrial locomotion differ between the forelimbs and hind limbs, likely resulting from the different functions of these structures. These examples contribute novel perspectives to our understanding of the diverse form-function relationships of bones across non-amniote vertebrates. Given that many fishes and salamanders serve as modern analogs of early stem tetrapods, these data could catapult new advances in modeling how changes in the material properties and mechanical performance of bones across the fish-tetrapod transition may have contributed to functional innovations, such as the invasion of land.

MAT2-2 12:00 pm

Contractile and connective tissue interactions in skeletal muscles.

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Abstract: Many diverse systems overcome the power limitations of skeletal muscle by operating in series with biological springs like tendons. The power output of muscle-tendon units depends on 1) the capacity of muscles to generate mechanical work, 2) the ability of muscle to transfer mechanical work to tendons, and 3) the rate energy is released to the environment. Here we examine how the changes in the mechanical properties of intramuscular connective tissue structures (ECM) affect the generation of muscle work and how changes in the mechanical properties of tendons affect the storage of elastic energy. To produce work, muscle fibers actively shorten and, as muscle is isovolumetric, expand radially. This radial expansion is likely to be limited by the extracellular connective tissue scaffolding (ECM) in which the fibers are embedded. We predict that changes in the mechanical properties of the ECM will compromise muscle work by restricting radial expansion and thereby constraining a muscle's capacity to shorten. We use natural perturbation to the ECM (aging), enzymatic disruption of the ECM (collagenase), and physical constraints applied to muscles to show that limiting the radial expansion of a muscle reduces mechanical work output. We also predict that the amount of energy transferred from muscle to tendon requires a well tuned relationship between the force profile of a muscle and the stiffness of a tendon. We show that differences in tendon properties explain variation in muscle-tendon unit power output across three anuran species. Our work suggests that

the muscle-tendon unit can be accurately characterized as a composite material where the tuned mechanical relationship between contractile and connective tissue structures define the upper limits of performance. Supported by NSF #1436476 and NIH #AR055295.

MAT2-3 12:30 pm

Evolution of crystal form and mineralization control in vertebrates.

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Abstract: During the evolution of vertebrates, an intricate relationship between the organic building blocks of life (proteins, carbohydrates) and silicates, carbonate, and phosphate minerals has evolved, which generated fantastic, complex hierarchical structures with unprecedented material properties. Optimized mechanical strengths, stiffness, toughness, and chemical stability with minimal material density, achieved with controlled hierarchy over a range of length scales, are hallmarks of biological materials. In the study of biomineralization processes, shedding light on the formation of these complex, composite structures is similar to discovering the Holy Grail, and also opens new perspectives for the synthesis of high-performance materials, and treating skeletal diseases. In this talk we will present an overview of proposals for mineralization control in vertebrate skeletons. Phosphate biomineral (carbonated apatite) formation remains elusive, therefore different hypotheses for calcium phosphate biomineralization continue to be tested. We will not only describe and differentiate these proposed pathways, but will propose how a marriage of both theories fits best our current knowledge on how biological organisms may produce these mineralized structures.

MAT3-1 2:30 pm

Co-evolution of teeth and food: Probing the interplay between tooth materials, tooth structures and foods.

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Abstract: Teeth are agents of fracture: their job is to access and reduce food to an ingestible size and increase the surface area of food to promote more efficient digestion. This means that teeth are subjected to a great deal of potential damage, via contact with foods, with themselves, and other environmental pollutants. Enamel serves as the front line of defence against this damage, and is a highly mineralised biological composite, composed of relatively few ingredients: hydroxyapatite plates (96%), organic protein (1%) and water (3%). Through a structural hierarchy of organisation, enamel manages to be optimised for seemingly competing selective pressures. Its high mineral content endows the material with high hardness and stiffness whilst the remnant proteins and hierarchical structural arrangement provide the material with toughness protecting against fracture. Therefore due to its composite nature, enamel can display quite different mechanical behaviour, dependent on the scale of measurement. In addition to changes in material structure, the arrangement of this material into different tooth morphologies also serves to control the damages dealt by everyday use. General patterns of tooth specializations associated with different diets have been well documented across taxa, mammalian and otherwise, and the functional significance of different tooth shapes remains a topic of interest. Here we present recent methodological advances and results that are allowing researchers a more in depth understanding of the behaviour of enamel and teeth, not only as standalone entities but also, through defining the interaction between tooth and food, helping to understand how the pressures of diet may be shaping dental optimisations at many scales.

MAT3-2 3:00 pm

Structure and mechanics of natural scales: inspiration for novel flexible protective systems.

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Abstract: Many animals need tough protection against predators, collisions and other mechanical threats. Their skin must be hard to resist puncture and lacerations, yet sufficiently compliant and light for unimpeded movements. These conflicting requirements can be resolved by the segmentation of hard materials into scales of finite size, a common strategy in nature. Individual scales combine hardness and toughness, and are also several orders of magnitude stiffer than the underlying dermis and other soft tissues (muscles and other internal organs). This extreme contrast of stiffness leads to a rich set of deformation and failure modes: Ring cracks initiated by contact stresses or radial cracks initiated by flexural stresses. Interestingly, we found that when flexural failure prevails, segmented hard scales are more resistant to puncture than a continuous protective layer of the same material (in addition to being also more flexible). Our experiments on natural and synthetic scales also recently highlighted a third failure mode where the tablet suddenly tilts under the action of the indenter, leading to the rapid sliding of the indenter onto its surface. From these results we built a comprehensive failure map that captures the effects of material properties and scale size on the failure mode of individual scales. In addition, we used mechanistic models and 3D printed synthetic scaled skins to show how the interaction between neighboring scales also controls puncture and flexural performance. These interactions are governed by the size of the scales, their overlap, their attachment, friction and the properties of the backing membrane. Enriching the geometry of the scales can also generate interlocking mechanisms between adjacent scales, resulting in improved stability. We now use these results to guide the design and optimization of

synthetic bio-inspired flexible protective systems for a variety of applications, from industrial gloves to touch screens.

MAT3-3 3:30 pm

Vertebrate skin in interaction with the environment: evolutionary solutions.

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Abstract: Vertebrates have conquered a wide range of climate zones and habitats. This evolutionary process required concerted adaptations of the whole body, including the musculoskeletal system, metabolism, diet, sensory organs, and behaviour. The skin, which constitutes the interface between the organism and the surrounding medium, plays a key role in the organisms adaptation to their environment. It protects the animals against chemical and mechanical influences, contributes to thermal control and locomotion, and determines the optical appearance fostering camouflage and signaling. The range of the available skin material is, however, genetically determined and therefore limited within the vertebrate clades. The talk sheds light on specific skin adaptations in reptiles, teleost fishes, and mammals to ecological niches and extreme habitats. The focus of this talk is more specifically on epidermal microstructures and scales being of particular importance for the optical appearance and contact mechanics. Specific skin adaptation is here discussed in reptiles (are epidermal features involved in the locomotion of arboreal lizards? The reduction of limbs to a snake like body is a radical solution in reptiles to conquer new niches: how does the skin contribute to the "new" limbless locomotion? Structural colors are known in birds and insects, but do reptiles have structural colors?), mammals (Is mammal skin adapted to climbing?), and fishes (fish scales are well known for their protective functions and their optimizations to reduce drag: which adaptations can be observed in benthic fishes?).

MAT4-1 4:30 pm

Biological attachment mechanisms; from dry to wet: examples and applications.

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Abstract: Attachment devices enable animals to move around or stay in place. The context in which attachment occurs however can be more complicated. While gravity and inertia rule the world of the gecko, fly and monkey, flow forces act on detaching stream and intertidal animals such as limpets or clingfish. To overcome these detachment forces, a variety of attachment mechanisms have evolved, including glue, friction, suction and mechanical interlocking. Some of these mechanisms show considerable differences in air and under water. Additionally, the concept of a submerged adhesive event and one that is dry is neither clear-cut nor simple. For example, a gecko's toe that adheres to a leaf seems to be a clear case of terrestrial adhesion, but depending on humidity there could be a monolayer of water on the leaf's surface, or there might be a patch of standing water on the leaf after rainfall. Here we discuss the attachment mechanism of two well investigated examples: geckos and clingfish. Geckos use a dry, van der Waals-based adhesive system. Small, hair-like projections allow geckos to cling strongly to virtually any substrate, however in the presence of surface water, adhesion becomes highly substrate dependent. On the other hand, aquatic clingfish use a ventral suction disc with specialized hierarchical structures to attach to wet substrates of a wide range of surface roughness. While there have been hundreds of gecko-inspired synthetic adhesives, many cannot capture all of the remarkable abilities of the natural system. Further, as our knowledge of the natural system grows, new applications, such as reusable and submersible adhesives, are only just being investigated. In contrast, bio-inspired adhesives that mimic the clingfish are still in the prototype stage of development. We believe that advancement in bio-inspired synthetics relies on an improved understanding of the natural system which focuses on both the ecology and evolution of these remarkable attachment mechanisms.

MAT4-2 5:00 pm

Mechanisms, evolution and biomimicry of color-producing nanostructures in birds and other dinosaurs.

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Abstract: Colors in animals can be produced by wavelength-selective absorption by pigments, or by scattering of light by nanostructured tissue. The latter offers a highly labile system that enables production of colors (e.g. blue) and color effects (e.g. iridescence) not easily attainable by pigments alone. Here I will first discuss how these colors are produced at the nanometer scale, using examples of color types spanning the visual spectrum and including both chromatic and achromatic colors. I will then discuss their evolutionary patterns (including some hints from the fossil record) and their potential effects on avian diversification. Finally I will describe our use of these materials as inspiration for new color-producing materials, including both non-iridescent and iridescent coatings.

Symposium — Muscle functional morphology: beyond gross anatomy (MFM)

Organizers: Adam Hartstone-Rose, Damiano Marchi

MFM1-1 2:30 pm

Stretch, strength, and speed: functional interpretations of muscle fiber architecture in limbs and the masticatory apparatus.

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Abstract: Traditional myological approaches to functional morphology focus almost exclusively on the gross anatomy of muscles and their osteological attachments. However, an expanding number of researchers are exploring muscle functional anatomy using new approaches that are enriching our understanding of the adaptations in the soft tissues of the musculoskeletal system—the focus of this symposium. Among these is a growing body of literature that focuses on coupling traditional gross anatomical dissections with chemical dissections resulting in deeper understanding of muscle fiber architecture. Through these techniques, we are learning new information about muscle stretch, strength and speed production abilities. Our muscle fiber architecture research, conducted with our students and numerous collaborators, has focused on primate and carnivore adaptations in masticatory and limb muscles as they correlate with variation in diet and locomotion respectively. Coupling these data with their osteological correlates has allowed us to estimate the masticatory abilities of extinct carnivores and primates and will eventually lead to more accurate analyses of the posture, locomotion and substrate use of extinct primates. In short, muscle fiber analysis has allowed us to expand our understanding of functional myology beyond the level of gross anatomy in ways that are adding depth to conversations about adaptations and niche partitioning in living and extinct species. This research was funded by NSF grant BCS-14-40599.

MFM1-2 2:45 pm

Modelling jaw muscle function in marsupials: from dissection to multibody dynamics analysis.

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Abstract: Multibody dynamics is a powerful modelling tool which is becoming increasingly popular for the simulation and analysis of jaw muscle function. It can be used to apply varying muscle forces to predict joint and bite forces during static and dynamic motions as well as investigating muscle activation patterns and how they vary to produce specific movements. The sequence of activity in the jaw muscles of macropods and wombats vary from those in other mammals including the closely related koala. Jaw movements are divided into a vertical phase and horizontal phase, but the number of muscles involved and the level of activity associated with each phase varies considerably between species. To investigate jaw muscle function in wombats, koalas and kangaroos, multibody dynamics models were constructed by combining data from gross dissection and 3D imaging techniques (Magnetic Resonance Imaging, MRI, and Computed Tomography, CT). MRI allowed 3D visualisation of soft tissues in situ, and through virtual dissection we estimated muscle forces and complex vectors of muscle action, allowing us to combine these data with electromyography data to simulate biting. Results show that the greatly enlarged masseter and medial pterygoid muscles in the wombat reflect their ability to exert very high compressive forces on the tooth row simultaneously with the dominant horizontal movement of the mandible. The unique activation pattern in wombats whereby only working-side muscles are active during the power stroke reduces rotation of the mandible to prevent the balancing-side molars from occluding and allows transverse movement of the jaw. These results vary considerably from those of the kangaroo, which has a dominant vertical phase, and the koala, in which the two phases are more even and muscle force is more equally distributed. Combining gross dissection with imaging techniques and multibody dynamics has given us new insights into how the jaw muscles of marsupials have adapted beyond their simple gross anatomy for various functions.

MFM1-3 3:00 pm

Jaw adductor muscle fiber architecture and estimated bite force in tree shrews (Mammalia: Scandentia).

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Abstract: The soft tissue of the masticatory apparatus is influenced by the properties of food ingested. Tree shrews (Order Scandentia) are omnivorous, and will eat a variety of leaves, fruit, arthropods and insects. It is hypothesized that tree shrews will reflect these dietary differences in their chewing musculature (soft tissue) and their mandibular morphology (hard tissue). Specifically, we look to see whether tree shrew species with a larger component of insects in their diet (*Tupaia tana* and *Tupaia montana*) will exhibit a higher ratio of temporalis to masseter musculature. Here, five species of tree shrew are dissected and their muscles of mastication chemically dissolved in order to measure muscle fascicle lengths and calculate physiological cross-sectional area (PCSA). Bite force is reconstructed for each species at the anterior premolar, first lower molar and posterior third molar from a combination of PCSA, muscle orientation, and fascicle length. Results indicate that bite force scales with positive allometry at each bite point ($\beta=3.07; 3.55; 4.12$). In each case, bite force increases when moving posteriorly along the tooth row, indicating increased force closer to the mandibular condyle. A comparison of the temporalis and masseter muscles indicate that neither *T. montana* nor *T. tana* had a higher ration of temporalis muscle than masseter. *T. nicobarica*, on the other hand, did. This suggests a larger proportion of insects in *T. nicobarica*'s diet, or a lesser dependence on insects in the diet of *T. montana* and *T. tana* than previously thought. These results suggest the need for more work into the feeding habits of *T. nicobarica*. In addition, understanding the morphology of tree shrew chewing mechanics could have the potential for reconstructing the same muscles of mastication in morphologically similar and phylogenetically closely related stem primates.

MFM1-4 3:15 pm

Biomechanics of the chewing musculature: osteological correlates of function and inferences from fossils.

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Abstract: There are many different approaches to the inference of chewing parameters in fossil mammals. These have included differing sources of data from extant analogues and have incorporated different levels of realism. The practical outcomes of such inferences include (more proximately) the input values for finite element and other biomechanical analyses and (more ultimately) conclusions regarding the diets and oral behaviors of extinct taxa. Here, we evaluate several different methods of inference focusing on the chewing muscles of primates. We compare the benefits of including more or less information on muscle position, orientation, size, and architecture. We generated inferences of muscle size, cross-sectional area, bite force, and gape adaptation in three extinct primate groups: Adapidae (Eocene, Europe), Notharctidae (Eocene, North America), and subfossil Lemuriformes (Pleistocene and Holocene, Madagascar). The data on extinct groups were compared with the corresponding values for extant strepsirrhine primates. Results indicate that adapids had large, powerful chewing muscles and great bite force; notharctids had large, powerful temporalis muscles and moderate bite force; and subfossil lemurs had large, powerful, masseter and medial pterygoid muscles. This suggests that some members of these extinct groups were using powerful bites to break their foods, but that different phylogenetic groups may have been emphasizing different individual chewing muscles. The fossil species have signs of gape limitations, consistent with processing small resistant foods (relative to their own body size). Here we also explore the relative merits of high-tech and low-tech methods for evaluating osteological correlates of muscle dimensions, and discuss some new, promising low-tech measurements. Funding came from Johns Hopkins University, Duke University, and Northwestern University.

MFM1-5 3:30 pm

Preliminary bite force estimations of Miocene giant mustelids (Carnivora, Mustelidae).

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Abstract: We use a sample of 22 modern carnivorans (Canidae, Felidae, Hyaenidae, Mustelidae and Ursidae) spanning the entire body size range of the order from *Mustela erminea* to *Ursus maritimus* to reconstruct the bite force (BF) in the Miocene giant mustelids *Megalictis*, *Eomellivora*, *Ekorus*, *Plesiogulo* and *Enhydritherium*. BF of the extant specimens was calculated following methods described by Hartstone-Rose et al., 2012: Specimens are dissected, their masticatory muscle fiber architecture is analyzed and the physiological cross-sectional area (PCSA) of each adductor is multiplied by its leverage and the muscle force constant, and the sum of those forces is divided by the leverage to the bite point. Since muscle origin areas correlate closely with PCSA in the extant sample, these areas were used to estimate PCSA in the fossils. Combining these with the leverage measurements allows us to estimate the BF of the extinct taxa. When regressing BF against a body size proxy—the geometric mean of 8 skull measurements (GM)—carnivorans overall scale with significant positive allometry (larger species have relatively higher BF $m=1.50$ at the canine bite point). This trend is even more pronounced in extant mustelids ($m=2.28$) likely influenced by the very high BF of the largest taxon *Gulo*. As expected, the fossil mustelids also have very high BF— all their residuals are statistically significantly higher than the extant carnivoran sample. Although their skulls are smaller, *Ekorus* and *Megalictis* have higher estimated BF than *Canis lupus*, *Lycaon pictus*, *Panthera pardus*, *P. uncia*, *Ursus americanus*, *U. maritimus*, and small *Crocota crocota* included in our extant sample. In fact, only the large *U. arctos* and *P. onca* and *P. tigris* exceeded their estimated BF. Also by our estimates *Ekorus* was able to produce BF ~ twice as powerful as those of the most powerful extant mustelid *Gulo*.

MFM1-6 3:45 pm

Functional adaptations of primate forearm muscle fiber architecture.

Leischner CL*, University of South Carolina School of Medicine; Allen KL, Washington University School of Medicine in St. Louis; Pastor F, Universidad de Valladolid; Marchi D, University of Pisa; Hartstone-Rose A, University of South Carolina School of Medicine leischne@email.sc.edu

Abstract: Distal humerus morphology is thought to reflect variation in the force production capabilities of the forearm musculature, necessitated by differences in substrate use and locomotion. Previously, we demonstrated that forearm muscle mass scales isometrically with body mass in primates and thus muscle mass alone is not an indicator of locomotor behavior. In preliminary data presented at the last ICVM, we found some functional correlates of muscle architecture, but the biases in the preliminary taxonomic sample precluded strong conclusions. We present new data from a greatly expanded sample including 55 specimens from 44 species: strepsirrhines (n=9), platyrrhines (n=15), and catarrhines (n=20). This final sample spans the entire size range of the order from *Microcebus* to *Gorilla*, and includes all major locomotor and substrate use groups. Contrary to our previous findings, forearm muscle mass actually scales with positive allometry across all primates ($m=1.12$, $r^2=0.98$). In terms of architecture, catarrhines

exhibit positive allometry in their physiological (and reduced physiological) cross-sectional areas (PCSA: $m=1.28$, RPCSA: $m=1.39$) indicating that larger catarrhines have relatively stronger forearm muscles. In terms of substrate use, while PCSA and RPCSA scale with isometry for terrestrial species, they scale with positive allometry (PCSA: $m=1.15$, RPCSA: $m=1.16$) for arboreal ones—thus larger arboreal primates have relatively stronger and faster forearms. Furthermore, terrestrial species have significantly greater PCSA ($p=0.0133$) and RPCSA ($p=0.0011$). Thus, terrestrial primates have greater forearm strength. We also studied subsets of these muscles, examining the architecture of wrist and digital flexors and extensors. Surprisingly, there are no statistical differences in the fiber architecture of quadrupedal primates when compared to vertical clinging and leaping or suspensory species. This research was funded by NSF grant BCS-14-40599.

MF2-1 4:30 pm

Leg muscle architecture in primates and its correlation with locomotion patterns.

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Abstract: Understanding the osteological correlates of the different locomotion patterns of extant primates is important to understanding locomotion of extinct primates. Bone biomechanical studies indicate that more arboreal primates have relative (to the tibia) more robust fibula than more terrestrial ones. Here, we test if the same pattern is seen in the differences in leg muscular architecture. Muscle mass, fascicle lengths (FL), physiological cross-sectional area (PCSA) and reduced PCSA (RPCSA) were studied in 34 primate species (6 strepsirrhines, 13 platyrrhines and 15 catarrhines). Muscles were grouped into toe and ankle flexors and extensors and studied for phylogenetic and functional signals. All variables strongly correlate with body mass: strength variables (mass, PCSA and RPCSA) scale with positive allometry, and speed/stretch measure (FL) scales with isometry across the whole sample. Thus, larger primates are relatively stronger though not faster or more flexible than smaller species. Residuals of the regressions show that strepsirrhines, catarrhines and platyrrhines are statistically indistinguishable. Surprisingly, the only variable that statistically distinguishes the arboreal vs. terrestrial species is total flexor/extensor RPCSA, with arboreal primates relatively stronger in this measure. The strongest functional signal emerged when comparing suspensory and vertical clinging and leaping (VCL) to more quadrupedal primates (QUAD). QUAD have statistically heavier leg mm. though they are not significantly greater in cross-sectional area or reduced in FL. Thus, although QUAD taxa are neither stronger nor slower than suspensory/VCL species, their muscles are more massive. Perhaps this is because of a mass constraint on suspensory/VCL locomotion. These results show the complex relation between leg bone biomechanics and muscle architecture and demand for further studies on this topic. Research funded by NSF grant BCS-14-40599.

MF2-2 4:45 pm

From bone to behavior: reconstructing habitual activity from muscle attachment site morphology.

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Abstract: Muscle attachment sites (entheses) are skeletal features frequently used to infer species-level locomotor patterns and individual activity patterns in the human archaeological and fossil record. Macroscopic surface analyses characterizing entheses size and complexity offer the opportunity to reconstruct behavior non-destructively under the assumption that increased habitual use results in larger and/or more rugose entheses. However, the precise relationship between soft tissue, bone and behavior remains unclear. This study uses a sample of sedentary, control laboratory mice ($n=33$) and others with experimentally increased ($n=32$) activity regimes to quantify activity-mediated effects on enthesal morphology and better understand this complex structure for use in paleontological research. We investigated cross-sectional geometry of the radius at two levels: radial tuberosity (the fibrocartilaginous biceps brachii insertion) and midshaft (a non-enthesal site). We used histological sections and microCT scans to investigate total subperiosteal (TSA), cortical (CA) and medullary area (MA) between midshaft and enthesal regions, and between entheses of control and experimental groups. In the activity group, TSA was significantly greater at the enthesis than at the midshaft. Additionally, though TSA and CA did not vary significantly between the exercised and control groups, MA was significantly smaller at the enthesal level in the exercised group ($p<.05$). This reduction in MA suggests that bone morphology is responsive to the mechanical environment, particularly at the enthesis. Thus, while recent experimental studies have questioned the reliability of enthesal surface morphology, there is potential for internal bone architecture to be an important tool in behavioral reconstruction from muscle attachment sites. This study was funded by the National Science Foundation [Graduate Research Fellowship DGE-1246908 to CT; DDIG BCS-0824552 to DG] and GWU's Lewis N. Cotlow Fund.

MF2-3 5:00 pm

Beyond function: muscle energetic and brain evolution.

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Abstract: Typically skeletal muscle fiber composition is used to evaluate functional differences in locomotion. However, because there are energetic differences among muscle fiber cells, muscle fiber composition could be used to address energetic questions. Muscle is composed of two main types of fibers: type I ("slow twitch") and type II ("fast twitch"). The difference between the two types can be reduced to differences in how these muscle cells use oxygen and glucose. Type I muscle fibers use oxygen to convert glucose to ATP, while type II fibers rely primarily on anaerobic metabolic processes. The expensive tissue hypothesis (ETH) could be improved upon by taking into consideration metabolic differences in skeletal muscle cells. The ETH proposes that the energetic demands imposed on the body by the brain result in a reduction in other expensive tissues (e.g., gastrointestinal tract). The original ETH dismisses the energetic demands of skeletal muscle because of its low metabolic demands at rest. However, its energetic demands can increase 100 fold when active. Furthermore, skeletal muscle is in direct competition for glucose with the brain. Because of skeletal muscle and the brain are competing for resources, we predict that larger brained primates will have relatively less muscle mass and that they will show a decrease in type I fibers. To test our predictions, we dissected 37 species of primates and obtain body mass and muscle mass values. We collected endocranial volumes from the literature. We also sampled pectoralis major, deltoid, gastrocnemius, and soleus for a subset of the primate sample (n=14). Using immunohistochemistry, a muscle fiber composition profile was created for each species sampled. Results show the percent muscle mass and type I muscle fiber [r(14) = -0.74, p = .02] negatively correlate with brain mass. Results clarify the relationship between muscle mass and brain mass and illustrate how muscle mass can be used to address energetic questions.

MFM2-4 5:15 pm

Old meets new: combining traditional and modern tools in the study of jaw adductor morphology and function.

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Abstract: The use of modern computational and imaging methods is significantly advancing the field of functional morphology by allowing scientists to more accurately document, measure, model and map the evolution of morphological complexes. In particular, X-ray Computed Tomography (CT) has opened a new niche in the study of anatomy; this imaging technique not only enables the observation and measurement of anatomical structures while they are still intact, but also the creation of three-dimensional renditions that can be used in modeling. Recently, and thanks to the development of diffusible iodine-based contrast enhanced CT (diceCT) protocols, these imaging tools have also started to show great promise for non-destructive imaging of soft tissues. Here, I illustrate the advantages and difficulties of using diceCT methods in the study of mammal jaw adductor anatomy and function. I use a morphologically and ecologically diverse sample of bats to highlight the utility of diceCT in uncovering interspecific variation in the compartments and attachments of jaw adductors. I also show how diceCT data can, and perhaps may always need to, be integrated with data produced via traditional approaches (e.g., dissections) to quantitatively study muscle function and evolution. By combining these traditional and modern tools into three-dimensional biomechanical models of biting function, I further demonstrate how they can complement each other for accurate predictions of interspecific variation in bite performance.

Symposium — Determinants of the mammalian feeding system design (MFS)

Organizers: Olga Panagiotopoulou, José Iriarte-Díaz

MFS1-1 9:30 am

Not all bones are created equal: Intrinsic and extrinsic influences on phenotypic expression in the developing skull.

Ravosa MJ*, University of Notre Dame; Weiss-Bilka HE, University of Notre Dame; Franks EM, University of Notre Dame; Scott JE, Southern Illinois University; McAbee KR, University of Notre Dame; Brill JA, University of Notre Dame; Pax KC, University of Notre Dame; Pasquinely AC, University of Notre Dame; Mazur MM, University of Notre Dame; Scollan JP, University of Notre Dame; Eastman MM, University of Notre Dame Matthew.J.Ravosa.1@nd.edu

Abstract: In vivo and ex vivo analyses facilitate a unique knowledge of how anatomical structures and their cellular constituents respond to external stimuli, information critical for understanding connective-tissue mechanobiology and phenotypic evolution. In mammals, diet-related variation in loading patterns induces a cascade of changes at the gross, tissue, cellular, protein and genetic levels, with such tissue modeling and remodeling maintaining the integrity of craniomandibular structures. Investigating these phenomena using a novel rabbit model of long-term dietary plasticity, we document the presence of considerable intracranial variation in reaction norms within and between masticatory and non-masticatory elements. In addition, we show that early onset and duration of a loading stimulus associated with a feeding behavior can result in levels of intraspecific variation that mirror morphological differences between sister taxa with disparate diets. Lastly, the rabbit longitudinal data are integrated with evidence about the intrinsic proliferative activity and load-induced responses of osteoblasts from the calvarium, basicranium and mandible in neonate mice. In highlighting the potential cellular bases of relative growth in the skull, our research suggests that cranial osteoblasts are not a homogeneous group of cells, but rather exhibit distinct behaviors depending on their anatomical location and embryological origin. Such findings are important for highlighting why bone should not be viewed as similar across skeletal regions with respect to its intrinsic growth potential or

osteogenic responses to external stimuli, an assumption inherent to most comparative and experimental studies. Funding: NSF (BCS-1029149/1214767), Indiana CTSI (NIH TL1TR001107 to A. Shekhar), Wenner-Gren Foundation, and Leakey Foundation.

MFS1-2 10:00 am

Tooth wear, textures, and feeding biomechanics.

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Abstract: Most mammals use differentiated cheek teeth for chewing, to divide food into small pieces. The occlusal surface and the occlusal gap are the spatial requirements of any tooth function. The dental tissues enamel, dentin and cementum built an antagonistic grinding system with the tooth tissues. Nevertheless the multi-body dynamics of the processes of wear are still not well understood. Therefore the review presented here aims to pinpoint these developments compiling an overview of the main controversies in the field of tooth wear analyses in vertebrate morphology. Main developments from the early days of traceology till recent discoveries analyzing surface textures are discussed. Wear traces on teeth have been described extensively and a guideline to the quantitative approaches that have been developed during the last fifteen years is given. The tribological concept understanding tooth surfaces as antagonists of a tribosystem is introduced and illustrated with data from controlled feeding experiments. Furthermore it is shown how surface textures can be related not only to dietary composition but additionally to chewing direction and feeding biomechanics. Some concluding remarks are given reminding to technical pit falls and presenting open questions for future research directions.

MFS1-3 10:30 am

Performance and integration in mammalian dentitions: from blade sharpness and dental complexity to the inhibitory cascade.

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Abstract: Teeth play a very important role in the mammalian feeding system, enabling effective breakdown of a variety of foods and helping to fuel the high metabolic rates of mammals. We can examine teeth as tools for the breakdown of food. Efficient mastication requires three important elements: 1) effective tool shape, 2) appropriate number of tools on the tooth, and 3) precise alignment of tool components. Fundamental tool types include blades, cusps and basins. Within each of these types, the shape of particular surfaces affects how much force or energy is taken by the tool to divide food. Here I report on experiments using idealised 3D printed tools to examine the specific effect of parameters such as blade sharpness, rake angle and approach angle on fracturing both simulant and real foods. The greater the number of tools on a tooth or toothrow, the more opportunity there is for food fracture during an occlusal stroke, but the less space between tools. The number of tools on a tooth can be estimated by the Orientation Patch Count (OPC) metric of dental complexity. Disparity in mammal diets is reflected in differences in their dental complexity, such that carnivores have simpler teeth than herbivores. While this information is useful for estimating diets of extinct species, it also gives clues to the limits on tooth function in mammals. For tools such as blades to work effectively, upper and lower teeth must precisely align during the occlusal stroke, but it is unknown how this alignment is established during development and evolution. Earlier work has shown that mammal teeth develop and evolve according to a pattern known as the inhibitory cascade. It is likely that the inhibitory cascade is instrumental in ensuring precise alignment of occluding teeth, and was a key characteristic enabling the evolution of mastication in mammals. As an example, we show that hominin dental evolution was tightly constrained by the inhibitory cascade.

MFS2-1 11:30 am

Variations in the material properties of mammalian and non-human primate jaws.

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Abstract: Cortical bone material properties including density and elastic properties (elastic and shear moduli, and Poisson's ratios) are essential for understanding the complex biomechanics of individual bones to muscle forces and extrinsic loadings. In particular, variations in cortical bone anisotropies are significant in determining the relationship between stress and strain in bone. In primate and human evolution, research on the craniofacial skeleton, including the mandible, suggest that variations in such properties may represent evolutionary adaptations to unique craniofacial functions or patterns of development. My laboratory has conducted comparative studies on the material properties of macaques, baboons, chimpanzees, gorillas, capuchins, alligators, bats, pigs, and humans. Methodology included measurements of bone density using Archimedes principle, and ultrasonic techniques modified to calculate 3D material properties of cortical bone. Such data are required to improve the accuracy of finite element models. Here comparisons are made across species to assess commonalities and differences in mandibular material structure. Overall, these results reveal complex patterns of skeletal maturation, much of which can be attributed to increasing bone density with age, especially regarding elastic and shear moduli. Other variables such as anisotropy and orientation of maximum stiffness are less related to bone density and differences suggest variations in internal microstructure with adaptation and growth. Interpretation of the impact of these differences between regions on the relationship between stress and strain patterns requires an understanding of the different loading and boundary

conditions at each region during function. For this reason, it is doubtful whether one can generalize from region to region and across species on the impact of including material properties in a functional analysis. Support: NSF Physical Anthropology HOMINID program NSF-BCS-0725141.

MFS2-2 12:00 pm

Impact of feeding behavior on the deformations of the macaque mandible.

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Abstract: Developmental studies reveal links between mandibular corpus morphology and diet. However, comparative research in primates does not strongly support links between food mechanical properties (FMPs) and mandibular corpus morphology. We investigated the effects of FMPs with variable stiffness (E , range=0.5-34MPa) and toughness (R , range=105-965Jm⁻²) on mandibular strain patterns and magnitudes using in vivo experiments and finite element models (FEMs). We hypothesized that variation in strain magnitudes and orientations when chewing items with different FMPs is minimal at the corpus and maximal at the lingual symphysis, since the latter is subjected to high strains during mastication. We further hypothesized that principal strain in the mandibular corpora is more strongly affected by variations in bite locations than is the symphysis. Results confirm that across all food items mean in vivo maximum principal strain (ϵ_1) in the corpus had a range of 13-227 $\mu\epsilon$ for nuts; 15-291 $\mu\epsilon$ for dry fruit and 9-149 $\mu\epsilon$ for soft food and comparative results were obtained from the FEMs. Nevertheless, the mean ϵ_1 in the symphysis in FEMs had a range of 19-1682 $\mu\epsilon$ for nuts, 3-1773 $\mu\epsilon$ for dry fruit, and 7-768 $\mu\epsilon$ for soft food, evidently higher than the corpus. Results also confirmed that ϵ_1 at the lingual symphysis is relatively insensitive to variation in bite location, whilst variations in magnitudes and patterns were encountered in the chewing side corpus. These data suggest that if variation in primate mandibular morphology is driven by variation in strain patterns and magnitudes, then it is likely related to a combination of both feeding behavior and FMPs, but with different factors being important at different mandibular sites. Funding: Marie Curie European Re-integration Grant ERG-MACACA 267207 to OP. SBMS, UQ start up Project Grant 606441 to OP. BBSRC Grant BB/J021504/1 to SW. NSF BCS 0962677 Grant to ABT.

MFS2-3 12:30 pm

What's gape got to do with it? Examining osteological correlates of jaw gape in primates.

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Abstract: Considerable attention has been given to bite force as a performance variable in vertebrate and mammalian feeding, yet until recently less interest has been given to the adaptive significance of variation in jaw gape. The publication of in vivo primate gapes by Hylander provides an opportunity to examine potential correlates between gape and osteology, which can help to elucidate the morphological patterns employed by primates to achieve large gapes, whether for dietary or social behaviors. The present study examines osteological features of the mandible, temporomandibular joint, and masticatory muscles in a sample of 21 catarrhine primates. The relationship between gape, canine projection, and body mass were examined, and osteological measurements were regressed on gape separately for females and males. A significant but weak relationship was identified between body mass and gape and, as in previous work, canine projection was significantly correlated with gape. Nearly all osteological features examined scaled with negative allometry and were significantly correlated with gape in both sexes; males showed especially strong relationships between gape and mandible length and measures of TMJ length and curvature. Similarly, geometric morphometric analyses found a strong relationship between overall craniofacial shape and gape. However, t-tests for relative differences between sexes within each species revealed that patterns of osteological differences varied considerably across taxa. Together, these data suggest that, though there are general patterns across catarrhine primates in how craniofacial morphology is linked to gape, species with considerable sexual dimorphism in gape achieve these differences in multiple ways. These differences in the osteological correlates of gape within species may be informative for understanding the trade-offs between gape vs. bite force production.

MFS3-1 2:30 pm

Functional and evolutionary relationships between jaw-muscle fiber architecture and behavior: a disturbance in the force.

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Abstract: Maximum bite force has long been recognized as a key performance variable related to biting and chewing and is believed to have played a critical role in the evolution of mammalian craniodental morphology. In the absence of fossilized soft tissues, paleobiological interpretations of craniofacial muscles have been forced to rely on the

assumption that muscle size is a reliable proxy for muscle force and hence the key functional property of the jaw muscles. Whole muscle function is primarily influenced by two architectural properties: physiologic cross-sectional area (PCSA), which is proportional to a muscle's maximum force-generating capacity, and fiber length (Lf), which is proportional to maximum muscle excursion/stretch. Here we highlight functional and evolutionary trends in the architectural features of anthropoid primate jaw muscles. We show that while some hard-object feeders, such as tufted capuchins, have jaw-muscle architectures that improve muscle and bite forces for feeding on mechanically resistant foods, others, such as sooty mangabeys, do not. Additionally, some species have architectural features that favor jaw-muscle stretch to improve access to foods, while others have evolved architectural features that favor jaw-muscle stretching to facilitate gape and canine display to potentially improve access to mates. Some primates experience trade-offs between maximizing muscle force and muscle stretch, but others circumvent this trade-off in ways that are potentially metabolically expensive. Collectively, these findings suggest there are multiple selection pressures placed on feeding-system morphology and a variety of ways species meet competing functional demands. The multiple potential morphological solutions emphasize the importance of incorporating muscle morphology in studies linking behavioral ecology and functional morphology of the feeding system. Supported by the National Science Foundation (BCS 0452160, BCS 0962677).

MFS3-2 3:00 pm

The effect of variation of the jaw adductor musculature and cranial morphology on the masticatory performance of primates.

Iriarte-Diaz J, University of Illinois at Chicago; Akif Y, University of Illinois at Chicago; Deshpande R, University of Illinois at Chicago; Al-Hamawi O, University of Illinois at Chicago* jiriarte@uic.edu

Abstract: Substantial variation in the structural relationships within the masticatory system (i.e., among teeth, joints, and muscles) through the evolutionary history of mammals has greatly influenced the mechanical performance of the system. These changes are typically viewed as evolutionary responses associated to specific pressures; such as the need to generate occlusal force, the need to resist masticatory stresses, or the need for delicate motor control. Thus, changes in the musculo-skeletal configuration are expected to reflect adaptations to these competing and varying demands. To evaluate the relative importance of these elements in shaping the evolution of the masticatory system necessitates adequate understanding of how variation in each factor affects the mechanical performance of the system as a whole. In this study, we created a 3D mechanical model of the masticatory system to evaluate how variation in various aspects of cranio-mandibular morphology affect feeding performance. The model takes inputs from 3D models to measure the location and relative force generation of the masseter, medial pterygoid and temporalis muscles, as well as the effect of asymmetrical activation patterns, like those needed for lateral mandible displacement during feeding. We collected 3D data from a morphologically and phylogenetically diverse group of primates to evaluate the evolution of the mechanical performance of feeding. We show that the musculo-skeletal configuration of the masticatory apparatus is mechanically labile and can be varied substantially while maintaining good masticatory performance. We also evaluated clade-specific morphological changes, such as elevation of the jaw joint with respect to the occlusal plane, and their effect on the mechanical performance of the feeding system.

MFS3-3 3:30 pm

Mandibular loading, jaw-muscle activity, and symphyseal performance: elucidating the relationships among mastication, morphology, and biomechanics of the mammalian jaw.

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Abstract: The morphology of the mammalian jaw is traditionally interpreted as reflecting the loading patterns it incurs during various oral behaviors such as chewing and biting. These loads are a result of jaw adductor muscle force as well as bite and temporomandibular joint reaction forces. This interpretation spans many different groups of mammals, from primates to carnivores, yet the available evidence suggesting that forces incurred during these behaviors has an evolutionary impact on jaw morphology is primarily limited to primates. Here, we relate *in vivo* jaw-muscle activity patterns and bone strains to patterns of jaw morphology and *in vitro* estimates of jaw strength in several pairwise comparisons across diverse groups of mammals including carnivores, ungulates and primates. Whereas some aspects of morphology (e.g., symphyseal fusion and a relatively large symphyseal cross-sectional area) have relatively consistent links to muscle activity patterns and strength estimates across mammals, the relationship between morphology and specific loading patterns derived from strain data is less clear. Moreover, mandibular strain patterns during mastication are varied and complex when considered relative to variation in symphyseal fusion across mammals, making links among specific *in vivo* loading regimes, performance and morphology more difficult to interpret across mammals. We consider the consistent features across these clade-specific relationships among activity, performance and form to help identify persistent factors driving the evolutionary changes in mammalian jaw form across mammals. Funding: National Science Foundation IOS-0520855 and DBI-1062327 to SHW, BCS-0959438 and DBI-1062332 to CJV, and BCS-0924592/1214766 to MJR and CJV.

MFS4-1 4:30 pm

Modulation of feeding energetic costs in primates: the impact of morphology and behavior across body size.

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West Virginia School of Osteopathic Medicine; O'Neill MC, Department of Basic Medical Sciences, University of Arizona College of Medicine; Toler M, Center for Functional Anatomy and Evolution, Johns Hopkins University cw19@duke.edu

Abstract: Our work to measure the energetic costs of feeding in primates seeks to evaluate the impact of morphology and behavior on feeding costs. Metabolic rate during feeding and chewing was measured by indirect calorimetry in 12 nonhuman primate species (70g–4.5kg) and humans (55–100kg) eating a variety of raw foods varying in size, toughness, stiffness, and energy content. Resting and postprandial metabolic rates were also measured. Food items requiring large amounts of pre-chewing processing (e.g., *Hapalemur* feeding on whole bamboo and *Daubentonia* gnawing wood) incur the largest feeding costs, and these are possibly due to the recruitment of trunk and limb muscles. Analysis of pre-cut pieces of food shows that, within species, net feeding costs per unit of food mass (W/g) are positively correlated with food size, toughness, and stiffness as predicted since jaw-adductors increase recruitment during large, tough, and stiff food chew cycles. A slope of 1.0 is expected if net feeding energetic costs (W) scale in proportion to jaw-adductor muscle mass across species, as predicted when recruitment is a major source of cost during chewing. However, we observe negative scaling of W relative to both body mass (slope=0.65, CI=0.05) and jaw-adductor mass (CIs of estimated slopes between 0.60 and 0.80). This negative relationship may be explained by aspects of morphology and behavior. For example, we find a strong association between high molar shear and low W during insect-feeding demonstrating empirically that tooth design increases the efficiency of food breakdown. Overall, the data provide evidence of significant correlations between energetic costs and food properties, tooth design, and behavior. We suggest that structural (e.g., muscle architecture and occlusal morphology), kinematic (e.g., chewing rate), and behavioral (e.g., food preparation) traits interact to modulate feeding costs. Supported by NSF BCS-1062239.

MFS4-2 5:00 pm

Symposium discussion.

Ross CF, University of Chicago rossc@uchicago.edu

Contributed Session — Morphological Integration & Modularity (MIM)

MIM1-1 2:30 pm

Role of FGF signaling during anterior-posterior patterning of zeugopod.

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Abstract: Zeugopod area displays large variability in bone patterning. In some species such as horse, the radius is the main load-bearing bone of the forelimb and the ulna can be significantly reduced in size. On the other hand, in chicken or alligator, the ulna is much larger than the radius. As fibroblast growth factors (FGFs) are key players in processes of cell proliferation and chondrocyte differentiation, we experimentally manipulated this pathway to test its effect on zeugopod modeling. We used loss-of-function approach, where FGFR inhibitor PD173074 was injected into chicken wings or limbs. The inhibitor treatment caused shorter and thinner humerus as well as partial or full absence of radius while ulna remained without morphological changes. The phenotype of hindlimbs resembles the wing phenotype with a more severe effect on the anterior skeleton. The application of PD173074 caused significant changes in cell proliferation and mesenchymal condensation formation during early stages of chondrogenesis in vivo, which was also confirmed in vitro. Moreover, we observed more significant inhibition of chondrogenesis in anterior micromass cultures in comparison to posterior ones. Next, we used gain-of-function approach where recombinant FGF ligands (FGF1 or FGF2) were applied into the right chicken wing bud at stage HH20-22. FGF implantation resulted in skeletal malformations resembling aberrant activation of FGFR/ERK MAP kinase signaling in the growth plate cartilage. Interestingly, humerus and ulna were shortened and thicker, while radius did not exhibit this phenotype. In conclusion, we found that a subtle modification of FGF level affects the size and shape of zeugopod bones during limb development. Based on our results, we propose that similar alteration of FGF signaling could play a role during limb evolution in vertebrates where different degrees of zeugopodial bones reduction are seen. The research was supported by Grant Agency of Czech Republic (14-31540S).

MIM1-2 2:45 pm

Bodies and fins exhibit correlated evolution towards locomotor specializations in cichlid fishes.

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Abstract: Cichlids comprise an explosive adaptive radiation of freshwater fishes, with tremendous variation in behavior and morphology. This radiation, and its well-studied evolutionary history, presents a unique opportunity to

test hypotheses about how functionally-related traits may exhibit correlated evolution in an appropriate phylogenetic context. In the case of fish locomotion, there are several hypotheses as to how fish bodies and fins may have evolved to support particular locomotor specializations: specifically, one would expect (1) swimming economy specialists to have deep anterior bodies with tapered narrow caudal peduncles, semi-lunate caudal fins, and anteriorly positioned median fins; (2) burst acceleration specialists to have cylindrical stout bodies with broad caudal fins and posteriorly-positioned, high surface area median fins and; (3) maneuvering specialists with laterally compressed, deep body profiles and large median fins with high surface area and broad bases. Using a combination of geometric and linear morphometrics in conjunction with partial-least-squares analysis, it was demonstrated that cichlid bodies, median fins, and caudal fins exhibit correlated shape evolution. Patterns of covariation largely agreed with existing hypotheses of evolution towards locomotor specialization. This is strong evidence that particular fin and body shape combinations have adaptive value. Future work will elucidate how morphology and kinematics vary with each other to produce swimming performance.

MIM1-3 3:00 pm

How many roads lead to Rome? Phenotypic and genetic convergence in two independent lines of mice selectively bred for increases in relative limb bone length.

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Abstract: Phenotypic convergence in limb bone morphology is common across terrestrial mammals. Limb proportions likely evolved in parallel in independent lineages under similar selection pressures, for example in the context of locomotor specializations. What is less clear, however, is how many distinct genomic, developmental and phenotypic pathways are possible in the evolution of convergent limb skeleton phenotypes. Put differently, if one were to “play the tape” of limb skeletal evolution again, how often would an ancestral taxon under the same selection pressures show the same changes in a descendant taxon, at phenotypic and genetic levels? Here, we addressed this question by looking at such changes in two independent lines of mice selectively bred for increases in tibia length relative to body mass (the Longshanks mice). Using a combination of genome sequencing, analyses of long bone trabecular architecture, and multivariate morphometric analyses of adult skeletons, we show that, while the two traits under selection (tibia length and body mass) are identical between the two Longshanks lines after 15 generations of selective breeding, changes in other skeletal traits differ between the two lines. Longshanks lines 1 and 2 can be readily distinguished on the basis of skeletal differences in their hands, feet and girdles, as well as in their long bone microarchitecture. These changes are reflected in subtle differences in the underlying genetic architecture, which shows a mix of parallel and lineage-specific genomic changes in regions with known roles in skeletal growth. These results suggest that, even among closely related lineages derived from the same ancestral population, parallel selection for the same skeletal phenotype can cause divergent changes in correlated skeletal traits, most likely through changes in distinct genetic and developmental processes.

MIM1-4 3:15 pm

Determinants of body shape and co-variation among elements of the bony torso in anthropoids (Primates: Anthropoidea).

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Abstract: A cornerstone assumption for reconstructing anthropoid evolution is that the hominoid torso differs from that of monkeys, with a broader rib cage and longer, broader pelvis to effect more laterally oriented glenohumeral joints, reflecting adaptation to below-branch arboreality. Furthermore, the transition to the hominin body plan is most commonly thought to have had African ape-like beginnings – long pelvis, short, stiff lumbar spine, cone-shaped rib cage. However, growing evidence for homoplasy in hominoid postcranial form appears to challenge these hypotheses. Further, the fossil record tends to leave only isolated bones, forcing paleontologists to rely on hypothesized co-variation among bones to infer torso structure. We test these assumptions about determinants of torso shape in anthropoids to provide a basis for inferring the evolution of torso form in the fossil record. We combine data on intact torso shape gathered from reconstructed CT scans of 68 extant anthropoids with linear and landmark data from 225 skeletons including ribs, vertebrae, sternum, and pelvis. Data reveal more and different patterns of variation among elements of the torso than previously appreciated, and do not support the idea that reorientation of the shoulder led to uniform modification of the torso. Iliac morphology is not tightly coupled with rib cage shape but is broadly related to lumbar form. Spinal musculature is a stronger determinant of pelvic form than previously recognized. Upper and lower portions of the rib cage are not tightly integrated and appear to respond to different adaptive constraints. These results reflect differing selective pressures across different regions of the torso, and provide data with which to more accurately infer aspects of torso form, and locomotor adaptation, in fossil anthropoids, and may provide clues to understanding variation in body shape across mammals. Supported by NSF BCS 0716244 and Leakey Foundation.

MIM1-5 3:30 pm

Building blocks: functional and developmental modularity in the axial skeleton of Felidae (Mammalia).

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Abstract: Geometric morphometric analyses of the axial skeleton in Felidae have shown heterogeneous ecomorphological specialisation in presacral vertebrae shape related to locomotion and prey size. While anterior vertebrae may either have evolved under stronger phylogenetic constraints or are ecologically conservative, posterior vertebrae, specifically in the post-T10 region, show clearer differentiation between ecomorphs. Whereas these results suggest that distinct vertebral sections are under different selection pressures and/or constraints, shape regionalisation in this complex serial structure can also reflect modular organisation of vertebrae, which may direct responsibility to selection. Here we have investigated hypotheses of modularity in the axial skeleton of nine living Felidae species spanning the full extant range in body size and ecology. Analyses were performed on a dataset of 1281 vertebrae composed of 19 vertebral types from 70 specimens. We assessed morphological, developmental, and functional modularity hypotheses both across and within vertebrae. Two-block Partial Least Squares analyses, with and without phylogenetic correction, identified five modules in the presacral axial skeleton (atlas – T1, C6 – T2, C7 – T8, T10 – T11, and T12 – L7), whose identities strongly correspond with hypotheses of morpho-functional modularity. Additionally, correlations between the cervical (atlas – C7) and posterior (T12 – L7) modules reflect timing of vertebral ossification. Intravertebral modularity was explored with analyses of relative eigenvalue standard deviation, RV coefficients, and covariance ratios. Our results support the developmental hypothesis of two widespread intravertebral modules (centrum vs. laminae). Exceptions showing different modular patterns are concentrated on regional morphological boundaries, specifically on the axis, C7 and T1, T8, T13, and L6 and L7. Additionally, the axis and vertebrae in the T10 - L7 region show the greatest overall integration.

MIM1-6 3:45 pm

Disintegrator: a new R package for evaluating phylogenetic trees while accounting for correlations between character states.

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Abstract: One of the assumptions of phylogenetic analysis is that all of the characters being assessed evolve independently of one another. However, morphological characters may be linked due to a shared developmental or epigenetic process, or because states are selected together because of shared functional or ecological pressures. The interdependence of characters is referred to as morphological integration and has been the basis for many arguments against using morphology to construct phylogenetic hypotheses. Morphological integration diminishes the reliability of phylogenetic analyses because it draws support for phylogenetic hypotheses from different characters out of proportion to the information that they actually carry. The most common method used to remove the effect of morphological integration has been for the investigator to identify a suite of correlated character changes, usually associated with a particular ecomorph, and then down-weight or delete those characters to reduce their collective contribution to tree length. Disintegrator is an R package that I developed to evaluate, among other things, the likelihood of a phylogenetic tree topology given a Brownian motion model of evolution. What sets Disintegrator apart from other programs is that it also uses the tree structure and the distribution of character states to create a model of correlations between characters, which it then uses to transform the original data to the expected set of states if there was no correlation between characters. The likelihood of the tree is then evaluated using the transformed data. Disintegrator is a step forward for the phylogenetic analysis of morphological data because it accounts for morphological integration in an objective way that diminishes the risk of introduced investigator bias.

MIM2-1 4:30 pm

Morphological modules within the avian skull evolve at different rates.

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Abstract: Modularity and integration are key features of biological systems, describing the degree to which individual components of organisms are interrelated with one another. Although these concepts are closely associated with evolvability and constraint, their macroevolutionary patterns have been investigated in very few vertebrate clades. We evaluated modularity and integration in a phylogenetic context and quantify phylogenetic signal and evolutionary rate in individual modules, using the avian skull as a focal system. Previous studies have found the avian skull to be generally integrated, more so than has been observed in mammals, but these analyses have been either phylogenetically restricted or based on limited shape data (i.e., using 2D data and/or excluding major cranial regions). Recent advances in data acquisition and analytical techniques for high-dimensional data allow for a more robust consideration of phenotypic evolution in the avian skull. Using 3D surface scans of a broad sample of Neornithines, we quantified cranial morphology using a high density of anatomical landmarks and semilandmarks. Covariance ratio analyses supported significant modularity between the braincase and face, with greater independence between these two regions than between random groupings of traits. Moreover, the facial skeleton exhibits higher evolutionary rate and higher morphological disparity than the braincase, whereas the level of within-module integration is significantly higher in the braincase. These results support the hypothesis that high integration constrains morphological evolution and suggest that the modular nature of the avian cranium facilitates individual subregions to respond to selective pressures and functional constraints in independent ways. This study also illustrates the utility of phenomic data for studying patterns of morphological evolution and serves to further our understanding of how modularity has influenced the evolution of morphological variation.

MIM2-2 4:45 pm

The timing of cranial lateral line morphogenesis and its implications for ontogeny of sensory function.

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Abstract: The pattern and timing of the ontogeny of the vertebrate sensory systems make critical contributions to an organism's ability to ultimately formulate appropriate behaviors. The mechanosensory lateral line system of fishes detects unidirectional or oscillatory water flows that arise from predators, prey, environmental flows, and obstacles. The cranial lateral line system of bony fishes goes through dramatic changes during the larval stage and then through metamorphosis to the juvenile stage. After the initial establishment of an array of neuromast receptor organs on the skin in young larvae, neuromasts may increase in number and size and change shape. Then, typically at metamorphosis, a subset of neuromasts becomes enclosed in pored lateral line canals in a conserved subset of dermatocranial bones, changing these receptors from velocimeters to accelerometers. In growing juveniles, the neuromasts continue to increase in size, and the relative pore size and canal diameter determine adult canal phenotype, which vary among taxa. Both the absolute and relative timing of each of these morphological changes (which speaks to modularity and integration in the dermatocranium and placode-derived sensory organs) is likely to have important implications for the ontogeny of flow sensing capabilities with respect to fish size, swimming behavior, and transitions in life history. This paper will compare the timing of lateral line development among fishes as structurally and ecologically diverse as zebrafish (*Danio rerio*), cichlids (*Aulonocara Stuartgranti*, *Tramitichromis* sp.), butterflyfishes (*Chaetodon ocellatus*), and gobies (*Elacatinus lori*, *E. colini*), and will consider implications for the ontogeny of lateral line function and lateral line-mediated behaviors. Supported by NSF grants 0843307 and 1459546 to JFW and the University of Rhode Island.

MIM2-3 5:00 pm

Constraint and convergent evolution of diprotodonty in therian mammals.

Cobb SN*, Hull York Medical School, University of York; Morris PJR, Hull York Medical School, University of Hull; Cox PG, Hull York Medical School, University of York sam.cobb@hyms.ac.uk

Abstract: Despite their high dietary and taxonomic diversity, living and extinct rodents share a conservative dentition consisting of a pair of enlarged and continually growing upper and lower incisors (diprotodonty), separated from a reduced posterior dentition by a large diastema. Diprotodonty has also independently evolved in a phylogenetically diverse range of non-rodent therian mammals, including hyraxes, lagomorphs and individual species of marsupials and primates. Here we examine whether the independent evolution of diprotodonty across therian mammals is limited to the dentition, or if it constrains the disparity of the whole masticatory system. Three-dimensional landmarks were collected from CTs of the cranium and mandible of non-rodent diprotodont species, species representing the main extant rodent families and non-diprotodont outgroup taxa. Geometric morphometrics methods were used to examine the convergence between the rodent and non-rodent specimens. The taxa in this study samples large phylogenetic distances, however in both the cranium and mandible morphospaces the diprotodont taxa group very tightly together. Within the rodents, taxa from the main groupings based on masticatory musculature (hystricomorphs, myomorphs, protrogomorphs and scuiromorphs) form discrete groupings in cranial results. Partial least squares (PLS) show a high level of covariation between cranium and mandible in all taxa. The findings of the study clearly demonstrate that convergent evolution of morphology in diprotodont mammals is not restricted to the dentition, but is also found in the cranium and mandible and their pattern of covariation. This indicates that there are strong functional constraints on the masticatory system associated with diprotodonty.

MIM2-4 5:15 pm

A maximum likelihood approach to assessing modularity with 3-D morphometric data.

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Abstract: Presently, identification of phenotypic modules can be accomplished through exploratory (e.g., cluster analysis) or confirmatory (e.g., RV coefficient analysis, Covariance Ratio analysis) approaches. Confirmatory approaches are more robust, but suffer from an inability to compare across different model parameterizations. For example, both a two-module neurocranial/facial model and a six-module model have been significantly supported for the therian mammalian skull using RV coefficient analysis. Here, we present an approach to analyzing modules with morphometric data in which model log-likelihoods of trait correlation matrices are compared using the finite-sample corrected Akaike Information Criterion, allowing for discrimination of hypotheses across different model structures. We validated this method on correlation matrices simulated to have no modularity and simple (2-module) and complex (6-module) patterns of integration, testing these simulated matrices against 31 model structures, including no modules, and various partitions of 2, 3, 4, 6, and 8 modules. We also assessed the effect of different degrees of integration magnitude, varying the average within- and across module correlations. In all cases, the correct model structure was recovered with greater than 0.99 posterior probability. We then focused on a published dataset of 61 landmarks measured on 181 macaque skulls (*Macaca fuscata*), spanning five age cohorts. Results for both coordinate and multidimensional vector correlations clearly supported a complex 6-module model for all cohorts, with separate estimates of within- and inter-module correlations as the best fit for all datasets, demonstrating that this pattern of integration is stable through the postweaning ontogeny of macaques. Subsampling analyses of the best-

sampled data set (M1 erupted) further demonstrates the ability to recover identical model structures and estimates of within- and among-module correlations with severely degraded sample sizes.

MIM2-5 5:30 pm

Modularity or integration or both? 3D analysis of 21 genera of frogs demonstrates phylogenetic conservatism in skulls and lability in limbs.

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Abstract: Quantifying morphological diversification across taxa can provide valuable insight into evolutionary processes, yet its complexities can make it difficult to identify appropriate units for evaluation. One of the challenges in this field is distinguishing between the morphological integration and modularity hypotheses, where morphological evolution of different structures is explained either by co-variation between them, or by independent evolution respectively. Here we used a 3D geometric morphometric approach with x-ray micro CT scan data of the skull and bones of fore-limbs and hind-limbs of representative species from all 21 genera of the ancient Australo-Papuan myobatrachid frogs, and analysed their shape both as a set of distinct modules and as a multi-modular integrative structure. We then tested three questions: (i) is morphological disparity similar between the two major subfamilies, (ii) do skulls and limbs show different levels of integration, and (iii) is shape variation correlated with locomotion, burrowing behavior, and ecology. We found that morphological disparity was similar in both species-rich subfamilies. Skull shape diversity was phylogenetically conserved, whereas limb shape was more associated with ecology, particularly in fossorial species. Morphological differences between different limb bones were highly correlated, depicting high morphological integration. In contrast, overall limb and skull shape displayed semi-independence in morphological evolution, favouring the modularity hypothesis. Our results show how form can be correlated with function, with the evolution of limb shape being driven by selective pressures imposed by the environment and functional requirements of locomotion and behaviour. Our results also illustrate how morphological evolution can display varying degrees of independence across different modules, and that quantifying this is crucial in order to make accurate predictions of complex evolutionary processes.

Symposium — Fundamental aspects of the spatial associations, development, and birth defects of the muscles and skeleton in non-pentadactyl limbs (NPL)

Organizers: Virginia Abdala, Tiana Kohlsdorf, Rui Diogo

NPL1-1 9:30 am

Non-pentadactyly, soft and hard tissue associations, birth defects, and implications for medicine.

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Abstract: Signaling for limb bone development usually precedes that for muscle development, such that cartilage is generally present before muscle formation. It remains obscure, however, if: (i) tetrapods share a general, predictable spatial correlation between bones and muscles; and, if that is the case, if (ii) such a correlation would reflect an obligatory association between the signaling involved in skeletal and muscle morphogenesis. We address these issues here by using the results of a multidisciplinary analysis of the appendicular muscles of all major tetrapod groups integrating dissections, muscle antibody stainings, regenerative and ontogenetic analyses of fluorescently-labeled (GFP) animals, studies of non-pentadactyl human limbs related to birth defects, mathematical insights concerning for instance the possible display of a Turing-model type of mechanism associated with digit formation, and new, state-of-the-art systems biology tools such as anatomical network analyses. Our synthesis suggests that there is a consistent, surprising anatomical pattern in both normal and abnormal phenotypes, in which the identity and attachments of distal limb muscles are mainly related to the topological position, and not to the developmental primordium (anlage) or even the homeotic identity, of the digits to which they are attached, thus providing a starting point towards the resolution of a centuries-old question raised by authors such as Owen about the specific associations between limb bones and muscles. This question has crucial implications for evolutionary and developmental biology, and for human medicine because non-pentadactyly is the most common birth defect in human limbs. In particular, this synthesis paves the way for future developmental experimental and mechanistic studies, which are needed to clarify the processes that may be involved in the elaboration of the anatomical patterns described here, and to specifically test the hypothesis that distal limb muscle identity/attachment is mainly related to digit topology.

NPL1-2 10:00 am

The genetic basis of mammalian limb diversification.

Sears KE*, *University of Illinois*; Maier JA; Rivas-Astroza M; Cao X; Zhong S; Zhao K; Sinha S; Ma J; Behringer R; Cretekos C; Rasweiler J ksears2@illinois.edu

Abstract: From bat wings to horse hooves, mammalian limb diversification has been crucial to the evolutionary success of the group. Indirect evidence from studies of mammalian limb evolution suggests that mammalian limb diversification, including the frequent limb reduction that characterizes many mammalian groups, has not occurred primarily by the evolution of new genes, but by differential regulation of existing genes shared by all mammals and

inherited from an ancestral genetic toolkit. However, the specific genes and regulatory mutations that are responsible for limb diversification remain unknown for most mammalian groups. To begin to identify these genes and regulatory mutations, we used RNASeq to compare the transcriptomes of the developing limbs of several mammals, including pentadactyl mice, bats, and opossums, and tetradactyl pigs. Results suggest that gene expression varies more during later than earlier stages of limb development, both within and among species. Consistent with this, results suggest that the evolutionary age of each species' transcriptome decreases as developmental age increases. Within the more variable, later-expressed genes, we identified significant differences in the expression levels of HoxA and HoxD genes (N = 9) within and among species. WISH generally confirmed these RNASeq results, and uncovered key differences in expression domains as well. We used computational approaches to identify candidate enhancers for HoxA and HoxD genes, and functionally tested candidate enhancers using in vitro luciferase assays. Through this approach we identified several candidate enhancers with the potential to drive lineage-specific Hox expression levels. Taken together, our results support the hypothesis that the hierarchical nature of development translates into increasing variation as development progresses, and that divergence of Hox gene expression during these later stages of development plays a role in mammalian limb diversification.

NPL1-3 10:30 am

What determines the identity of the distal limb muscles? A myological analysis of mammals with digit reduction/digit loss.

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Abstract: Using the pentadactyl limb as a reference, muscles and bones are usually superimposed in a sharp spatial association. But does this spatial correlation reflect an obligatory association during morphogenesis? The somatic limb muscle progenitor cells apparently do not carry intrinsic positional information; the presence of the first tissue formed during limb development (condensations that will give rise to bones) may provide the positional signaling for the subsequent development of the muscles. According to this scenario, it can be expected that in non-pentadactyl limbs bones and muscles are still spatially superimposed. How the loss of bony structures affects muscle anatomy? Does the muscle reduction parallel the bone reduction in non-pentadactyl limbs? Addressing these questions will help us clarify the specific correlation existing between limb bones and muscles. However, the studies of limb development and evolution have emphasized skeletal tissues, while soft tissues such as muscles have been neglected. With those questions in mind, we dissected representatives of the main groups of mammals with different grades of digit reduction or digit loss to test the hypothesis that the identity and configuration of the autopodial muscles is mainly related to the topological position of the digits to which the muscles attach. Our results suggest that there is a consistent, anatomical pattern in which the identity of the muscles of the autopodium are mainly related to the topological position, and not to the developmental primordium (anlage) or even the homeotic identity, of the digits to which they are attached. Those results agree with previous studies focused on other tetrapod groups with non-pentadactyl as a wild-type phenotype, such as lizards, crocodiles, frogs, salamanders, and chickens, as well as humans with birth defects, and are therefore a new step towards the resolution of the old question about the specific associations between limb bones and muscles. Supported by CGL2014-52611-C2-2-P and PNPD/CAPES Brazil.

NPL2-1 11:30 am

Adapting the vertebrate limb neuromuscular system to changes in dactyly.

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Abstract: The morphology of the vertebrate limb has greatly diversified over the course of evolution, to accommodate for various modes of locomotion, as well as distinct uses of its most distal part, the autopod. In order to provide meaningful mobility, the formation and attachment of distinct limb muscle groups to their corresponding bony elements, as well as the correct innervation of these muscles by motoneurons, has to be tightly coordinated. This task is complicated by the diverse developmental origins of the limb's musculoskeletal system: the somites (muscle), lateral plate mesoderm (bone) and the spinal cord (motoneurons). While a pentadactyl state of the autopod is the norm amongst mammals, there is considerable variation outside of this clade. Moreover, in a number of human and other mammalian congenital disorders, the autopod skeleton deviates from this digit formula. Interestingly enough, however, in many of these cases the extra digits seem to be functionally incorporated into the musculoskeletal apparatus, i.e. they appear movable in a controlled fashion. The goal of our study is to understand how changes in the digit formula of the autopod skeleton are integrated with regards to its neuromuscular system. To do so, we are using mouse genetics, in particular the mutant Gli3-Xt as well as a conditional Prx1-Cre/Gli3 allele, and grafting experiments in chicken and emu embryos. We map out changes in embryonic musculature and muscle innervation patterns, and try to trace back the molecular identity of these additional neuromuscular units. Overall, we find distinct changes in the limb's neuromuscular system that seem to be largely dictated by skeletal topology. We discuss this

apparent developmental flexibility and its implication for evolutionary transitions in vertebrate digit formulas.

NPL2-2 12:00 pm

Ecomorphology and biomechanics of digit reduction.

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Abstract: Ecomorphology is the study area that correlates anatomical features to ecological variables. A classic example in comparative anatomy is the hand structure of mammals as diverse as humans, cetaceans, bats and horses. Such obvious links with ecology, in this case locomotor modes like walking, swimming, flying and running are easily stated and lead to adaptive story telling. In practice however, these patterns prove to be more difficult to assess. Comparative biomechanics is a mechanistic approach to study how structures are used to perform certain ecological tasks. One of the most notable features in a hand is the number of digits. A wide variety of mammals have diverged from the ancestral pentadactyl condition, with various degrees of digit reduction. Examples include artiodactyls, perissodactyls, xenarthrans and the extinct meridiungulates. We will use a simple theoretical geometrical model of a segmented limb of a running animal to determine the mechanical advantages and constraints on the number of digits. Changing the number of digits has consequences to the compression and bending strength of the hand, and to the inertial properties, which in turn might have consequences to cost of transport. We will demonstrate that even though intuitively digit reduction seems beneficial and straight forward in terms of COT that from a mechanical standpoint several trade-offs and constraints emerge that must have been at play during evolution. An extreme example of digit reduction is monodactyly. Equids (horses, asses and zebras) are the only extant monodactyl mammals. We will discuss the future direction of our projects currently underway, and how the evolution of equids fit into the context of comparative biomechanics.

NPL2-3 12:15 pm

Chameleon hand/foot clefting, a tweak on the pentadactyl design and a challenge to limb congenital malformations.

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Abstract: While a handful of vertebrate models have provided the majority of what we know about limb development, the recent wave of evolutionary developmental research has allowed for a seemingly exponential growth in taxa used in the lab to answer a variety of questions within a clinical and evolutionary framework. While squamate reptiles represent >33% of all living amniotes, very little is known about their embryonic development and how body plans within this group have diversified over the course of evolution. Within squamates, the chameleon body plan has been modified for a specialized lifestyle of arboreality and are structurally divergent from other terrestrial tetrapods with respect to the cranial, trunk, tail and limb skeletons. To begin to understand how the body plan of a chameleon develops, we take advantage of the slow development of the Veiled Chameleon (*Chamaeleo calyptratus*) to study the development of their split-hand/split-feet and ask the following questions. 1) At which developmental time point do we see a break from the typical pentadactyl phenotype? 2) Has early limb genetic patterning been modified? 3) How is hand/foot splitting being controlled? 4) How does our work on the veiled chameleon challenge what we know about congenital cleft formation in humans and other tetrapods?

NPL2-4 12:30 pm

Patterning and post-patterning modes of evolutionary digit loss in mammals.

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Abstract: A reduction in the number of digits has evolved many times in tetrapods, particularly in cursorial mammals that travel over deserts and plains, yet the underlying developmental mechanisms have remained elusive. Here we show that digit loss can occur both during early limb patterning and at later post-patterning stages of chondrogenesis. In the 'odd-toed' jerboa (*Dipus sagitta*) and horse and the 'even-toed' camel, extensive cell death sculpts the tissue around the remaining toes. In contrast, digit loss in the pig is orchestrated by earlier limb patterning mechanisms including downregulation of *Ptch1* expression but no increase in cell death. Together these data demonstrate remarkable plasticity in the mechanisms of vertebrate limb evolution and shed light on the complexity of morphological convergence, particularly within the artiodactyl lineage.

Contributed Session — Paleontology (PAL)

PAL1-1 2:30 pm

Puzzle of the earliest vertebrates: "Blessed are the meek"

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Abstract: Why are vertebrates such complex animals, compared to almost all the invertebrates? Some paleobiologists say vertebrate complexity arose when the prevertebrates evolved from filter feeders into predators.

However, the earliest fossil vertebrates such as the jawless Cambrian fishes *Haikouichthys* and *Metaspriggina* are unlikely to have been predators and more likely were filter feeders on food-rich remnants of “microbial mats” on the sea floor. The main predators of the Cambrian were arthropods, with their grasping, manipulative limbs. Both the arthropods and their vertebrate prey participated in the Cambrian’s “predatory arms race,” which led in both clades to rapidly improving distance senses, enlarging brains, increasing cognition, and more complex behaviors. It also led to the most basic, sensory, type of consciousness (having any kind of experience at all), although a better case can be made for consciousness in the first vertebrates than in the arthropods. But why did the limbless, jawless, unarmored, harmless, and rarer proto-vertebrates – so low on the food chain – exceed the arthropods and other invertebrates in brain complexity (many more neurons) and genomic complexity (two rounds of genomic duplication), with their larger genomic repertoire allowing more evolutionary innovations (such as the later evolution of the predatory, jawed vertebrates)? The proposed solution is two-fold. First, ancestral vertebrates were unusual filter feeders with access to highly concentrated and nutritious food particles in the patches of microbial mat. Second, they had superior locomotor motility based on their streamlined, myomere-propelled bodies, unhindered by a heavy or awkward exoskeleton of the arthropod type.

PAL1-2 2:45 pm

Osteology of the Cretaceous †Ctenothrissiformes and †Pattersonichthyiformes: clues to primitive structure in eurypterygian fishes.

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Abstract: Eurypterygian fishes contain over a third of extant vertebrate species and comprise three major lineages: the myctophiforms and acanthomorphs (collectively the ctenosquamates), and the aulopiforms. There are also a number of exclusively fossil eurypterygian groups, including †Ctenothrissiformes and †Pattersonichthyiformes. Relationships among the three major eurypterygian clades are clear, but there is no consensus as to how these extinct groups fit into this framework. We studied three fossil taxa: †*Aulolepis*, †*Ctenothrissa* (†Ctenothrissiformes) and †*Pattersonichthys* (†Pattersonichthyiformes), by re-examining fossils and visualizing internal anatomy using computed tomography (†*Aulolepis*). We developed a new morphological matrix, used in isolation and combined with a molecular dataset, in order to place the three fossil among living teleosts. Finally, we used topological hypothesis testing to evaluate contrasting systematic interpretations. We find strong support for a stem ctenosquamate placement for the two fossil groups, with two favoured topologies: 1) †ctenothrissiforms and †pattersonichthyiforms are a clade, 2) †ctenothrissiforms and †pattersonichthyiforms are a grade, with †*Ctenothrissa* closest to the ctenosquamate crown and †*Aulolepis* the most remote. We tentatively prefer the second hypothesis, which demands fewer independent derivations of morphological specializations. Our internal examination of these stem ctenosquamates suggests more complicated patterns of character evolution among eurypterygians than is suggested by living species alone. For example, we found that a key aulopiform synapomorphy, an enlarged uncinat process on the second epibranchial, is present in †*Aulolepis* suggesting that it is a eurypterygian synapomorphy subsequently lost in derived ctenosquamates.

PAL1-3 3:00 pm

A reconsideration of the aïstopod *Lethiscus stocki* (Tetrapoda: Lepospondyli) via micro-Computed Tomography (microCT), with implications for tetrapod phylogeny.

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Abstract: To investigate larger trends in tetrapod phylogeny, we revisited microCT dataset of *Lethiscus*, the oldest lepospondyl. Digital dissection shows for the first time fine structure of the skull, revealing previously unrecognized primitive morphology despite its derived body plan, including a spiracular notch, narrow, anteriorly-restricted parasphenoid, palatal fang-pit pairs, Meckelian ossifications, and previously noted deep circular atlantoccipital articulation. The braincase is elongate and atop a dorsally projecting septum of the parasphenoid, similar to what is seen in stem tetrapods such as embolomeres. This morphology is corroborated by that of a second aïstopod, *Coloraderpeton*. Lower jaw morphology is completely preserved, facilitating comparison with stem tetrapods. Phylogenetic analysis of a newly expanded matrix of early tetrapods, including critical new microsaurian braincase data, demonstrates lepospondyl polyphyly, placing aïstopods onto the tetrapod stem, whereas recumbirostrans are displaced into amniotes. These results show that stem tetrapods were much more diverse in their body plans than previously thought. Furthermore, our study requires a change in commonly used calibration dates for molecular analyses, and emphasizes the importance of taxonomic and character sampling for early tetrapod evolutionary relationships.

PAL1-4 3:15 pm

Morphological innovations in the earliest post-Devonian tetrapods: adaptations towards increasing terrestriality?

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Abstract: Although the earliest Carboniferous (early Mississippian) Tournaisian stage has been considered a

depauperate interval for vertebrates and particularly tetrapods (known as “Romer’s Gap”), our recent work has unearthed a rich and diverse suite of Tournaisian fossils from the UK. These include many new tetrapod genera, spread across the phylogenetic and morphological divide between Devonian and Carboniferous forms. While some retain plesiomorphic characters, others demonstrate a number of innovations to morphology that are seen for the first time in the Tournaisian tetrapods. 1) Parasphenoids that cross the ventral cranial fissure and underplate and fuse to the braincase base, in one case also underlying the basiptyergoid processes. This may relate to strengthening and consolidating the braincase as it is increasingly subjected to gravity and the forces of muscle contraction during head movements. 2) An exoccipital separate from the basioccipital in contrast to the conjoined ex- and basioccipital of more primitive tetrapods may relate to development of a more mobile occipital joint, also associated with more flexible head movement. 3) Deeply emarginated jugals may imply enlarged orbit and eye sizes compared to Devonian forms and suggest the increased importance of vision in terrestrial forms. 4) Humeri in which the foramen for the brachial artery and median nerve passes from the dorsal to the ventral side of entepicondyle. This is related to 5), humeri that show greater than 25 degree twist, related to increasing stride length, and 6) humeri in which the deltopectoral crest becomes more proximally placed and which show the development of a true shaft. 7) The earliest occurrence of a five-digit autopod. Some of these innovations, seen for the first time in small animals, may be directly linked to increasing terrestrialization among post-Devonian taxa.

PAL1-5 3:30 pm

A re-description of *Amphibamus grandiceps* (Temnospondyli: Dissorophoidea) from the Francis Creek shale, Mazon Creek, Illinois.

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Abstract: The Carboniferous temnospondyl *Amphibamus grandiceps* (Cope, 1865) is one of the oldest known members of Amphibamidae from the Middle Pennsylvanian aged (309 Mya) Mazon Creek deposits in Grundy County, Illinois, USA. *Amphibamus* was once considered a pivotal taxon in the debate over the origins of modern amphibians. It has since been usurped by the closely related amphibamids *Dolesempetron* and *Gerobatrachus*. Despite this, several features, including the presence of small pedicellate bicuspid teeth, an abbreviated skull table, reduced ribs, a pectoral girdle incorporating a small interclavicle and bar like clavicles, link *Amphibamus* to modern amphibians. Taxonomic revision of *Amphibamus* has been hindered by the loss of the original type specimen in a fire, and a lack of subsequent descriptive papers on significant specimens, including the near complete neotype YPM 799. In addition, many specimens from Mazon Creek have since been reassigned to *Amphibamus*, including *Micrerpeton caudatum* (Moodie, 1909), *Miobatrachus romeri* (Watson, 1940), *Mazonerpeton longicaudatum* (Moodie, 1912), as well as a variety of larval specimens. Many of these specimens vary in their morphology and their ontogenetic stages have not been assessed. Anatomical features including the shape of the skull and cranial elements, morphology of the terminal phalanges, length of the limbs, and number of caudal vertebrae (tail length) all remain unclear. Here we re-describe the neotype of *Amphibamus* and include a discussion of new anatomical and ontogenetic data from reassigned specimens. Exceptional preservation of soft tissues found in Mazon Creek nodules also allows for a new analysis of labile structures including the integument (scale impressions), and structures of the eye (scleral ossicles). A phylogenetic analysis including YPM 799 was performed for the first time, recovering it as the sister taxon to *Amphibamus*.

PAL1-6 3:45 pm

Evolution of genome size in recent and fossil salamanders.

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Abstract: Modern salamanders possess giant genomes, and directly correlated with this, the by far the largest cells among tetrapods. While no entire genome of a salamander has been sequenced thus far, recent studies have shown that large introns and novel genes contribute to the enormous genome sizes. The extreme cells size impacts many aspects of salamander biology and has been suggested to be closely associated with the enormous plasticity in life history pathways and their high regenerative capacity that includes limbs, eyes, spinal cord and other complex tissues. In the current study, we sectioned long bones (N>18, mostly femora) of members of all modern salamander families with known genome sizes as well as long bones of members of several fossil amphibian lineages to investigate (1) if the correlation between genome size and cell size that has been established based on leucocytes holds with respect to osteocyte size and (2) when within the long evolutionary history of the clade the large genome sizes evolved. For outgroup reference, we sampled femora of a number of modern amniote and frog taxa with known genome sizes. Understanding the correlation between osteocyte lacuna size and genome size in modern taxa is vital for an investigation of the genome sizes in fossil taxa. In order to minimize errors caused by variation in location and orientation of sections, we aimed to sample homologous elements in the same location and the same plane of sectioning. Our results show that genome size and osteocyte size are tightly correlated in salamanders. Moreover, the large genomes of urodeles were already present in stem-group salamanders (Karaauridae) and most likely evolved early in the evolutionary history of the salamander lineage, possibly as early as Paleozoic dissorophoid

temnospondyls. This provides new insights into the deep time genomic evolution of urodeles and a novel dataset for understanding salamander origins and the evolution of central aspects of their biology, such as life history patterns, miniaturization, and developmental rates.

PAL2-1 4:30 pm

A new important stage in the evolution of the turtle body plan.

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Abstract: The phylogenetic relationships of turtles have been a particularly contentious issue in the study of vertebrate evolution. This is due to conflicting evidence from molecular and anatomical data but also a lack of transitional fossils from the critical time interval. The stem-turtle *Odontochelys*, from the early Late Triassic (~220 mya) of China, has a partially formed shell with an already fully developed plastron and other turtle-like features in its postcranial skeleton. Unlike *Proganochelys*, from the Late Triassic (214 mya) of Germany and Thailand, it retains marginal teeth and lacks a complete carapace. A large temporal gap separates *Odontochelys* from *Eunotosaurus*, from the late Middle Permian (~260 mya) of South Africa, which has been plausibly hypothesized as the oldest known stem-turtle. The recently discovered *Pappochelys*, from the late Middle Triassic (~240 mya) of Germany, represents a structural and chronological intermediate between *Eunotosaurus* and *Odontochelys*. It shares with the latter two taxa the possession of anteroposteriorly broad trunk ribs that are T-shaped in cross-section and bear sculpturing, elongate dorsal centra, and modified limb girdles. Unlike *Odontochelys*, *Pappochelys* has a cuirass of robust paired gastralia but no plastron. It provides new evidence for the hypothesis that the more posterior portion of the plastron formed through serial fusion of gastralia. Except for the modified trunk ribs *Pappochelys* has no carapace. The cranium of *Pappochelys* has upper and lower temporal fenestrae as well as a suborbital foramen, supporting diapsid affinities for turtles. The upper and lower jaws bear teeth. Phylogenetic analysis found Pantestudines as the sister-group of Sauropterygia and, in turn, this pair as the sister-taxon of Lepidosauriformes. However, statistical support for this result is not strong, at least in part due to our still inadequate knowledge of basal saurians.

PAL2-2 4:45 pm

Macroevolution of the crocodylomorphs.

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Abstract: Extant crocodylians might be considered something of a failure. Since the emergence of the Crocodylomorpha in the Late Triassic their diversity has declined to just 23 species, compared to over 10,000 species in their sister clade, the birds. The extant crocodylians also show low morphological disparity, with all species being semi-aquatic ambush predators with a similar body plan. This low diversity and long fossil range has led to the crocodylians being described as 'living fossils', but is this justified? The Crocodylomorpha in the fossil record show great morphological diversity, including terrestrial, cursorial, fossorial and marine forms, insectivores, omnivores, herbivores and durophages. In this study we present a new super tree phylogeny of the Crocodylomorpha and evaluate the tempo and mode of crocodylomorph evolution using morphology. We find extreme conservatism of in the evolution of body size in the Crocodylomorpha and a number of its subclades. Rates of evolution are predominantly stable, but punctuated by environmental changes with rate-shifts in the crown-group associated with mass extinctions. Time-series modelling of Crocodylomorph diversity and morphological disparity compared with environmental variables finds evolution to be driven and constrained by temperature and the diversity of competing clades such as dinosaurs. We conclude that the Crocodylomorpha adhere strongly to the punctuated equilibrium and Court-Jester models of evolution. Therefore the limited diversity and disparity of the extant Crocodylomorpha is likely a reflection of their rather narrow range of ecological tolerances when compared to birds, and massively changed global environmental conditions that restrict the potential diversity of the group today.

PAL2-3 5:00 pm

Ornithischian dinosaur 'cheeks' are evolutionary epiphenomena of previously undescribed reorganization and enlargement of jaw musculature.

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Abstract: Numerous jaw muscle reconstructions in ornithischian dinosaurs have influenced over a century of jaw mechanics studies. These reconstructions, although loyal to extant phylogenetic bracketing (EPB), pose concerns of small adductor muscle bodies and caudally displaced insertions relative to mandibular proportions. Also, the presence of a buccal dental emargination bounded by a lateral dentary ridge (LDR) has led to reconstructions of novel buccinator-like 'cheeks', a trait requiring unlikely muscle differentiation and fiber reorientation. Here I present a new interpretation of jaw muscle anatomy in ornithischians with in-depth examination of osteological correlates and muscle scars in taxa spanning the entire clade, with reference to EPB. M. adductor mandibulae externus (mAME), a major jaw muscle group, has historically been reconstructed as inserting along the apex and caudal margin of the coronoid process. Although this is likely for deeper layers, the most superficial mAME layer is reconstructed here as a rostralateral expansion of muscle along the coronoid process and its rostrally extending margin creating the LDR, a trait observed in some extant lepidosaurs with coronoid processes. Laterally flaring jugals in ornithischians, especially ceratopsids, create an opening allowing direct communication between the endocranial adductor chamber and the LDR. MAME exits this opening and fibers insert as a large muscle fan along the LDR extending farther rostrally than

previously proposed. This new mAME reconstruction rejects a novel buccinator-like muscle and repurposes mAME as a major jaw adductor, cradling the jaw bilaterally, as well as a secondarily functional 'cheek' containing food within the oral cavity. Along with reorientation of pterygoideus musculature accommodating for orthal components, this new mAME reconstruction holds new and important implications for much stronger orthopalinal feeding strokes and long-axis dentary rotation in ornithischian jaw mechanics.

PAL2-4 5:15 pm

Distribution of purported cursorial adaptations in Mesozoic theropod dinosaurs through phylogeny, time, and space.

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Abstract: Cursoriality is broadly defined as adaptations towards increased terrestrial locomotor performance at less energetic cost. One such clade which has been previously studied is Theropoda (the carnivorous dinosaurs and their descendants, including birds). Exclusive of the fully volant birds (the clade Ornithothoraces, containing crown-group birds Aves), terrestrial theropods were striding obligate bipeds with a parasagittal stance, despite a size range of <1 to over 8000 kg. But within this group osteological traits associated with cursoriality are variably developed. The present analysis examines these traits in the context of increased knowledge of theropod diversity (especially the early branches of lineages long known from the Late Cretaceous); of new comparative techniques to reconstruct the trait evolution, and new more phylogenetically-informed myology of the pelvic-hindlimb-caudal complex. A new species-level supertree of theropod dinosaurs and their outgroups is assembled. Traits affiliated with increased locomotory performance are mapped onto this tree. These include: proportional increases in the pre- and postacetabular portions of the ilium from the ancestral condition; elongation of the distal limb elements (tibia; metatarsus); alternative morphologies interlocking and reducing the mediolateral width of the metatarsus; size and position of the lesser and fourth trochanters; and size and distribution of the caudal transverse processes. These traits are not randomly distributed, but phylogenetically co-associated. Clades in which they are strongly expressed are the Jurassic "elaphrosaurs" and Cretaceous Noasauridae within Ceratosauria, sporadically expressed in Oviraptorosauria and Troodontidae within Maniraptora, and especially well-developed Tyrannosauridae, Ornithomimidae, and Parvicursorinae in basal Coelurosauria. The strongest examples are present only in the Late Cretaceous Asian (Asia plus North America) landmass.

PAL2-5 5:30 pm

Measuring morphological diversity and tempo using discrete characters: advantages and disadvantages of including additional phylogenetic information.

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Abstract: Discrete characters offer a rich resource of morphological data, the ability to compare extremely disparate organisms, and a mature set of tools for dealing with missing data. In addition, they offer the opportunity to ask questions relating to both morphological diversity (often termed simply "disparity") and tempo. Here I present two case studies exploring how the combination of discrete characters and phylogeny affects: 1) properties of an ordination ("phyломorphospace"), and 2) time series of evolutionary rate. The respective data sets are: 1) a coelurosaurian theropod dinosaur matrix of 152 taxa and 853 characters, and 2) a lungfish matrix of 86 taxa and 91 characters, and I used the recent R package Claddis for all analyses. For the former case I compared five different phyломorphospaces using scree and ordination plots, time series, and correlations. Overall, these suggested a pre-ordination ancestral state reconstruction that limits the amount of missing data estimated should be favoured as this minimises the amount of introduced phylogenetic signal. For the latter case I compared four different time series using the Wobble Index of Alroy, showing that use of a likelihood algorithm and a rudimentary correction for missing data creates dramatically smoother time series than a parsimony algorithm and no correction. In conclusion, the usage of phylogenetic data in analysing morphological diversity and tempo offers some clear benefits. However, results are highly contingent on algorithm choice and at present clear optimality criteria for comparative tests can be hard to identify.

PAL2-6 5:45 pm

Dynamics of morphological evolution in Cretaceous and Paleocene eutherian mammals.

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Abstract: The end-Cretaceous mass extinction marks a transition in mammal evolution from small Cretaceous taxa to more diverse faunas of larger taxa in the Cenozoic. Despite this, many studies have found no change in evolutionary parameters across the Cretaceous-Paleogene (K-Pg) boundary, although few of these studies have explicitly considered early Paleogene taxa, largely due to a lack of a resolved phylogeny. We conducted the largest phylogenetic analysis (177 taxa) of Paleocene placentals to date. We dated the resulting trees using a recently described stochastic method, predicting a latest Cretaceous origin of Placentalia, but earliest Paleocene interordinal diversification. We reconstructed ancestral states for 680 characters and binned character transitions, identifying significant increases in rate of evolution at the K-Pg boundary and at the origin of Placentalia. We binned morphologies of ancestral nodes as well as those of the tips, and estimated morphological disparity for Cretaceous and Paleogene time bins. Range-based disparity metrics were low in the Cretaceous, but increased at the K-Pg

boundary. Variance-based metrics were stable during the Cretaceous, decreased from the Campanian to the Maastrichtian, before increasing only in the middle Paleocene. We reconstructed body size for all sampled taxa, testing several models of evolution. Our results support an increase in rate of body size evolution at the origin of Placentalia. Combined, these results suggest a three phase model of eutherian morphological evolution. First, extinction of most stem eutherians in the Campanian, alongside a diversification of near-crown eutherians and early Placentalia and an increase in rate of body size evolution. Second, further extinction of stem eutherians at the K-Pg boundary, rapid diversification of Placentalia and exploration of morphospace. Third, niche specialisation and morphospace clustering through the Paleogene. Together, our results support the diversification of Placentalia as an archetypal adaptive radiation.

PAL3-1 9:30 am

Intraspecific variation and the evolution of the ancestral dinosaurian growth condition.

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Abstract: Understanding growth patterns of extinct clades has been a persistent problem in vertebrate paleontology, especially for dinosaurs and other archosaurs, which possess the widest range of body sizes and growth rates of any group of terrestrial vertebrates. Determining the ontogenetic stage of an individual is important for paleontological interpretation, but there are few non-destructive methods for determining skeletal maturity. Understanding the ancestral dinosaurian growth condition is vital to interpreting the evolution of this clade. To better understand this question, I analyzed 29 ontogenetically variable characters in the early theropod dinosaurs *Coelophysis bauri* and *Megapnosaurus rhodesiensis*. These taxa are temporally and phylogenetically close to the origin of dinosaurs and are known from large growth series from single populations. I used ontogenetic sequence analysis to reconstruct growth pathways and quantify the amount of intraspecific variation in growth, then used non-metric multidimensional scaling (NMDS) to test if these characters vary continuously. These data suggest a high level of intraspecific variation, with >50 equally parsimonious developmental sequences found for these taxa. NMDS analysis found a single cluster of individuals with no evidence of bimodality, suggestive that these characters are not dimorphic. In these results, size is a poor predictor of skeletal maturity. Variation in growth patterns is widespread among early dinosaurs and other dinosauriforms, suggesting that this high level of variation in growth is the ancestral dinosaurian condition. Given that strong variation in ontogeny is absent in more derived theropods (e.g., Coelurosauria), this intraspecific variation was lost during the evolution to living birds. Such variable characters should be used with care in cladistic analyses. High variation should be assumed in early dinosaur taxa and may not be indicative of taxonomic diversity or sexual difference.

PAL3-2 9:45 am

Wing-bone thickness and bending resistance in pterosaurs.

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Abstract: Pterosaurs were both the first true flying vertebrates, and the largest animals to fly, with wingspans up to 11m. They have long been studied for their biomechanics and flight capabilities, especially the larger species. Classical and recent literature describe pterosaurs as having extremely thin-walled bones, particularly in proportion to the bone diameter, (except for known outliers like dsungaripteroids), as well as having the highest degree of pneumaticity of any animals. A new large-scale comparative dataset was analysed to test this proposition. Over 60 pterosaur wing bones from several families were studied. Air/marrow space proportion (ASP/MSP) and radius/thickness (R/t) values were calculated and compared to previous studies. Pterosaur ASP and MSP values range from 0.12 in apneumatized bones to 0.90 in highly pneumatized bones. The lower ASP and MSP values are similar to those seen in extant birds, while higher values remain greater than those seen in any other animal. Contrary to previous studies, there is a high occurrence of low R/t values in pterosaurs (R/t between 1 and 7.99) with 75% of values falling within this range, more similar to R/t values seen in birds, with smaller animals having the lower R/t values. R/t values and diameter are related to the Second Moment of Area (I), a geometrical property correlated with bending stiffness, an important property of pterosaur wing bones supporting flight loads. I varies with the fourth power of diameter, with values ranging from as low as 30 mm⁴ for small diameter thick-walled pterosaur bones to 17,000 mm⁴ for large thin-walled pterosaur wing bones. The allometry of scaling dictates that mass reduction becomes increasingly important with size. Consequently as pterosaurs become larger, the bone wall thickness is reduced relative to overall diameter, providing adequate bending stiffness in combination with relatively low mass, at the cost of increased bone fragility.

PAL3-3 10:00 am

Evolutionary increases in vertebral regionalization within the mammalian lineage: evidence from fossil synapsids.

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Abstract: Tetrapods primitively have a vertebral column that is divided into distinct neck (cervical vertebrae) and trunk (dorsal vertebrae) regions. In contrast, strong regionalization of dorsal vertebrae into thoracic (ribbed) and lumbar (ribless) regions is thought to be an independently derived feature of mammals and archosaurs. Recently,

however, subtle regionalization has also been found in the trunks of lepidosaurs that corresponds to HOX expression boundaries, suggesting that underlying regionalization patterns may be more universal than previously thought. To resolve the evolutionary origin of the strongly differentiated trunk in mammals, we determined the degree of regionalization in their extinct stem-group, the non-mammalian synapsids. Axial regionalization was measured in non-mammalian synapsids, extant mammals and sauropsids, using a likelihood-based method that requires no a priori knowledge of region boundaries. Vertebral shape was quantified using linear measures, and multivariate segmented regressions were used to model variation in all possible vertebral regions. Finally, the 'best' model for region boundaries was selected from the data using the Akaike Information Criterion based on regression residuals. Among extant species, we find support for four presacral regions in mammals, archosaurs and lepidosaurs, reflecting cervical, cervicothoracic, anterior dorsal and posterior dorsal modules; irrespective of the presence of a ribless lumbar region. Conversely, non-mammalian synapsids show more variable regionalization patterns, with a minimum of two regions in basal "pelycosaurs" and up to four in advanced non-mammalian cynodonts. Thus, despite the ubiquity of regionalization among extant amniotes, our data suggest increasing regionalization through synapsid evolution, and raises questions about the ancestral amniote condition for axial patterning.

PAL3-4 10:15 am

The cave bear story: integrating paleontological and developmental evidence.

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Abstract: The fields of paleontology and developmental biology contribute the significant element of time to evolutionary theory. Though these timescales differ greatly, the integration of these disciplines is key to understanding mechanisms of morphologic expression and evolutionary change. Paleontological data, especially fossil collections, provide our only direct evidence of past biodiversity and how individual species, communities, and ecosystems respond to environmental change on evolutionary and long-term ecological timescales. The development of proxies and models for predicting environmental or genetic stress associated with extinction is a major research challenge and has important economic and societal implications. The European cave bear, *Ursus spelaeus*, was part of the Pleistocene megafauna that went extinct during the Last Glacial Maximum. Why the cave bear went extinct, whereas other bears such as the brown bear did not, has been a central question in evolutionary biology. In our study of the evolution and development of the dentition in bears, we try to understand not only morphological variation, but also extinction. The shape of the mammalian dentition, which is determined prior to eruption and modified only by wear, is strongly correlated with diet. Tooth shape can be described by the patterns of cusps that compose the crown, or chewing surface, of the tooth. We use a metric called dental complexity to reconstruct the diet of cave bears and develop a system whereby dental variation can be measured as an indicator of environmental and genetic stress in a population.

PAL3-5 10:30 am

Morphometry and behavioural biology: As seen in the humerus of Pleistocene tiger

(*Panthera cf. tigris* Pocock 1929) from Manjra Valley, India.

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Abstract: The palaeobiogeography of large predators in India is largely based on scanty and fragmented fossil materials. In fact, carnivore fauna in Indian Pleistocene is mostly elusive and as a result any interpretation of their behavioural biology tends to be theoretical and conjectural. Presently in India, the niche of apex predator is almost always filled by large felids, while canids have occupied a secondary level in the trophic system. Therefore, the study of predator biology and behaviour in Pleistocene fauna must look extensively at large felid fossils, at least at this initial stage. It is here that the recent discovery of a well-preserved, almost complete humerus of *Panthera cf. tigris* from Pleistocene formations in the Manjra River valley near Harwadi (Latur dist. Maharashtra), is of particular interest, since it provides a hitherto unprecedented potential for systematic palaeontology and morphometric analysis. Its state of preservation has allowed a near-complete set of measurements, which have hitherto not been available given the paucity of the fossil record of carnivore specimens in India. The availability of a humerus is an additional convenience since the humerus is an important element in the biomechanics of any animal, particularly one as mobile and active as the tiger. Studies have been carried out on the connection between humerus morphometry and behavioural biology of various felid species, such as the recent study by Meloro and his team, which compared the humerus measurements of several different felid species worldwide. This was done as an attempt to correlate the morphology of various parts of the humerus with certain activities and behaviour involving predation and hunting patterns of the respective felids. The present study utilises a similar methodology in measuring the aforementioned specimen from Harwadi and offers some insights into the behavioural biology of Pleistocene tiger in India.

PAL3-6 10:45 am

Evolution and function of the angular process in early mammalian jaws.

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Abstract: The lower jaws of mammaliaforms of the Mesozoic Era (252-66 million years ago) have shown disparate morphologies, and it is expected that such major differences correlate with modifications in biomechanical functions. To address this issue I use fossil data to analyze morphological and functional changes in lower jaws of mammaliaforms and early mammals. In particular, I focus on the angular process, which is functionally important as the insertion site for two primary jaw adductor muscles: the medial pterygoid and the superficial masseter. Morphometric analyses are used to establish macroevolutionary trends. A key result is that the angular process of cladotherians (i.e., eutherian-placentals, metatherian-marsupials, and eupantotherians) does not appear to be homologous with the angular process of non-mammalian mammaliaforms (e.g., *Morganucodon*), and the process is more posteriorly positioned in cladotherians. The results of the morphometric analyses are used as the framework for three-dimensional modeling to examine the functional effects of evolutionary changes to the angular process. The position and size of the process is artificially manipulated to mimic evolutionary changes, and relative mechanical advantages of jaw adductor muscles are calculated. Results indicate that the posterior extension of the cladotherian angular process reduces the mechanical advantage for orthal jaw moments. However, molar morphologies of cladotherians suggest that the chewing cycle is not purely orthal, and instead includes mediolateral movement, which is likely produced by rotation around a vertical axis of rotation. When the jaw model is restricted to this type of rotational movement, the presence of a posterior angular process increases the mechanical advantages by lengthening the moment arms of the jaw adductor muscles. These results suggest that molar and jaw morphologies evolved in concert to produce a more complex chewing cycle involving increased mediolateral movement.

PAL4-1 11:30 am

Extreme longirostry in Miocene odontocetes: the ecomorphology and biomechanics underlying the repeated evolution of a superlative snout.

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Abstract: Different odontocete lineages evolved cranial elongation during the Miocene, resulting in skulls that are proportionally more extreme than any living or extinct aquatic tetrapod. In some taxa, the rostrum comprises as much as 80% of total skull length; others have as many as 350 tooth sockets in the cranium and mandible combined. In this study, we CT scanned a range of long-snouted fossil odontocetes from the middle and late Miocene, including *Parapontoporia sternbergi*, *Xiphiacetus bossi*, *Pomatodelphis inaequalis*, *Zarhinocetus errabundus* and *Zarhachis flagellator*, to characterise and quantify their extreme morphology, which provides a basis for inferring performance and behaviour. We used beam theory to predict the biomechanical limitations of this morphological specialisation compared to extant pelagic longirostral taxa, including odontocetes and billfishes. Predicted stress in the rostrum of some fossil taxa is higher than those found in extant odontocetes, indicating a more limited dietary niche. Second moment of area of rostral cross sections from the CT data also show that there is substantial variation in the shape of the rostrum between fossil species. Dorsally flattened taxa such as *Zarhachis flagellator* and *Pomatodelphis inaequalis* likely fed using lateral rostral sweeps. In contrast, *Xiphiacetus bossi* appears to be convergent on the cranial morphology of swordfish, using an elongate rostrum to sweep in a wide range of directions. The repeated and phylogenetically disparate origin of longirostry among odontocetes raises questions about how it evolved, and why such extreme longirostry went extinct. Given our results, we suggest that these traits likely originated in association with prey capture, potentially fast-start swimming fish. For several coeval middle Miocene taxa, eustatic sea level maxima and high ocean temperatures might have provided ideal environments the evolution of this cranial morphology in odontocetes.

PAL4-2 11:45 am

Morphological consequences of tooth loss: A comparison of the course of the mandibular canal in mysticete cetaceans using 3D models.

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Abstract: Mysticete cetaceans (baleen whales) are a diverse and successful clade of mammals that have evolved to include the largest animals in the history of the earth. The success of this clade has been, in large part, to a shift in their feeding mechanism. Over their evolutionary history mysticete cetaceans lost functional teeth and instead evolved baleen plates. These keratinous structures hang down from the palate and allow mysticetes to bulk filter feed on small to medium sized prey. While baleen plates replace the dentition of the palate, no secondary structure is developed in the mandible whatsoever. Though tooth buds are known to form in embryonic mysticetes, they are completely resorbed prior to birth. The result is an entirely edentulous mandible in mysticete cetaceans. Despite the lack of teeth, a shallow alveolar groove persists on the dorsomedial surface of the mandible. The internal anatomy of the mandible, specifically the course of the mandibular canal and any connections made with the alveolar groove, have never been studied and described. Here, we use computed tomography scans to create 3D models of the internal anatomy of the mandibles of a typical artiodactyl (*Sus scrofa*), an archaeocete cetacean (*Zygorhiza kochii*), and an extant mysticete (*Balaenoptera acutorostrata*). In doing so, we compare the internal anatomy of the mandible by charting the course of the mandibular canal and all of its distributaries. Our results confirm a highly unique morphology in the mandibles of mysticete cetaceans compared to their artiodactyl relatives and archaeocete

ancestors. Our results verify the persistence of dorsomedial branches of the mandibular canal to feed the alveolar groove.

PAL4-3 12:00 pm

The diversity and evolution of supraorbital crests in Platanistoidea (Cetacea: Odontoceti), and their implications for echolocation.

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Abstract: Cetacean skulls are dramatically different in construction from their closest mammalian relatives. Many skull elements are posteriorly "telescoped" with overlapping of facial bones that were once adjacent in ancestral configurations. In odontocetes, telescoping has layered the maxilla over the frontals in the antorbital notch region. This coincides in some groups with supraorbital crests surrounding the melon, an organ involved in sound generation. The most elaborate crests occur in the Ganges and Indus River dolphin (*Platanista* spp.), where they rise above the level of the nuchal crest as heavily pneumatized, extremely thin wings. Their position wrapping around the melon suggests that they may be involved in the generation or propagation of sound in the head (though this hypothesis is difficult to test). Supraorbital crests also appear in other lineages (e.g., Ziphiidae, Iniodea) but are composed of different skull elements and are less extreme than in *Platanista*. To better understand the origin of the crests in this lineage, we examined the supraorbital crests in a group phylogenetically allied with *Platanista*. Termed Platanistoidea, this group of cetaceans spans from the Oligocene to the present, including almost exclusively marine forms. We measured the physical extent of their crests and categorized the crests' position relative to key skull elements. In addition, we used computed tomography to examine the internal morphology and relative bone density of the crests. Preliminary results reveal that marine fossil platanistoids, such as *Pomatodelphis* and *Zarhachis*, have elevated, robust crests that do not exhibit pneumatization as *Platanista* does. Oligocene platanistoids, older and with smaller crests, also show no patent pneumatization. We propose that the elaboration and pneumatization of the crests in *Platanista* is a relatively recent innovation, plausibly linked with the reinvasion of freshwater river systems.

PAL4-4 12:15 pm

Digital reduction patterns in terrestrial artiodactyls: how many mechanisms?

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Abstract: Artiodactyls show strong reduction of lateral digits around the paraxonic axis to varying degrees. This pattern had been used early on as a phylogenetic character, with the general assumption that digit reduction and loss should be irreversible, but more recent phylogenetic work and additional fossil material has shown this to be improbable. Digit reduction seems to have followed a complex evolutionary pathway among lineages. The first digits of both fore and hindfeet have been lost at least three times, while reduction of the side toes shows a minimum of four disparate morphologies: digits 2 and 5 reduced in diameter to less than half of the median digits, but similar in length to digits 3-4; digits 2 and 5 reduced in length, but similar in diameter to digits 3-4; digits 2 and 5 reduced to metapodial splints or nodules, lacking phalanges; and, rarely, asymmetrical reduction of digit 5 to a nodule with a full-sized digit 2. Developmental work on digit reduction in pigs, cows and camelids shows that more than one developmental trajectory can produce reduction of lateral toes (Cooper, 2014; Lopez-Rios et al. 2014). In both pigs and cows, derived changes in early patterning established by *Shh* have resulted in the reduction of lateral toes without extensive apoptosis in the lateral limb bud. In camelids, the developing limb bud shows the ancestral patterning of *Shh*, with extensive apoptotic activity in the lateral digits. Because these living clades of terrestrial artiodactyls show different mechanisms of digital reduction, this suggests a basis for convergence in digit reduction. The complex patterns of digit reduction found among extinct taxa highlights the possibility that additional potential developmental mechanisms for digit reduction may have existed.

PAL4-5 12:30 pm

Beam mechanics of digit reduction in fossil horses.

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Abstract: The evolutionary history of equids is a classic story—initially told as a straightforward, orthogenetic progression from small to large, many- to single-toed, low-crowned teeth to hypsodont teeth, and browsing to grazing. While the relationship between hypsodonty and the spread of grasslands has since been shown to be less than linear, few studies have quantitatively approached related hypotheses about digit reduction. Proposed drivers for the transition to a single toe include locomotor economy, speed and straight-line locomotion, and increased body mass. To investigate this last hypothesis, we modeled the beam mechanics of metapodials through the evolutionary history of horses using micro-CT scans. Taxa include *Hyracotherium* (tetra- and tridactyl), *Equus* (monodactyl), and six other fossil equids at varying stages of digit reduction. We analyzed stresses in compression and bending under simulated body-weight loads, both in forward locomotion and lateral dodging. Without accounting for the lateral toes offloading some force, stresses at midshaft in tridactyl horses surpass the tensile strength of bone, with the exception of later horses with more reduced digits, such as *Neohipparion*. If the force is scaled according to "toedness index," a measure of the relative proportions of the digits, all equid metapodials experience similar low levels of stress when

loaded. Finally, we make forelimb-hindlimb comparisons, with the hypothesis that if body weight is a mechanical driver of digit reduction, evolutionary shifts should appear first in the forelimb because it carries more weight. We conclude that selection for reduced distal limb mass, combined with the mechanical demands of increasing body mass, is a plausible driver for digit reduction in equids. Future work incorporating gait data from extant tapir (a perissodactyl with the same digit configuration as *Hyracotherium*) and wild equids will provide more nuanced force and digit loading data.

PAL4-6 12:45 pm

Limb evolution of North American Equidae.

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Abstract: The pattern of environmental change throughout the Cenozoic is characterized by a trend toward increasing ecological dominance of open habitats (e.g., grasslands) at the expense of closed habitats (e.g., forests). Numerous lines of evidence constrain the spatial and temporal pattern of this transition. Traditionally, the radiation of hypsodont horses in North America has been assumed to signal the spread of open, grass-dominated environments. However, grass phytoliths show a rise in the numerical abundance of open-habitat grasses at least 4My earlier. A possible reason for this discrepancy is that dental evolution was slow to respond to the spread of grass-dominated environments. Limb evolution might show a more immediate response to the spread of open environments. Many studies of extant taxa demonstrate a link between morphology of the limb skeleton and habitat, which are corroborated by biomechanical studies of locomotion. Studies of fossil taxa have leveraged these relationships to establish patterns of limb evolution within clades of mammals in the context of Cenozoic environmental changes. In this study, we analyze the evolution of limb evolution in the family Equidae. We use both linear measurements and geometric morphometrics to quantify the morphology of six limb elements. We use a dated estimate of North American equid phylogeny to estimate rates between 55 and 5 Ma, spanning most of horse evolution in North America. Our results show a generally low rate of evolution between 35 and 25Ma, followed by a rapid increase in evolutionary rate that persists across the Oligocene/Miocene boundary. This rapid increase is coincident with estimates of grassland expansion based on phytoliths, and precedes the radiation of hypsodont horses. These results also corroborate previous studies of ungulate limb evolution and suggest that limb evolution might be more sensitive to environmental change than dental evolution.

PAL5-1 2:30 pm

The cartilage cone of archosauromorphs: biomechanical implications for hip joint loading and femoral ossification.

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Abstract: The cartilage cone is a convex extension of the epiphyseal hyaline cartilage that inserts into the metaphyseal growth plate of long bones. Among extant archosaurs, the cartilage cone results from delayed endochondral ossification relative to perichondral ossification during embryological development, and is absent in neonates. In contrast, the proximal femora of many post-neonatal fossil archosauromorphs possess evidence of uncalcified cartilage cones. This study investigated the evolutionary transitions, functional roles, and ontogenetic significance of the cartilage cone in archosauromorphs. Femora of 140 taxa were studied and digitized. Key phylogenetic transitions in cartilage morphology were estimated using likelihood ancestral state reconstruction on the osteological correlates, and analyzed using phylogenetically corrected correlation to reveal trends in body size evolution. The cartilage cone arose independently in multiple lineages, including dinosauriforms and paracrocodylomorphs, but was secondarily reduced in sauropods, theropods, crocodylomorphs, and phytosaurs. Although adult body size does not predict the presence of the cartilage cone, it is often absent in large adults but persist in locomotor patent conspecific juveniles. The cartilage cone likely provided mechanical support to the thick epiphyseal hyaline cartilage against tensile and shear strain by increasing metaphyseal surface contact. In sauropods and phytosaurs, reduction of the cone coincides with highly rugose growth plates; whereas reduction of the cone in theropods coincides with smooth growth plates. These divergent adaptations are hypothesized to associate with transitions in cartilage thickness and locomotor-induced loading regimes. Overall this study indicates that multiple lineages of basal archosauromorphs used uncalcified hyaline cartilage as load bearing tissues on par with subchondral bones, illustrating a key innovation in locomotor tissues.

PAL5-2 2:45 pm

Developmental trajectories of convergence, recapitulation, and evolutionary novelty in the crocodylian skull.

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Abstract: The crocodylian skull is a unique and complex structure that has been extensively used in phylogenetic and functional studies, and it has served as a model system for interpreting the paleobiology of extinct species. Despite this great interest, we still know very little about how the crocodylian skull evolved or how it is shaped through development. Here we present a geometric morphometric (GMM) analysis that integrates and explores the ontogeny

of craniofacial development in extant crocodylian species. Our dataset includes embryonic series for nine species that represent all major adult cranial shapes found in extant crocodylians (i.e., generalized, slender-snouted, and blunt-snouted), as well as post-hatchling ontogenetic series for all extant crocodylian species. Our shape analysis finds that all embryonic specimens cluster together in a unique region of morphospace characterized by blunt rostra, even though adult alligatorids, crocodylids, and *Gavialis* occupy distinct regions. Slender-snouted crocodylids and *Tomistoma* have similar ontogenetic trajectories, suggesting a shared developmental pattern. However, the ontogenetic trajectory for *Gavialis* proceeds in the opposite direction. These results suggest the long, slender snout of *Gavialis* may have developed via a novel developmental pathway. In addition, analysis of the palate appears to “recapitulate” the evolutionary modification of the internal nares, with the opening moving posteriorly through development, and only later exiting through the pterygoid. Overall, our data suggest that ontogenetic changes in the crocodylian palate better reflect crocodylomorph evolution, while snout shape captures later, crown group, evolutionary divergence. We intend to test this further by incorporating fossil taxa, from across the crocodylomorph clade, into our shape morphospace.

PAL5-3 3:00 pm

Evolution of the flexible avian neck: insights from 3D cervical joint kinematics in wild turkeys.

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Abstract: Birds have extremely flexible necks, as demonstrated by the variety of elaborate poses they adopt during preening, feeding, and sleeping. Evolution of this flexible musculoskeletal system from non-avian theropod dinosaurs is not well-understood – particularly the acquired capacity to achieve complicated neck configurations. Historically, measuring inter-vertebral joint motion in the neck has been challenging, due to overlying skin, abundance of soft tissue, and the numerous serially repeating, inter-articulating bones. To overcome these obstacles, we used X-ray Reconstruction of Moving Morphology (XROMM) to measure 3D joint kinematics during simple (e.g. dorsoventral/lateral bending) and complex (e.g. multiple-axis twisting, looking over shoulder) neck maneuvers in cadaveric wild turkeys (*Meleagris gallopavo*), with soft tissues intact (e.g. skin, muscle, ligament). Our results reveal that inter-vertebral joint movements are not strongly regionalized, although the middle portion of the neck (C5-C6, C7-C8) appears to be somewhat less flexible than other regions. Furthermore, joints in the middle portion appear to work together, rotating similarly to achieve poses, while cranial and caudal joints behave more independently. We recorded torsion in joints caudal to the atlas-axis complex (C3-C4, C4-C5), indicating that heterocoelous centra do not always restrict axial rotations. We also discovered that zygapophyses maintain very little overlap during certain poses (e.g. dorsiflexion). Our use of XROMM to record 3D cervical joint kinematics is thus revealing a hidden world of complexity that has not been fully appreciated using previous methods. We aim to further our investigations of the evolution of the avian neck by integrating experimental and modeling approaches, including *in vivo* measurements of cervical joint function in living birds and musculoskeletal simulations of cervical joint motion in extinct non-avian theropod dinosaurs.

PAL5-4 3:15 pm

Paleobiology of caseids (Synapsida: Caseidae) and the functional morphology of their respiratory apparatus: implications for the evolutionary origin of the mammalian diaphragm.

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Abstract: The origin of the diaphragm remains a poorly understood yet crucial step in the evolution of terrestrial vertebrates as this unique structure serves as the main respiratory motor for mammals. We analyzed the paleobiology and the respiratory apparatus of one of the oldest lineages of mammal-like reptiles: the Caseidae. Combining quantitative bone histology and functional morphological modeling approaches we conclude that an auxiliary ventilatory structure must have been present. Histology of the long bones revealed an extremely osteoporotic-like microstructure in the phylogenetically advanced caseids. This biomechanical impediment renders the traditional hypothesis that these taxa were primarily terrestrial functionally implausible. Putting the barrel-shaped, short-necked and tiny-headed animals into water furthermore solves the problems that were associated with their limited feeding envelope and their difficulty to drink. An aquatic lifestyle, on the other hand, resulted in severe constraints on the caseian ventilatory system, which consequently had to cope with diving-related problems. Our modeling of breathing parameters revealed that these caseids were capable of only limited costal breathing and must have employed some auxiliary ventilatory mechanism to quickly meet their oxygen demand upon surfacing. The bucket-handle articulation of the ribs allowed for a maximal vital capacity of only about 40% of total lung capacity, which is far from being physiologically plausible. Given caseids' phylogenetic position at the base of Synapsida, it is most parsimonious to assume that a homologue of the mammalian diaphragm was already present about 50 Ma earlier than previously assumed. This early origin is interpreted as an exaptation that allowed the large caseids to become aquatic and also paved the way for the evolution of the bronchioalveolar lung towards crown synapsids

through the formation of a negative-pressure intracoelomic compartment: the pleural cavity.

PAL5-5 3:30 pm

Functional morphology of the pectoral girdle and forelimbs of a new burrowing cistecephalid dicynodont (Therapsida: Anomodontia).

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Abstract: Dicynodonts were one of the most abundant and successful clades of Permo-Triassic synapsids, and provide early examples of the evolution of new ecomorphologies. Cistecephalid dicynodonts were specialized scratch diggers, with mole-like forelimbs and highly modified box-like skulls. Fieldwork conducted in the Zambezi Basin of Zambia uncovered a new partially articulated Permian cistecephalid (NHCC LB366). Despite its likely earlier stratigraphic occurrence than other cistecephalids, the specimen shows markedly derived characters, including reduced orbits and a flared snout. Micro-CT scan data reveal that the specimen includes the whole pectoral girdle, complete humeri, and the proximal ends of both ulnae. Here we present a description of this new specimen along with biomechanical analyses, emphasizing the forelimbs and associated soft tissue anatomy as it pertains to fossoriality. Although the forelimbs differ in some details from later cistecephalids it is clear that they were still optimized for very powerful movements. Specifically, the elbow joint possesses an enlarged olecranon, and the humerus shows a unique combination of primitive articulation surfaces with robust muscle attachment sites. An analysis of Index of Fossorial Ability (IFA), an established functional index informative of digging ability, across dicynodonts and extant burrowers confirms the strong potential for digging habits in NHCC LB366. To further validate the inferred fossorial ecology, we conducted comparative geometric morphometric analysis on extant burrowing mammals and reptiles, and used both physical 3D-printed models and computerized models, to quantify joint surface area and range of motion in the humerus (55.56° anterior-posterior) and the ulna (54.39° anterior-posterior; 88° laterally). Together, these analyses demonstrate that cistecephalids evolved sophisticated specializations for digging earlier in dicynodont history than previously recognized.

PAL5-6 3:45 pm

Triassic wheelbarrow race: revisiting cynodont forelimb posture with a musculoskeletal model.

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Abstract: Highly adducted limbs operating in a parasagittal plane are a key mammalian innovation, decoupling pectoral and pelvic limb function and enabling the selection of dynamic, asymmetrical gaits by decreasing the lateral component of ground reaction forces. By contrast, tetrapods with more abducted stances typically employ stable, symmetrical gaits where mediolateral bending of the axial skeleton contributes substantially to stride length. As the immediate evolutionary precursors to mammals, cynodonts are reconstructed with sprawling forelimbs and parasagittal hindlimbs. However, no extant tetrapod has reliably been observed to employ this combination of limb stances—in the absence of a clear modern analogue, new methods and a broader, comparative perspective are necessary for inferring the locomotory ability and kinematics of these animals. It has been hypothesized that full hindlimb parasagittalism in the synapsid line was preceded by a period of facultative adduction, as seen in modern crocodilians. Here we consider the possibility of the cynodont forelimb following a similar dual-stance path to parasagittalism, and explore the gait implications of dissimilar fore- and hind-limbs. We present preliminary data from a musculoskeletal model of *Massetognathus pascuali*, a cynodont from the middle Triassic, combining μ CT-data with muscle anatomy based on an extant phylogenetic bracket reconstruction of forelimb and pectoral girdle myology. By looking at how skeletal geometry and simulated muscle function interact across a series of hypothesized poses, we are able to evaluate the potential postural space available to this organism and shed light on the acquisition of mammalian parasagittalism.

PAL6-1 4:30 pm

Testing the buoyancy of an immersed *Spinosaurus* (Dinosauria: Theropoda) with a digital model.

Henderson DM*, Royal Tyrrell Museum of Palaeontology don.henderson@gov.ab.ca

Abstract: A recent interpretation of the fossil remains of the enigmatic, large predatory dinosaur *Spinosaurus aegyptiacus* proposed that it was specially adapted for an aquatic mode of life – a first for any predatory dinosaur. A detailed, three-dimensional, digital model of the animal was generated and the flotation potential of the model was tested using specially written software. It was found that *Spinosaurus* would have been able to float with its head clear of the water surface. However, a similarly detailed model of *Tyrannosaurus rex* was also able to float in a position enabling the animal to breathe freely, showing that there is nothing exceptional about a floating *Spinosaurus*. The software also showed that the centre of mass of *Spinosaurus* was much closer to the hips than previously estimated, implying that this dinosaur would still have been a competent walker on land. With regional body densities accounting for pneumatized skeletons and system of air sacs (modelled after birds), both the *Spinosaurus* and *Tyrannosaurus* models were found to be unsinkable, even with the air sacs substantially deflated. The conclusion is that *Spinosaurus* would still have been a competent terrestrial animal.

PAL6-2 4:45 pm

Correlated and stepwise evolution of tail weaponry in mammals, turtles, and dinosaurs.

Arbour V. M.*, North Carolina Museum of Natural Sciences; Zanno L. E., North Carolina Museum of Natural Sciences ymarbour@ncsu.edu

Abstract: Weaponry is a pervasive trait among amniotes that appears to evolve in predictable patterns when underpinned by similar socioecological and habitat parameters. Most animal weapons are located on either the head or the limbs, despite the trade-offs that must occur given the critical functions these parts of the body must perform. In contrast, tail weaponry is an extremely rare occurrence in amniotes, with specialized tail weaponry present in only three highly disparate clades: mammals, turtles, and dinosaurs. This suggests that 1) tail weapons evolve only under very specific selective regimes, and/or 2) there may be anatomical constraints that prevented the repeated evolution of tail weaponry in amniotes. Here we examine the evolution of stiff tail clubs in these three clades, by investigating which anatomical and ecological features are correlated with this feature. All amniotes with stiff tail clubs also bear osteoderms, are quadrupedal, and have ornamentation anteriorly on the body (horns and crests on the skull, and/or humps and spikes in the pectoral region). The tail clubs of ankylosaurids, glyptodonts, and meiolaniids all share a broadly similar gross morphology, but each evolved through unique evolutionary pathways. Ankylosaurids had modified distal vertebrae that tightly interlocked to form a rigid handle, and enlarged osteoderms at the tip of the tail forming an axe-like knob of bone. In contrast, glyptodonts and meiolaniids enveloped the tail in anteriorly in rings of osteoderms and posteriorly in an immobile distal tube of osteoderms. Similar to ankylosaurids, glyptodont tail clubs went through a stepwise acquisition of characters, with stiffening of the distal tail via encasement in an osteodermal tube preceding the expansion of the terminus of the tail, a feature only found in the doedicurine glyptodonts.

PAL6-3 5:00 pm

Modeling fragmentary dentaries as beams to test hypotheses of differing diets.

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Abstract: Differences in diet correlate with various morphological traits, permitting inferences about the feeding behavior of extinct taxa from fossil material. For mammals, most studies rely on complete cranial material or unworn teeth, but this excludes the many taxa known only from fragmentary fossils. Here we explore a method that requires only partial dentaries and provides an additional line of evidence for dietary reconstructions. This method exploits the relationship between the resistance of the dentary to bending and the capacity of an animal to process mechanically tougher food types, and places measurements of bending in a comparative context to determine to what extent different taxa may have fed on mechanically tough foods. Micro-CT scans were prepared for 16 dentaries representing ten late Paleocene to early Eocene (57 to 52 million year old) mammals from the Western Interior of North America that have been hypothesized to process prey with different mechanical properties. For each specimen, the thickness and distribution of mandibular cortical bone were analyzed at homologous cross-sections along the tooth row to calculate section moduli (geometric properties of beams) using the BoneJ plugin to ImageJ. Comparison of section moduli allowed an assessment of each taxon's relative resistance to the bending stresses experienced during prey processing. Although members of the Pantolestidae, a group of otter-like mammals, have been hypothesized to take mechanically tougher foods, analysis of their mandibular cortical bone distribution did not reveal any specialization for resistance to dorsoventral or mediolateral bending compared to contemporaneous mammals. The biomechanical properties of the dentary can be calculated from fragmentary material, are independent of phylogeny, and reflect bone remodelling in response to forces encountered during life.

PAL6-4 5:15 pm

Specialized wear facets in mammalian dentitions.

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Abstract: Tooth wear provides important information about the life of fossil and extant mammals. Nevertheless, wear is not appreciated very much among paleontologists, for wear eliminates details essential to phylogenetic studies. Bunodont teeth, e.g. human teeth, are often worn gradually and continuously. In contrast to such functional "unspecialized" teeth, specific wear facets characterize other teeth. This paper concentrates on the three types of wear facets that are widely distributed in the dentitions of herbivorous and carnivorous mammals, fossil and recent. They are discussed in their function and compared to technical tools. A sequence of wear stages was deduced from the functional "unspecialized" teeth based on the amount of dentine exposed. As a result of continuous wear, these phases are of almost equal functional significance and can be interpreted as phases of the late ontogeny of the teeth. However, those teeth that are characterized by the discussed wear facets do not show continuous wear, but function only during one of the ontogenetic phases. Each facet can be correlated to a specific phase. This phase becomes considerably prolonged during ontogeny and the preceding or subsequent phases correspondingly shortened. Thus, the specialization marked by wear facets show a heterochronic pattern in the life history of teeth.

Symposium — The vertebrate pharynx: crossroads in evolution and development (PHA)

Organizers: Ann Huisseune, Abigail Tucker

PHA1-1 9:30 am

Pharyngeal remodelling in development and evolution.

Graham A*, King's College London anthony.graham@kcl.ac.uk

Abstract: Pharyngeal segmentation is a characteristic of all vertebrates and during development it is first seen in the appearance of a series of bulges on the lateral surface of the head, the pharyngeal arches. In all gnathostomes, the first two pharyngeal arches form the jaw and hyoid while the more posterior arches will generate different components in different vertebrate clades. In many chondrichthyans, the embryonic segmental organisation of the pharynx is maintained in the adult arrangement of the gills slits. Conversely, in many osteichthyans, the posterior gill bearing arches are covered by the operculum. However, with the evolution of the tetrapods there has been a loss of segmentation in the adult form as a result of the remodelling of the pharynx that occurs during metamorphosis in amphibia and embryogenesis in amniotes. This process involves the expansion of the second arch such that it comes to cover and enclose the more posterior arches. This remodelling event is crucial in the organisation of the mature pharynx, and we have begun to identify the signalling pathways that direct this process and how these have been modified during evolution. The emergence of the tetrapods also involved a reduction in the number of pharyngeal segments. We will further discuss the mode through which this has been achieved and suggest that this can give us insights into how the number of pharyngeal segments can be controlled.

PHA1-2 10:00 am

Molecular basis of the lamprey pharyngeal development.

Jandzik D*, University of Colorado Boulder; Romasek M, University of Colorado Boulder; Square TA, University of Colorado Boulder; Cattell MV, University of Colorado Boulder; Medeiros DM, University of Colorado Boulder

Abstract: Lamprey, a member of the jawless vertebrate clade (cyclostomes), a sister group to jawed vertebrates (gnathostomes), is a fantastic model for the study of evolution and development of the vertebrate pharynx. Using comparative approach between these two groups has a great potential to reveal the core vertebrate patterns and mechanisms of pharyngeal evo-devo. Simple morphology of the pharyngeal apparatus, serial organization, relatively slow development of lamprey embryos, and good amenability to genetic manipulations make it possible to study the morphogenetic and developmental processes in great detail. Similar to gnathostomes, morphogenesis of the lamprey pharynx is driven by the successive formation of bilateral outpocketings of endoderm, called pharyngeal pouches. Endoderm of these pouches fuses with overlying ectoderm and encloses a mesodermal core to form the pharyngeal arches. The arches are populated by ventrally migrating neural crest cells, which give rise to the pharyngeal skeleton and musculature. Formation of the lamprey pharynx and its derivatives involves expression of several members of the vertebrate pharyngeal gene regulatory network, including transcription factors *Pax1/9*, *Tbx 1/10*, and *Ripply3* and signaling molecules of FGF, Hedgehog, and WNT pathways. In addition, Retinoic acid signaling is critical for pouch formation and establishing anteroposterior pouch polarity, and together with FGFs and Endothelin signaling plays a role in later pharyngeal skeletogenesis.

PHA1-3 10:30 am

Tightly orchestrated epithelial transitions drive pharyngeal pouch formation in zebrafish.

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Abstract: Transitions in cell morphology are essential for the remodeling of epithelia during development. In the vertebrate head, remodeling of the pharyngeal endodermal epithelium generates a series of outpocketings, or pouches, which divide the developing face into its basic segmental units, the pharyngeal arches. Pouches are ancestral forms of head segmentation, likely common to all deuterostomes. In vertebrates, pouches generate a number of important organs, such as the thymus and parathyroid, and promote development of the posterior facial skeleton. Using time-lapse recordings and transgenic and mutant analysis in zebrafish, we have found that pouch formation involves a series of epithelial transitions controlled by signaling factors in the neighboring mesoderm and ectoderm. The formation of pouches is initiated by localized Wnt11r signals from the mesoderm, guided to the periphery by Fgf8a signaling, and finally reshaped into mature pouch bilayers by combined Wnt4a and Eph-ephrin signaling. I will discuss how these multiple signaling pathways are integrated to generate the precise stereotypical branching pattern of the pharyngeal endoderm.

PHA2-1 11:30 am

Endoderm out of the mouth: pre-oral gut in non-teleost fishes reveals an ancient mode of foregut development.

Cerny R.*, Department of Zoology, Charles University in Prague, Czech Republic; Metscher B.D., Department of Theoretical Biology, University of Vienna, Austria; Arias Rodriguez L., Laboratorio de acuicultura tropical, Universidad Juárez Autónoma de Tabasco, Villahermosa, Mexico; Gela D., Research Institute of Fish Culture and Hydrobiology, University of South Bohemia in Ceske Budejovice, Czech Republic; Minarik M., Department of Zoology, Charles University in Prague, Czech Republic robert.cerny@natur.cuni.cz

Abstract: In all vertebrates, oro-pharyngeal development is considered rather uniform. From anterior to posterior, it comprises progressive formation of mouth and pharyngeal arches, where ectoderm generally outlines the outer, whereas endoderm the inner surfaces and structures. Here we present evidence that in all non-teleost fishes, development of the mouth is preceded by considerable foregut evagination that forms a distinct "pre-oral gut" along

the roof of the prospective mouth. MicroCT imaging of complete embryonic series of African bichirs, American gars, and European sturgeons detailed an early pouching of their anteriormost archenteron with subsequent formation of prominent diverticula in the premandibular domain. Further in vivo lineage tracing mapped a contribution of this pre-oral endoderm to orofacial epidermis, including lips, sensory barbels, attachment organs, and teeth. This presents the first direct evidence of external surfaces and structures of the vertebrate head to be thoroughly derived from the endoderm. Embryonic formation of the pre-oral gut is prominent in all three basal (non-teleost) fish lineages and thus seems arguably ancestral for ray-finned fishes (Actinopterygii). In teleosts, such a foregut morphogenesis has been suppressed probably due to radical transformation of their early embryonic development and foregut compression. On the other hand, pre-oral gut formation seems to be at least rudimentarily present in many other vertebrates and the early foregut expansion that forms diverticula with a central lumen continuous with the buccal cavity appears in many Deuterostomes. Hatschek's diverticulum of embryonic *Amphioxus* (Cephalochordates), oral (buccal) glands of appendicularian tunicates, or stomochord (buccal diverticulum) of hemichordate acorn worms are all examples of this kind of foregut morphogenesis. The above-described peculiar formation of the prominent pre-oral gut in non-teleost fishes thus reveals an ancient blueprint of foregut morphogenesis rather than a clade-specific curiosity.

PHA2-2 12:00 pm

The first pouch in formation and evolution of the amniote middle ear.

Tucker AS*, King's College London abigail.tucker@kcl.ac.uk

Abstract: The endodermally derived first pharyngeal pouch classically forms the middle ear cavity in tetrapods with a tympanic ear, creating an air filled space that is continuous with the pharynx. In mice, however, the endoderm of the first pouch breaks during embryonic development creating a middle ear that is lined by both endoderm and neural crest derived mesenchyme. A similar break does not appear to occur in birds and reptiles but has been observed in a variety of mammals. This has consequences for the development of the tympanic membrane, with the Pars flaccida of mammals appearing to have no contribution from the first pouch. This new consideration of the role of the first pouch has consequences for our understanding of evolution of the tympanic ear and for our understanding of why the mammalian middle ear appears particularly susceptible to disorders.

PHA2-3 12:30 pm

Evolutionary and developmental relationships between pharyngeal pouches and teeth.

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Abstract: During vertebrate development, the pharyngeal endoderm produces a series of pouches separating the pharyngeal arches. The pouches may extend towards, and eventually make contact with, the ectodermal cover (skin). In primary aquatic osteichthyans, gill slits develop at these contact points. Based on paleontological and neontological evidence, we have previously proposed that the places of contact allow the interaction between ectoderm and endoderm and that this interaction is required for pharyngeal tooth formation (Huysseune et al., 2009). Likewise, the need for a close correlation between pouch formation (more specifically, ectodermal/endodermal contacts) and pharyngeal tooth development could explain the evolutionary loss of pharyngeal teeth in tetrapods. We have tested this hypothesis using mutant and transgenic zebrafish (*Danio rerio*), a teleost fish species possessing pharyngeal teeth only. For example, zebrafish *van gogh* mutants, defective in the transcription factor *tbx1*, display impaired pouch formation and defects in their pharyngeal dentition. Dentition defects coincide with the level of impairment of ectodermal-endodermal contacts. We have further tested the association between pouches and teeth by blocking endogenous retinoic acid synthesis, which also leads to defective tooth formation. We propose that impaired tooth formation is not a direct result from blocking endogenous retinoic acid (as suggested by Gibert et al., 2012), but is a byproduct of defective pouch formation. Together, our results lend support to the association between pouch and (pharyngeal) tooth formation. The authors acknowledge support from the Special Research Fund (BOF, 2-4 yr project) of Ghent University. Huysseune et al., 2009. *J. Anat.* 214: 465-476. Gibert et al., 2010. *FASEB J.* 24: 3298-3309.

PHA3-1 2:30 pm

What happened to the gills during the fish-to-tetrapod transition?

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Abstract: The internal gills of bony fishes were long thought to have been lost before tetrapods evolved, with lungs and the skin forming the main respiratory organs in terrestrial vertebrates. Fossil evidence and phylogenetic bracketing instead reveal that the story was more multi-faceted. In fact, many early tetrapods were aquatic throughout life, and some of these retained internal gills homologous with those of their sarcopterygian ancestors. In the stem-group of modern amphibians, these gills were retained in some aquatic clades, whereas in stem-amniotes, they were lost. A novel feature that evolved only in tetrapods are external gills of larval forms, absent in the immediate ancestors of tetrapods, but which are known to have existed in both stem-amphibians (temnospondyls) and stem-amniotes (seymouriamorphs). A survey of different breathing mechanisms in early tetrapods reveals complicated patterns of respiratory organs and mechanisms, highlighting that morphological disparity correlates with respiratory diversity.

PHA3-2 3:00 pm

Lungs to gas bladders: homology, novelty and transformation.

McCune A.R.*, Cornell University; Cass A.N., North Carolina State University; Longo S.J., University of California, Davis; Riccio M.L., Cornell University arm2@cornell.edu

Abstract: An important evolutionary novelty among vertebrates is the gas bladder of ray-finned fishes, which develops dorsally as an outgrowth of the pharynx. Having a gas bladder characterizes nearly 30,000 species of the Actinopteri (all ray-finned fishes except polypterids). This air-filled organ may function in respiration, buoyancy, sound production, hearing or in some combination of these roles. Since the late 19th century, gas bladders have been regarded by most as homologous to lungs, although there continue to be those who disagree. Using data from micro- and nano- computed tomography (CT), we will illustrate the difference between lungs and gas bladders, review the evidence for and against homology, and present preliminary genetic data implicated in the transformation of lungs to gas bladders.

PHA3-3 3:30 pm

Diverse embryonic and evolutionary origins for the hypoxia-sensitive cells of the vertebrate respiratory reflex.

Baker CVH, University of Cambridge; Hockman D, University of Cambridge; Burns AJ, UCL Institute of Child Health; Mongera A, Max-Planck Institut für Entwicklungsbiologie; Fisher S, University of Pennsylvania; Unlu G, Vanderbilt University; Knapik EW, Vanderbilt University; Kelsh RN, University of Bath; Kaufman CK, Harvard Medical School; Mosimann C, Harvard Medical School; Zon LI, Harvard Medical School; Tucker AS*, King's College London

Abstract: Carotid body glomus cells respond to hypoxia by releasing neurotransmitters, triggering the respiratory reflex. It has been proposed that these neural crest-derived cells, which develop in association with the third pharyngeal arch artery, are homologous to the hypoxia-sensitive "neuroepithelial cells" (NECs) of fish gills. We test this hypothesis using genetic lineage-tracing and neural crest-deficient mutants in zebrafish, and physical fate-mapping in frog and lamprey. NECs in anamniote gill and orobranchial epithelia are not neural crest-derived, hence are most likely homologous to hypoxia-sensitive pulmonary neuroendocrine cells in lung airway epithelia, whose endodermal origin we confirm in mouse and chicken. We propose that carotid body glomus cells evolved instead from chromaffin cells associated with large pharyngeal arch blood vessels, which lineage-tracing in zebrafish shows are neural crest-derived.

PHA4-1 4:30 pm

Neural crest-pharyngeal interactions that underlie the evolution of jaw size.

Fish JL, University of Massachusetts Lowell; Vavrušová Z, University of California San Francisco; Chakrabarti D, University of Massachusetts Lowell; Gambino K, University of Massachusetts Lowell; Rose N, University of California San Francisco; Schneider RA*, University of California San Francisco rich.schneider@ucsf.edu

Abstract: The evolutionary success of vertebrates is due in large part to variation in jaw size. Developmental mechanisms that generate species-specific differences in jaw size involve neural crest mesenchyme (NCM), which is the progenitor population that migrates into the mandibular arch and forms the jaw skeleton. In particular, precisely timed interactions between NCM and pharyngeal endoderm facilitate the patterned outgrowth of the mandibular arch, and these interactions are mediated by the Sonic Hedgehog (SHH) signaling pathway. We hypothesize that the species-specific response of NCM to Shh expression in pharyngeal endoderm can alter the proliferation and differentiation of skeletal precursor cells, and ultimately lead to evolutionary variation in jaw size. We test our hypothesis by examining expression of members and targets of the SHH pathway qualitatively and quantitatively on the mRNA and protein levels in quail and duck embryos, which are two birds with distinct jaw sizes. We also analyze the cell cycle and proliferation dynamics since these are known to be closely tied to SHH signaling. Our results reveal species-specific levels of expression and differential responses to SHH signaling in quail versus duck. When we make chimeric "quack" by transplanting NCM from quail to duck, we find that donor NCM maintains its quail-like expression in duck hosts and gives rise to shorter, quail-like jaws. Overall, these experiments reveal that species-specific differences in SHH signaling are intrinsic to, and mediated by NCM, and that developmental changes to the SHH pathway in NCM may modulate jaw size during evolution. Funded in part, by NIDCR R01 DE016402 to R.A.S.

Symposium — New insights into the functional relationship between anatomy and physiology of extinct and extant vertebrates (PHY)

Organizers: Wm. Ruger Porter, Glenn Tattersall

PHY1-1 2:30 pm

Vascular anatomy and thermophysiological strategies in the heads of extinct and extant dinosaurs.

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Abstract: Diapsids emphasize different sites of thermal exchange (oral, nasal, and orbital regions), yet share conserved vascular patterns known to facilitate thermoregulation. Given the impact of surface-to-volume ratio on heat

balance, we hypothesized that the higher heat loads of large-bodied dinosaurs would require enhanced sites of cephalic thermal exchange, potentially promoting selective brain cooling (SBC), in comparison with smaller-bodied members of the same clade. Evidence for vascular anatomy was collected from dinosaur fossils and their extant relatives using CT scans, vascular injection, and/or gross dissection. Cross-sectional areas of bony vascular canals were measured and analyzed using principal components and partial least squares analyses to test hypotheses of thermally-relevant vascular networks in small- and large-bodied dinosaurs of the same clade. Generalized vascular patterns and equivalent vascular canal sizes were found in smaller-bodied dinosaurs with modest-sized oral and nasal regions. Large-bodied dinosaurs likely experienced selective pressures to emphasize regions of physiological heat-exchange, and indeed the blood vessels in these emphasized sites were found to have different sizes and combinations of blood vessels. Sauropods had a large subnarial foramen indicating a rich blood supply to the nasal and oral regions. Ankylosaurs had evidence of an enhanced blood supply to the nasal region, but not to the oral region. Theropods had modest supply to nasal and oral regions but an enhanced blood supply to the paranasal sinuses, indicating a novel physiological role for these sinuses. This evidence supports the hypothesis that larger-bodied dinosaurs evolved anatomically expanded and richly vascularized sites of thermal exchange to support the SBC necessary to buffer neurosensory tissues from extreme body temperatures. Moreover, different clades evolved different vascular strategies, reflecting convergent evolution of large size and different evolutionary paths to SBC.

PHY1-2 2:45 pm

Avian bills as thermoregulatory structures.

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Abstract: Avian bills rest at the cross-roads between form and function. Known for their diversity of forms as adaptive feeding structures, bills are also mechanosensory, chemosensory, and respiratory structures. Avian bills should not be viewed as simply feeding structures, but rather as living structures, served by a network of nerves and blood vessels. As endotherms, birds also must contend with heat conservation in the cold and heat dissipation under warm conditions. As uninsulated structures, bills are therefore potential sites of significant heat exchange to and from their environment. We initially demonstrated the dramatic potential for heat exchange to the bill of the toco toucan. The toucan bill is well vascularised, and blood flow appears to be altered according to ambient temperatures or changes in internal heat loads. The capacity for heat loss is impressive, up to 4-5 times the rate of resting heat productions. We have also demonstrated that bill size is a thermally plastic trait in terms of developmental plasticity; larger bills will exchange heat more effectively through both surface area effects as well as changes to vascular conductance. Japanese quail reared in the cold show slower bill growth than birds reared at warm temperatures, and as adults are more effective at conserving heat loss from the bill, suggesting permanent alterations in the vasculature. This pattern of bill size-temperature dependency is a widespread evolutionary response. In over 200 species of non-migratory birds, we found strong evidence for smaller bill sizes in species living in cold environments, with the strongest relationships in avian families with the highest latitudinal ranges. Combined, the story emerging is that avian bills may be subject to selection by environmental temperatures, in addition to their functional role in feeding. Research funding provided to GJT by the Natural Sciences and Engineering Research Council of Canada and the National Geographic Society.

PHY1-3 3:00 pm

Mathematical models and bone histology shed light on maximal aerobic capacities of both extinct and extant tetrapods.

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Abstract: Our study aimed to test the hypothesis that there is a relationship between vascularity of musculoskeletal tissues, lung design, red blood cell (RBC) dimensions, and maximal rates of oxygen consumed during vigorous exercise in extant tetrapods. If such a relationship exists and its mechanistic basis is understood, it could be used to infer maximal aerobic capacities of extinct tetrapods. Maximal aerobic capacities are important in many ways. For example, they intertwine with mode of locomotion, they can determine the outcome of intraspecific competition and predator-prey interactions, and they are inversely correlated to genome size. We used mathematical models to understand the relationship between RBC dimensions, lung design, and oxygen uptake under different levels of inspired oxygen, and histology to study the link between RBC size and bone microvasculature in both extant and extinct lineages. Our models show that as levels of inspired oxygen decrease, maximal rates of oxygen uptake become increasingly sensitive to RBC size and hemoglobin concentration. In contrast, shifts of P50, for example by organic phosphates, had a very modest effect on oxygen uptake. We believe these results predict strong selection for reduced RBC size and thin blood gas barriers for highly active animals living in low oxygen conditions (e.g., in burrows, at altitude, during geologic periods of low environmental oxygen). Our histological analysis is the first to focus on the relationship between RBC dimensions and minimum canal caliber in cortical bone. Femora of several tetrapod species were sectioned at the midshaft and digitally imaged for histometric measurements and analysis. Multiple regression models support the hypothesis that minimum and harmonic mean canal caliber covary with RBC width and area. We use these results to retrodict the acquisition of mammal-like physiology in the synapsid lineage, focusing on Permo-Triassic therapsids. Supported by: NSF-BIO 1309040 to AKH and NSF-IOB-1055080 to CGF

PHY1-4 3:30 pm

Insular dwarfism and the distinct physiology in island deer: bone histology of Japanese extinct island cervids indicates interrupted growth.

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Abstract: Miniaturization of island mammals is a well-known phenomenon in the evolutionary history of vertebrates, and therefore, a relationship between morphological reduction and physiological modification has been argued for. However, because of limited samples and a lack of ancestral taxa and/or kin, this relationship is still poorly understood. Here, we examine long bone histology of two extinct island cervids (*Cervus astylodon* and Muntiacini genus et sp. indet.) discovered from the Pleistocene deposits on Okinawa Island, Japan, to infer their life history and discuss their potential physiology in comparison to that of living relatives (*C. nippon* and *Muntiacus reevesi*). Bone histology of the two extinct island cervids is similar to each other and characterized by poorly vascularized parallel-fibered bone. Another peculiar characteristic of their histology are large amounts of lines of arrested growth (LAGs) with an external fundamental system (EFS), showing 13 LAGs with an EFS in *C. astylodon* and 6 LAGs with an EFS in Muntiacini gen. et sp. indet. The zones between LAGs are consistently narrow throughout the cortex, suggesting slow growth rates throughout life. In contrast to these island taxa, bone histology of the living relatives exhibits a highly vascularized fibro-lamellar bone and few LAGs with wider intervals throughout most of the cortex, agreeing with known observations of rapid body growth in the wild. Extinct island deer show distinctly slower growth and longer life histories compared to their living relatives. This life history strategy is similar to that typical for reptiles and an extinct island bovid, *Myotragus*; all having a low metabolic rate in common. Taken all together, dwarfism of *C. astylodon* and Muntiacini gen. et sp. indet. might be associated with a decrease in metabolic rate, and the extended life history could be due to a lack of predators on Okinawa Island until the invasion of humans in the Late Pleistocene.

PHY2-1 4:30 pm

The function of the carotid rete—the unique "wonderful net" of the Cetartiodactyla.

Strauss WM*, University of the Witwatersrand (WITS); Hetem RS, University of the Witwatersrand (WITS); Mitchell D, University of the Witwatersrand (WITS); Maloney SK, University of Western Australia; Meyer LCR, University of the Witwatersrand (WITS); Fuller A, University of the Witwatersrand (WITS) strauwm@unisa.ac.za

Abstract: Retia mirabilia have been described in all vertebrate groups, and are generally involved in counter-current exchange, be it the exchange of gas (e.g., oxygen in teleost fish and birds), or heat (e.g., tuna, mammals). A well-developed carotid rete is common only among members of the Order Cetartiodactyla - the artiodactyls (even-toed ungulates like sheep, goats, and antelope) and also cetaceans - and members of the Felidae (Order Carnivora). In the carotid rete of artiodactyls, warm arterial blood destined for the brain loses heat to cooler venous blood draining into a cavernous sinus, mainly from the nasal mucosa. The arterial blood leaving the rete en route to the brain is therefore cooler than when it entered the rete, resulting in selective brain cooling, defined as a hypothalamic temperature lower than arterial blood temperature. Using Dorper sheep dosed with Deuterium, we show that selective brain cooling serves a water conservation function. Sheep that used selective brain cooling more frequently, and with greater magnitude, lost less body water than did conspecifics using selective brain cooling less. We show that a 50 kg sheep can save 2.6 L of water per day (ca. 60% of daily water intake) when it employs selective brain cooling for 50% of the day during heat exposure. We then investigate whether selective brain cooling differs between free-living artiodactyls with varying water dependencies. Using generalised linear mixed-effect models we show that carotid arterial blood temperature and brain temperature affect selective brain cooling attributes. Neither heat load, nor species, had an effect on selective brain cooling attributes. Indeed, variability in selective brain cooling was greater within a species than between species. The carotid rete, which may have helped facilitate the evolutionary success of artiodactyls, may play an important part in individual adaptability to a changing climate.

PHY2-2 5:00 pm

Complicated noses keep cool heads: the thermoregulatory effects of nasal passage shape in extant birds and reptiles, with implications for dinosaurs.

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Abstract: Sauropsids (reptiles and birds) evolved a diversity of nasal anatomies, but how this diversity affects nasal airflow and thermal physiology is largely unknown. In general, bird noses are thought to offer superior heat and water savings due to the presence of nasal turbinates. To test this hypothesis, we simulated nasal airflow in various birds, lizards, and crocodylians using computational fluid dynamics (CFD) software. Bird noses are relatively short and compact, disrupted by multiple nasal convolutions (turbinates) that increase surface area within the confined space. Turbinates split the air field into multiple, parallel air channels. In contrast, lizard airways are relatively long due to elongation and convolution of the nasal vestibule. However, with only minor invasions by turbinates, air travels through lizard noses in a single channel, or serially. Crocodylian noses are intermediate, being long like lizards but having more turbinate invasions as in birds. Our CFD analyses found that serial and parallel nasal arrangements

provided similar benefits for reducing heat and respiratory evaporative water loss. Air-cooled nasal mucosa reduces the temperature of the underlying blood vessels, and many of these veins pass from the nose to the brain, offering the potential for substantial selective brain cooling. Drawing on our analyses of extant sauropsids, we extended our analysis into the fossil record by simulating airflow through the noses of the dinosaurs *Stegoceras*, *Panoplosaurus*, *Euoplocephalus*, and *Majungasaurus*. Most reconstructed dinosaur noses provided thermoregulatory results on par with extant animals. *Majungasaurus* proved to be an outlier with a fairly inefficient nasal passage. We suggest that theropods emphasized their paranasal sinuses for brain cooling, rather than the nasal passage. Enhancing the nose appears to have been necessary for large-bodied dinosaurs, likely as a means of maintaining brain temperatures within safe limits.

PHY2-3 5:30 pm

Macroevolutionary impact of selective brain cooling on artiodactyl diversity patterns throughout the Cenozoic.

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Abstract: Artiodactyls are known for having the highest diversity of extant large-bodied mammals. They are also known to have a number of unique physiologies, particularly foregut-fermentation-based digestion. This digestive physiology is considered key to artiodactyl success in modern environments. While the link between digestion and herbivore evolution is undisputed, there is an additional feature that may also bolster artiodactyl diversity over Cenozoic environmental shifts: the carotid rete [CR]. The CR is an intracranial arterial meshwork that replaces the internal carotid artery. Sitting in a sinus of turbinate-cooled venous blood, the CR drives brain cooling and delays water-costly responses to heat stress (panting, sweating). Thus, the CR may be selectively advantageous across Cenozoic periods of warming or aridification. Much is known about CR physiology, but its macroevolutionary impact is heretofore unknown. This study uses both soft- and hard-tissue morphological surveys to identify presence/absence of the CR across 10 extant and 16 extinct artiodactyl families. Evolutionary modeling was then used to test whether hypothesized innovations (digestion and the CR) have a demonstrable effect in generating modern diversity. When modern lineages are examined in a phylogenetic comparative framework, results show that diversification is not significantly different per trait, but that extinction probability is lower for artiodactyls with a CR. These physiologies are significantly correlated in living animals (87%), but when fossil data is added, only 8 of 26 families exhibit trait overlap. When evolutionary models of speciation and extinction take extinct groups into account, artiodactyls with a CR diversify earlier, speciate faster, and are more insulated from extinction. The results of both suites of models suggest that brain cooling may be a prerequisite for ruminant digestion, protecting the brain from the higher core temperatures that are needed to support fermentation.

Symposium — Palate development, function and evolution (PLT)

Organizers: Joy Richman, Casey Holliday, John Abramyan

PLT1-1 9:30 am

Molecular patterning of the hard palate during mammalian palatogenesis.

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Abstract: The mammalian palate is anatomically divided into the anterior hard palate and the posterior soft palate. However, how the anterior hard palate is patterned and how the palatal osteogenesis is controlled remain unknown. It was recently demonstrated that in the developing branchial arches, the TALE superclass homeodomain proteins particularly Meis proteins set up a ground state that is common to all the arches and their derivatives whereas Hox transcription factors act as tissue-specific cofactor to specify the arch identity. However, this raises a fundamental question as what factors interact with Meis to specify and pattern the Hox-free first arch and its derivatives including the palate. The homeobox gene *Shox2* is expressed specifically in the anterior palatal mesenchyme, overlapping with the future bony hard palate domain. We have shown previously that *Shox2* mutation leads to not only anterior palate clefting, but most intriguingly, to significantly reduced bone formation in the hard palate. Together with the loss of the stypolod in *Shox2*^{-/-} limb, there is an essential role for *Shox2* in organ patterning and skeletogenesis. Our recent studies present evidence that inactivation of *Shox2* leads to premature/ectopic expression of *Runx2* in *Shox2*⁻-expressing palatal mesenchymal cells. Our RNA-Seq studies on *Shox2*⁺ cells from E13 palatal shelves and limbs demonstrate a genome-wide elevated expression of osteogenic genes in the absence of *Shox2*, consistent with our results that *Shox2* overexpression in CNC lineage cells causes cleft and inhibits osteogenesis. Moreover, *Shox2* ChIP-Seq on the developing palate and limb reveals genome-wide preferential occupation of *Shox2* on the responsive cis-regulatory elements of these genes bound by Hox and Meis proteins. These results suggest that in the Hox-free developing palate, *Shox2* interacts with Meis to pattern the hard palate and regulates osteogenesis by antagonizing the transcription output of Meis proteins to prevent premature osteogenic differentiation. (supported by NIH grants R01 DE14044 and R01DE17792).

PLT1-2 10:00 am

Differing effects of *Fgfr* mutations on palate morphology in non-cleft mouse models.

Martinez-Abadias Neus*, Center for Genomic Regulation; Motch Perrine Susan, Pennsylvania State University; Melkonian Freya, Universitat de Barcelona; Pankratz Talia, Pennsylvania State University; Rhodes Katie, Pennsylvania State University; Wang Yingli, Icahn School of Medicine at Mount Sinai; Zhou Xueyan, Icahn School of Medicine at Mount Sinai; Wang Jabs Etyli, Icahn School of Medicine at Mount Sinai; Richtsmeier Joan, Pennsylvania State University nmartinezabadias@gmail.com

Abstract: FGFR1-3-related craniosynostosis syndromes are autosomal congenital disorders that involve craniofacial, neural and other malformations caused by mutations in the FGF/FGFR signaling pathway. Even though the syndromes present overlapping phenotypes and mutations can reside on neighboring amino acids of the same gene, the craniofacial phenotype shows marked variation within and between syndromes. Focusing on palate development, our goal is to pinpoint differences in the emergence and severity of palatal dysmorphologies between some of the most prevalent craniosynostosis syndromes using murine models for Apert (Fgfr2+/S252W and Fgfr2+/P253R), Crouzon (Fgfr2+/C342Y) and Muenke (Fgfr3+/P244R) syndromes at two different developmental times (embryonic day 17.5 and day of birth P0). Results based on palatal suture patency and comparative 3D shape analysis of landmark-based data recorded on high resolution micro CT scans of mutant and non-mutant littermates confirmed that across these mutation groups, the posterior aspect is the most affected region of the palate. However, the Apert Fgfr2 S252W mutation caused earlier onset (before E17.5) and resulted in the most severe palate dysmorphology by P0. The remaining mutations are associated with later onset (between E17.5 and birth) and less severe palatal defects. The least disruptive mutation was the Muenke Fgfr3 P244R mutation, which induced palatal dysmorphologies only when present in two copies (Fgfr3P244R/P244R). We conclude that the onset time, gene dosage and spatio-temporal expression patterns of the Fgfrs affected by these mutations may explain the phenotypic dissimilarities between FGFR1-3 related craniosynostosis syndromes. Further experimental analyses guided by our morphometric results may reveal the mechanisms leading to the most severe palatal anomalies in craniosynostosis syndromes. Grant support: NIH/NIDCR (R01 DE018500, 3R01 DE018500-02S1, R01 DE022988, P01HD078233), FP7-PEOPLE-2012-IIF 327382, SEV-2012-0208.

PLT1-3 10:15 am

An open and shut case; Variation in morphogenesis of the secondary palate in amniotes.

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Abstract: The secondary palate forms the roof of the oral cavity, posterior to the primary palate. The bones supporting the palate in mammalian line of amniotes consist of the palatine process of the maxillary bone and the palatine bone whereas in the reptilian line, the pterygoid also makes an important contribution. The mammalian amniotes have an unbroken evolutionary record of intact palates. Furthermore, the mammalian secondary palate includes the muscular soft palate which is not preserved in the fossil record. In contrast, in the reptilian line, squamates and aves have open secondary palates but lack an equivalent to the soft palate. Many studies in the mouse have documented anterior-posterior differences in gene expression that correlate with the putative border of the hard and soft palate. We hypothesized that in the avian embryo, such positionally restricted patterns would not exist. In the chicken, the medial surfaces of the maxillary prominences grow outward to form the palatal shelves starting at stage 29, by stage 33 the palate has fully formed and ossification begins at stage 34. The posteriorly restricted genes examined included BARX1, TBX22, BMP4, PAX9 and MN1. We also looked at SHOX2 and MSX1 which are anteriorly expressed in mice. In the chicken the majority of genes varied in their expression patterns compared to the mouse. PAX9 is ubiquitously expressed while MSX1 is absent from the anterior palatal shelves. Interestingly, TBX22 is expressed medially throughout the palatal shelves at stage 31 and 32 but is downregulated posteriorly at stage 33. Only one gene, BARX1, is correlated with the posteriorly positioned pterygoid bones. Therefore the molecular patterning in the bird does not follow the anterior-posterior regionalization seen in the mouse. We uncovered a set of genes with conserved expression in the palates of birds and mammals however our detailed examination suggests the regulatory regions may be slightly different.

PLT1-4 10:30 am

Mechanisms of crocodilian palate formation.

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Abstract: Amniote embryos develop a connection between the embryonic mouth (stomodeum) and the nasal cavities. Subsequently, a secondary palate forms in most lineages. In snakes, lizards and birds, palatal shelves bud out from the maxillary prominences but do not fuse, leaving a natural cleft. In mammals and crocodilians, the secondary palate completely separates the oral and nasal cavities. However, the details of crocodilian secondary palate formation are unclear. Here we describe the ontogeny of the secondary palate in alligator embryos using histology, immunohistochemistry and 3D reconstruction. We found that at stage 14 and 15 (Ferguson staging), the choanae open into the oral cavity unobstructed, although slight thickening of the medial sides of the maxillary prominences are visible posterior to the choanae. The midline mesenchyme inferior to the nasal septal cartilage also projects into the stomodeum. At stages 16 through 17, the medial sides of the maxillary prominences become enlarged so that by stage 17, fusion initiates between the medial maxillary prominences and nasal epithelium. At

stages 18-19, the zone of fusion between the palatal shelves extends posteriorly, retaining connection to the nasal septum and furthermore, beginning to contact each other directly. Anti-cytokeratin staining confirms the presence of epithelial contact between the maxillary prominences over a limited distance (14-21 microns), indicating an extremely short period of epithelial seam retention. In mammals, palatal shelves develop vertically and then reorient horizontally to make extensive epithelial contact in the midline. The medial edge epithelium persists throughout the length of the palate, gradually degrading and being replaced by mesenchyme. The crocodilian maxillary prominences enlarge medially, make anterior contact with the premaxilla and the nasal septum first, and then gradually merge down the midline in a posterior direction to form a complete, flat secondary palate.

PLT1-5 10:45 am

Morphology and development of secondary palate in chameleon.

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Abstract: In some groups of reptiles such as turtles, crocodiles and lizards, various degree of secondary palates have developed. In chameleons, the secondary palate is supported by palatine processes of the premaxilla and maxilla as well as by the palatal and pterygoid bones. The vomer is situated medially. In some post-hatching individuals, we observed open palates while in others there was partial fusion of palatal shelves in the midline. Here, we focus on the analysis of developmental processes underlying secondary palate formation and their differences in comparison to mammals. During pre-hatching development, lateral palatal shelves in chameleons grow dorso-medially toward each other, covering the interorbital septum and choanae. The palate was open rostrally and caudally while closer approximation of the shelves was found in the centre. The growing medial edge of palatal shelves was covered by cylindrical epithelial cells containing apical nuclei. On the other hand, epithelial cells of the nasal and the oral cavity were flattened. Immunohistochemical analysis of PCNA revealed massive proliferation in multilayered oral epithelium as well as in the medial part of the mesenchyme. To experimentally affect the palate development, we dissected palatal shelves from embryos in the middle of pre-hatching development. We did not observe any sign of fusion when palatal shelves were cultured next to each other. On the other hand, the full fusion was found in cultures treated with TGFβ added to the culture medium. Our preliminary results revealed that fusion of the chameleon palate can be enhanced by growth factors. Future work will uncover the cellular and molecular processes responsible for secondary palate fusion in chameleons. The research was supported by Grant Agency of Czech Republic (14-37368G).

PLT2-1 11:30 am

Structure and strain in the chondrichthyan palatoquadrate.

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Abstract: Functional morphology of the palatoquadrate in several species of chondrichthyan fishes was compared horizontally in adults and ontogenetically in selected species. Meckel's cartilage was also compared due to its morphological coupling to the palatoquadrate and their key role in feeding and ventilation. Shape change in these elements over ontogeny and across species was analyzed using geometric morphometric analyses, percent mineralization, cross-sectional area, and second moment of area. Similarly, functional changes were analyzed using mechanical stiffness, Poisson's ratio, and Young's Modulus. Interspecific shape changes were greater in the palatoquadrate than Meckel's cartilage. Ontogenetic shape changes varied with elements showing isometric or negative allometry. Cross-sectional area and percent mineralization also varies leading to consistent stiffness over ontogeny. An inflection point exists in the stress-strain curve that may indicate mechanical property changes in tesserae-ligament interactions during compression. Tessellated cartilage has a complex heterogeneous structure that varies among species leading to functional differences that may be correlated with feeding style and diet.

PLT2-2 12:00 pm

Relative kinetic competency in the palatal complexes of birds and other diapsids.

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Abstract: Cranial kinesis, or flexibility among intracranial joints, defines many clades of birds and other reptiles.

Numerous evolutionary and functional transitions occurred during avian cranial evolution where the primitive, vertically-thin palate of non-avian theropods was modified into either a flat, sutured, weakly-flexible assembly in palaeognaths or a strut-like, often highly-flexible palate in neognaths. Palatal elements and their braincase articulations are key features of the kinetic feeding apparatus as they must promote or restrain movements of the facial skeleton such as in propalinal (rostrocaudal) or pleurokinetic (mediolateral) excursions. However, kinetic movements remain challenging to assess without in vivo data or among extinct taxa such as non-avian dinosaurs. Here we share an experimental methodology designed to test hypotheses of kinetic excursions and ultimately of the evolution of avian kinesis. We developed 3D finite element models of birds and other diapsids (e.g., *Tyrannosaurus*, *Edmontosaurus*, *Gekko*) which differ markedly in palatal morphology as well as known kinetic behaviors. Palatal complexes (pterygoids, palatines, quadrates) were repositioned in three different postures (neutral, propalinal, pleurokinetic) in each taxon to represent hypothetical excursions of palatal kinesis. Jaw and protractor muscles were mapped onto the models, 3D moments about multiple joints were calculated using BoneLoad, muscle orientations were tracked among the different postures, and force propagation through the models were evaluated using finite element analysis. We found palatal posture to greatly influence muscle orientation and loading environment among our sample. These methods are powerful for reconstructing and understanding the complex biomechanical environment of the skulls of kinetic species as well as vertebrates in general. This research was funded by the National Science Foundation (NSF IOS-1457319), Missouri Research Board, Missouri Research Council and the Dept. of Pathology and Anatomical Sciences.

PLT2-3 12:15 pm

The significance of novel palatal joints in the adaptive radiations of archosaurs.

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Abstract: From the origin of the mammalian temporomandibular joint, to the iterative evolution of piscine intramandibular joints, to the Paleozoic rise of gnathostomes, vertebrate adaptive radiations often accompany major innovations in linkages of the feeding apparatus. Here we explore equally significant, arthrological adaptations evolved by crocodyliforms and dinosaurs using imaging, histology, biomechanics, and comparative approaches. Although both extant archosaur clades underwent significant transformations in palatal articulations, they did so in divergent ways. Crocodyliforms evolved hard-biting, akinetic crania further stabilized by their characteristic pterygomandibular joint. Avian clades frequently develop novel articulations to either better canalize kinetic movements (e.g., ducks, parrots) or to stiffen the skull (e.g., woodpeckers). These novel, secondary articulations are mediated by a spectrum of skeletal tissues including secondary cartilage, chondroid bone, vestiges of the palatoquadrate cartilage, fibrous entheses and flexion zones all of which reflect a fascinating interplay of developmental origins, loading environment and phylogenetic history during the radiations of archosaurs.

PLT2-4 12:30 pm

Why (and how) the long face? The evolutionary and developmental bases of Anolis facial diversity.

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Abstract: Evolved differences in craniofacial form and function have been critical to the success and diversification of vertebrates. To obtain an understanding of the factors that have constrained and/or facilitated the production of this diversity evolutionary biologists must embrace an organismal approach to the study of anatomy, integrating developmental, ecological, and behavioral perspectives. We have taken this broad approach to the study of craniofacial variation in *Anolis* lizards, a textbook model of adaptive diversification. Despite decades of research on this diverse genus, few studies have addressed variation in head shape until recently. Previously we showed that the most striking changes in craniofacial shape among anoles are associated with differences in male facial length. Our behavioral observations in field have not yet revealed ecological differences that can explain this variation, but have led us to propose hypotheses based on sexual selection. Through comparative developmental analyses we have shown that variation in facial length is the result of modifications in facial growth rates, not changes in patterning as observed in other lineages. Our analysis of anoles illustrates that the mechanisms driving facial outgrowth are distinct from those in birds and mice. The ongoing collaborative research among our labs is aimed at understanding how these mechanisms have been modified in anoles with different facial morphologies.

Contributed Session — Sensory Biology & Neuroscience (SBN)

SBN1-1 9:30 am

Using the brain-neurocranial relationship in the extant Australian lungfish to interpret fossil endocasts.

Clement AM*, Flinders University; Strand R, Uppsala University; Nysjö J, Uppsala University; Long JA, Flinders University; Ahlberg PE, Uppsala University alice.clement@flinders.edu.au

Abstract: Lungfish first appeared in the geological record over 410 million years ago, and are the closest living group of fish to the tetrapods (limbed animals and their descendants). Palaeoneurological investigations into the group show that unlike numerous other fishes -but more similar to that in tetrapods- lungfish appear to have had a close fit

between the brain and the cranial cavity that housed it. As such, researchers can use the endocast of fossil taxa (an internal cast of the cranial cavity) both as a source of morphological data but also to aid in developing functional and phylogenetic implications about the group. Using fossil endocast data from an exceptionally and 3D-preserved Late Devonian lungfish from the Gogo Formation, *Rhinodipterus*, and the brain-neurocranial relationship in the extant Australian lungfish, *Neoceratodus*, we present the first virtually reconstructed brain of a fossil lungfish. Computed Tomographic data and a newly developed 'brain-warping' method are used in conjunction with our own distance map software tool to both analyse and present the data. The brain reconstruction is adequate, but we envisage that its accuracy and wider application in other taxonomic groups will grow with increasing availability of tomographic data sets.

SBN1-2 9:45 am

Comparative morphology of snake (Squamata) endocasts: evidence of phylogenetical and ecological signals.

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Abstract: Endocasts obtained from computed tomography are now widely used in the field of comparative neuroanatomy. They provide an overview of the brain morphology and the associated tissues located in the cranial cavity, and thus, through anatomical comparisons, information about the senses, the behaviour and the ecology of the species. Although there are many studies dealing with mammal and bird endocasts, those performed on the endocasts of squamates are comparatively rare, thus limiting our understanding of their morphological variability and interpretations. Here, we provide the first comparative study of snake endocasts, in order to bring new information about the morphology of this structure and to test if it encompasses an ecologic signal. For this purpose, the digital endocasts of 45 snake specimens, encompassing a wide diversity of snakes in terms of phylogeny and ecology, were digitized using computed tomography, and compared both qualitatively and quantitatively (using traditional morphometrics). Snake endocasts present a great variability. Beyond a strong phylogenetical signal, the endocast morphology reflects some notable ecological trends: e.g., 1) fossorial species present a reduction of the optic roof; 2) both fossorial and marine species have cerebral hemispheres with a small lateral projection; 3) cerebral hemispheres are more developed in arboreal and terrestrial species. This study provides the first elements of comparative neuroanatomy in snakes, and shows that this structure, as in mammal and bird endocasts, carry both phylogenetical and ecological information.

SBN1-3 10:00 am

The bones and genes of smell: Cribriform morphology and olfactory receptor gene repertoires.

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Abstract: Mammals are assumed to have a keen sense of smell. Yet, the mammalian olfactory system has undergone losses as well as gains throughout its evolutionary history, generating a diverse olfactory profile, morphological and molecular, across all orders. The anatomy of olfaction varies markedly in mammals and includes the complete loss of the olfactory bulb in toothed whales. Annotated genomes reveal that some species, such as the elephant, have experienced an expansion of their olfactory receptor (OR) gene repertoire, while others, such as the great apes have experienced strong reductions. OR genes code for specific odorant receptors types, each of which is found on thousands of sensory neurons distributed across the olfactory epithelium. For this reason, we hypothesize that there is a relationship between the relative number of OR genes and olfactory anatomy. To test this, we quantified cribriform plate (CP) morphology in 26 mammal species for which we know the total number of OR genes and percentage of non-functioning pseudogenes. The CP was chosen for two reasons: 1) its perforations offer a direct imprint of all olfactory innervation passing from the nose to the brain, and 2) the CP is retained in dry skull samples and fairly well preserved in fossils. Using high resolution CT scans and 3D imaging software we estimated the surface area of the CP as well as the cumulative cross-sectional area of its foramina. Preliminary results show a significant positive correlation between the number of functioning OR genes and cribriform plate morphology. A second molecular metric, percentage of pseudogenes, shows no relationship to CP size. This is interesting, given that

the percentage of OR pseudogenes is regularly used in the literature as a predictor of the relative loss of olfactory function. The results of this study, when applied to the CP morphology of fossil mammalian skulls, may help us gain insight into the relative size of the olfactory subgenome in extinct species.

SBN1-4 10:15 am

A comparison of the fluid dynamics and odorant deposition of unsteady sniffing versus quasi-steady breathing in the nasal cavity of the coyote.

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Abstract: The mammalian nose is a complex organ responsible for conditioning and filtering of inspired air, as well as sensing chemicals in the environment. Most carnivores have a complex nose with a convoluted airflow path that increases surface area for respiratory heat and moisture exchange, and odorant deposition. The coyote, in particular, possesses a complex nasal airway with a significant amount of olfactory epithelium for its size, likely reflecting its enhanced olfactory ability. Physically, airflow and odorant deposition in the nose are the first steps that influence olfactory function. In this regard, previous studies have shown that unique airflow patterns develop in the canine nasal cavity during sniffing that are optimized for delivering odorants to the olfactory region. To date, however, no studies of mammalian olfaction have compared the influence of unsteady sniffing versus quasi-steady breathing on olfactory function. This is especially important given that most studies of nasal airflow and odorant deposition assume quasi-steady conditions and do not consider the unsteady effects of sniffing. In this work, we examine how the dynamics of sniffing influence nasal airflow patterns and the deposition of odorants in the nasal cavity of the coyote. A three-dimensional model of the coyote nose is reconstructed from high-resolution magnetic resonance imaging (MRI) scans, and used in computational fluid dynamics (CFD) simulations of airflow and odorant deposition for steady-state inspiration, steady-state expiration, and unsteady sniffing. A comparison of the nasal airflow patterns, flow distribution in the nose, and odorant deposition will be shown to elucidate the influence of sniffing on olfactory function.

SBN1-5 10:30 am

Nasal morphometry and airflow dynamics in a nocturnal primate, *Nycticebus pygmaeus* (Mammalia: Primates).

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Abstract: "Macrosmatic" mammals, those most highly adapted for olfaction, have dedicated olfactory regions within their nasal cavity, and segregated airstreams for olfaction and respiratory air-conditioning. Here we examine the distribution of olfactory surface area (SA) and nasal airflow patterns in the pygmy slow loris (*Nycticebus pygmaeus*), to determine whether their complex nasal cavities are similar to "macrosmats" such as canids. Using the head of one adult loris cadaver, we co-registered micro CT slices and histology sections to create a 3D reconstruction of the olfactory mucosa distribution. Histological sections were photographed and converted to binary images for morphometric and functional analyses using custom image processing software. CT reconstructions of bone coded for mucosa type reveal the loris has a complex olfactory recess (~19% of total nasal SA), with multiple olfactory turbinates. However, the first ethmoturbinate has a rostral projection that extends far anterior to the olfactory recess, and ~90% of the SA of this turbinate is covered with non-olfactory epithelium. A computational fluid dynamics simulation of airflow indicates that high speed flow is restricted medially, along the respiratory surfaces of the first ethmoturbinate and maxilloturbinate. The slowest moving airstreams are found laterally in paranasal regions and posteriorly within the olfactory recess. Moreover, some airflow that reaches the olfactory recess does not pass through the dorsal meatus. This pattern is notably different than reported for canids, in which olfactory airstreams are shunted through the dorsal meatus, separately from respiratory airstreams, to an olfactory recess in which all ethmoturbinates are mostly covered with olfactory epithelium. The results indicate that lorises may be said to have certain macrosmatic anatomical characteristics (e.g., olfactory recess), but not segregated nasal airflow patterns as in the dog. Funding: NSF BCS-1231717, BCS-1231350, IOS-1120375.

SBN1-6 10:45 am

Comparative morphology and histology of the nasal fossa in four mammals: gray squirrel, bobcat, coyote, and deer.

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Abstract: Comparative studies of the quantity and distribution of olfactory epithelium (OE) in mammals have been largely limited to species <1kg due to the difficulty of applying traditional histological approaches to larger specimens. Here we present data on olfactory and non-sensory tissue distribution in the nasal fossa of 4 mammals: gray squirrel, bobcat, coyote, and deer, ranging from 0.42 kg to 62 kg. These species were chosen because they could be acquired fresh from hunters in accordance with local regulations. Moreover, they exhibit a range of skull shapes and diets that might affect OE quantity and distribution. Nasal cavities were scanned using high-resolution MRI and then prepared for histological analysis. The noses were sectioned and OE was highlighted using staining and immunohistochemistry. On selected sections, the perimeters of the septum, maxilloturbinates, nasoturbinates and

ethmoturbinals were measured using ImagePro Plus software. We quantified the total surface area of OE and non-sensory epithelium in the nasal cavity as well as its anatomical distribution. In all four species, OE was entirely absent from the maxilloturbinals and was confined to the caudal half of the nose on the septum, nasoturbinals, and ethmoturbinals. Total surface area of OE did not correlate well with body mass. Although the squirrel had the least OE, the similarly sized 15 kg coyote and 12 kg bobcat differed greatly in total OE surface area, with the canid having a much larger area comparable in extent to that of the 62 kg deer, suggesting greater olfactory ability in the canid. The gray squirrel differed from the other 3 species in having a much greater proportion of its nasal fossa lined with OE, which is similar to what has been observed in other small mammals. Our results suggest that both skull size and shape influence OE distribution, as has been shown for some primates.

SBN2-1 11:30 am

Adaptive signals in the morphological evolution of vertebrate eyes.

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Abstract: The morphology of vertebrate eyes often seems to match the visual requirements imposed by the photic environment of the organism. In particular the preferred activity time in the 24 hour cycle (diel activity pattern) is considered to strongly influence the morphological evolution of eyes. For example, the eyes of night-active (nocturnal) organisms often feature traits consistent with improved light sensitivity, whereas eye shape of day-active (diurnal) organisms tends to reflect bright light levels. Even though empirical data strongly point towards adaptive evolution as the underlying mechanism producing the observed patterns, rigorous analyses of the tempo and mode of evolution are rare. Using the R-package SLOUCH and time-calibrated phylogenies, I characterized the phylogenetic half-life and stationary variance of visual performance features in three different vertebrate clades. Two of the investigated clades represent avian radiations (Strisores, n=59 sampled species; Afroaves, n=74), whereas the third clade is mammalian (Euarchontoglires, n=109). All clades feature a large diversity of diel activity patterns (nocturnal, diurnal, as well as day/night or twilight activity, grouped as cathemeral/crepuscular) and multiple evolutionary trait reversals, making them ideal for studying adaptive evolution. In the presence of strong selection, phylogenetic half-life (time to evolve half the distance from an ancestral state towards the optimum of a novel selective regime) and stationary variance (tendency to deviate from the optimum) are expected to be low, whereas both phylogenetic half-life and stationary variance may approach infinity when non-selective mechanisms are prevalent. My results suggest strong selection on eye shape evolution in both bird clades, whereas selection is much reduced in mammals. It is possible that non-visual senses are more important for fitness in mammals and hence weaken the functional constraint on eye shape evolution.

SBN2-2 11:45 am

Drivers of visual field evolution in mammals.

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Abstract: Mammals have highly varied visual systems, which is likely due to the extraordinary diversity of their ecological niches. Among mammals, visual field overlap, measured as orbital convergence, varies from a high degree of convergence (i.e. binocular vision) to the non-overlap of visual fields (i.e. panoramic vision). Three primary hypotheses have formed the basis of understanding visual field evolution in mammals: the predation risk, nocturnal restriction, and arboreal-depth perception hypotheses. Among mammals, binocular vision is most strongly associated with the primates. The 'nocturnal visual predation hypothesis' incorporates the predation risk, arboreal-depth perception and nocturnal restriction hypotheses to explain visual field convergence among primates. We used phylogenetic generalized least squares regression to simultaneously test the various hypotheses that have been proposed to explain visual field evolution using a large sample of mammalian species (~329). We include data relevant to the hypotheses outlined above including body mass, habitat, activity period, social behavior, and trophic level. We fail to support the nocturnal restriction hypothesis. However, we find that habitat openness has interacted with body size and activity period during the evolution of orbital convergence in mammals. We show that a single hypothesis is insufficient to explain the evolution of morphological characters that are evolutionary mosaics, reflecting ecological and behavioral evolution among mammal clades.

SBN2-3 12:00 pm

Exploring the evolution of the auditory morphology of primates using *in-situ* soft-tissue visualization and geometric morphometric.

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Abstract: Extant primates show substantial diversity in their auditory morphology. Such variation is known to be related

to aspects of hearing and/or could also reflect morphological alterations of surrounding structures. Studying the ear region of fossil primates could thus shed light on their auditory capacities while potentially providing information on the evolution of the cranial base as well. Studying the ear region, however, remains methodologically challenging due to the complex three-dimensional morphology of its delicate structures hidden inside the temporal bone. Individual structures of the ear are thus commonly measured separately and hardly anything is known about their spatial relationships. Moreover, precisely inferring auditory function requires quantitative data about soft-tissues to be obtained, which remains to be done for primates. Here, we present an approach to quantitatively study the three-dimensional shape and functional relevant measures of the middle ear and cochlea, including essential soft-tissue structures. Applied to 27 primate species, this approach is based on contrast-enhanced *in-situ* visualization of micro-CT images and semilandmark-based geometric morphometrics (GM). Results of the GM analysis show in detail distinct differences in shape, size and spatial configuration of the ear region from tympanic membrane to cochlea across primates. Furthermore, functionally important measures like tympanic membrane area and cochlear duct volumes will be discussed. This approach expands the knowledge of the morphological diversity of the auditory region and provides a strong basis for reliably reconstructing its morphology and function in fossil primates. This research was funded by the Max Planck Society.

SBN2-4 12:15 pm

Some chameleons really do "hear it through the grapevine."

Huskey S.H. *, Western Kentucky University; Anderson C.V., Brown University; Smith M.E., Western Kentucky University; Barnett K.E., New York State Department of Environmental Conservation steve.huskey@wku.edu

Abstract: Though less studied than airborne, acoustic communication, a number of animals communicate via substrate vibrations. For example, many bird species communicate with conspecifics via vibrations and elephants have been shown to communicate over long distances with vibrations through the ground. Further, it's believed that >90% of insects use some sort of vibration to communicate. One group that has been understudied in terms of vibratory communication is reptiles, likely because their vocalization abilities are often lacking and entire reptilian groups are deaf to airborne sounds (e.g. snakes). An exception is the veiled chameleon, *Chamaeleo calyptratus*, which can produce a low-frequency, buzzing sound emanating from the throat region, which we hypothesize to be produced by a specialized out-pocketing of the trachea known as the gular pouch. This sound results in a vibratory signal transmitted through a tree branch and is often used when the animal feels threatened or during courtship/mating. This is the first documented case of plant-borne, vibratory signaling in any reptile, and while anecdotally noted in other chameleon taxa as a threat response, this phenomenon has not been examined in detail in *C. calyptratus* or other chameleon species. Here, we compare gular pouch morphology among chameleon taxa and relate it to reported abilities to produce vibratory threat responses. We then hypothesize how these structures are used to generate seismic vibrations. Producing and detecting vibrations by chameleons may represent the earliest means of seismic communication among terrestrial vertebrates. As chameleons have neither the vocal cords or syrinx known to produce seismic vibrations in other terrestrial vertebrates, their vibrations must be produced in a completely novel way. These results therefore provide valuable insights into the evolution of key tracheal modifications and a novel communication strategy.

SBN2-5 12:30 pm

The origin of ultrasonic hearing in whales: new insights from morphometric studies of the inner ear.

Churchill M*, New York Institute of Technology; Geisler JH, New York Institute of Technology; Martinez-Caceres M, National Museum of Natural History, Paris France mchurchi@nyit.edu

Abstract: Odontocetes (toothed whales) are rivaled only by bats in their ability to hear ultrasonic frequencies. However, the origin of ultrasonic hearing within whales is still unknown, and most studies on whale inner ear morphology have been qualitative, with few rigorous statistical analyses. To determine how and when ultrasonic hearing evolved, we performed PCA on 8 measurements of the cochlea taken from HR-CT scans of 25 whale and outgroup taxa. Several fossil odontocetes were sampled, including an early diverging xenorophid. Measurements analyzed included length of cochlea, length of secondary bony lamina, 2 measures of width of the basal turn, height of cochlea, maximum distance between turns, radius of the spiral ganglionic canal, and area of the fenestra cochlearis. Approximately 86% of the variation was explained by the first two components. PC 1 explained 56% of the variation and reflected overall variation in body size. PC 2 explained 29% of the variation and separated taxa into two discrete morphospaces: taxa that hear at ultrasonic frequencies, comprised of all odontocetes, and an infrasonic hearing morphospace, comprised of mysticetes and hippopotamids. Basilosaurids occupied an intermediate zone between both morphospaces. Xenorophid whales possess a high basal ratio and very long secondary bony lamina, both traits associated with ultrasonic hearing. However they possess a relatively small spiral ganglionic canal when compared to odontocetes, suggesting a lesser degree of acoustic signal processing ability than modern odontocetes. Using ancestral character state reconstructions generated by Mesquite 2.75, we determined that ultrasonic hearing evolved at the base of Odontoceti. Our study also demonstrated that initial enlargement of the spiral ganglionic canal and an increase in the length of the secondary bony lamina occurred within Archaeoceti, indicating that adaptation towards high frequency hearing preceded the evolution of echolocation in odontocetes.

SBN2-6 12:45 pm

Functional morphology of mysticete sound reception: constructing the first baleen whale audiogram using finite element modeling.

Cranford T/W*, San Diego State University; Krysl P, University of California, San Diego; Potter C/W, Smithsonian Institution tcranfor@mail.sdsu.edu

Abstract: Vocalization frequencies in baleen whales (Mysticeti) overlap with low-frequency anthropogenic sound sources, but mysticete sound reception mechanisms are essentially unknown. Synthetic audiograms were generated for a fin whale by applying finite element modeling (FEM) tools to X-ray CT scans. We scanned the head of a small fin whale (*Balaenoptera physalus*) in an industrial CT scanner designed for solid-fuel rocket motors. Our custom FEM toolkit allowed us to visualize the interactions between sound and the anatomic geometry within the whale's head. Simulations reveal two mechanisms that excite each of the bony ear complexes (TPCs): (1) the skull-vibration enabled bone conduction mechanism and (2) a pressure mechanism transmitted through soft tissues. Bone conduction is the predominant mechanism that contributes to low-frequency sound sensitivity (Cranford and Krysl, 2015). Recent preliminary simulations suggest a sensory basis for directional hearing based on phase differences between waves that arrive at the TPCs through skull deformation. We have also succeeded in reconstructing an entire minke whale specimen (*Balaenoptera acutorostrata*) from CT scan data. These results have important implications for assessing mysticete exposure to levels of anthropogenic noise and for understanding various aspects of ecological morphology associated with baleen whale sound reception. [Cranford, T. W., and Krysl, P. (2015). "Fin Whale Sound Reception Mechanisms: Skull vibration enables low-frequency hearing," in PLoS ONE (Public Library of Science, San Francisco), p. e116222.] Funding for this project was provided by Dr. Michael Weise at the Office of Naval Research (N00014-12-1-0516).

Symposium — Segmentation and serial homology: surprising new insights for long-standing central questions in vertebrate morphology (SEG)

Organizers: Rui Diogo, Gunter Wagner, Fritson Galis

SEG1-1 9:30 am

Serial homology: how does it fit into the picture?

Wagner G. P. *, Yale University gunter.wagner@yale.edu

Abstract: While biologists have developed a reasonably coherent understanding of homology as it applies to "the same organ in different species regardless of form or function", the concept of serial homology is more controversial. One argument is that, reasonably, serial homology applies to different parts of the same organism, and for that reason the phylogenetic definition of homology does not fit; ergo serial homology is not homology at all. In this contribution I will present another perspective, which applies to both "special" homology (homologous parts of different species) as well as to parts of the same organism, namely the notion of genetic/developmental individualization. For the phylogenetic homology concept to be meaningful it has to be limited to the comparison of developmentally individualized body parts (this point will be argued more in detail in the talk). However, as soon as we include the notion of developmental individuality, we are also freed from the strictures of the phylogenetic definition and can consider the identity of body parts within the same body. In doing so one has to recognize that we need to distinguish between two categories of serially homologous characters: homomorph and paramorph characters. Homomorphs are simple reiterations of the same developmental program, like multiple instances of the same cell type. The term paramorph derives from the concept of a paralog gene, i.e. two body parts are paramorph if they ancestrally derive from a homomorph reiteration of the same character but each acquired developmental individuality such that they are now two individualized body parts. The notion of paramorph characters is particularly clear in the case of cell type evolution according to the sister cell type concept. The notion of paramorph characters also implies that groups of characters have a hierarchical structure of relatedness. Finally I will address the recent hypothesis that tetrapod fore- and hind limbs are not serially homologous.

SEG1-2 10:00 am

Serial homology vs. derived similarity of pectoral and pelvic appendages: comparative, genetic, evo-devo and network studies in fish, tetrapods, and human birth defects.

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Abstract: Most evolutionary and medical textbooks state that the pectoral and pelvic appendages of fish, and therefore the fore and hindlimbs of tetrapods, are serial homologues. However, such statements are mainly the consequence of a repetition of older ideas that were formulated based on romantic ideas and/or the notion of an 'archetype', and that were never tested against empirical data. Here we show how such statements are contradicted by regenerative studies of axolotls, developmental studies of tetrapods, and comparative and evolutionary studies of all major vertebrate groups, including recent re-analyses of the appendicular muscles of chondrichthyans, dipnoans and coelacanth contradict this old dogma, a literature review on the available paleontological data, and the use of novel, state-of-the-art systems biology methods such as anatomical network analyses. That is, the integrative analysis of the data available strongly supports the idea that the similarity of the muscles and bones of the fore and

hindlimbs of tetrapods such as salamanders and modern humans is not due to serial homology, but is instead the result of independent evolutionary changes (homoplasy) occurred mainly during the origin of tetrapods due to the co-option of similar genes for the development of both limbs. In fact, contrarily to the limbs, and particularly their most distal regions, the pelvic and pectoral girdles were seemingly very different from the moment they appeared, and have remained very different from each other since then, an idea supported by recent studies of both anatomical and genetic networks. More than becoming lost on specific definitions of what is serial homology, the important take-home message is therefore that the similarity between the pectoral and pelvic fins of fish, and particularly of the fore and hindlimbs of tetrapods, is a derived - and not an ancestral, as has been dogmatically assumed for more than 250 years - similarity.

SEG1-3 10:30 am

The evolution of head segmentation in the Phylum Chordata.

Holland L*, *University of California San Diego*; Gilland E, *Howard University* lzholland@ucsd.edu

Abstract: A major controversy in evolution of vertebrates from their invertebrate ancestors is whether vertebrate head is fundamentally segmented and inherited this segmentation from an amphioxus-like ancestor. In amphioxus, segmented musculature extends the full length of the body. The pharynx also contains a segmental series of gill slits. While it is generally agreed that the head cavities of agnathans (premandibular, mandibular, and hyoid) evolved from the anterior somites of an amphioxus-like ancestor, the relationship between the head cavities of sharks and those of lampreys remains controversial as does the relationship between head muscles of bony vertebrates and the head cavities and head muscles of sharks. Evidence from comparative morphology of vertebrates and amphioxus and from patterns of gene expression is consistent with an evolutionary scenario in which the anterior somites of an amphioxus-like ancestor gave rise to the head cavities of the lamprey and shark, and into the eye and jaw muscles in bony vertebrates.

SEG2-1 11:30 am

Medial-lateral aspects of anterior-posterior patterning in the vertebrate body plan.

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Abstract: The regionalization of the anterior-posterior (AP) axis is an important feature of vertebrate diversity and varies widely between taxa. An axial Hox code is strongly correlated with AP patterning of somite-derived tissues, especially the vertebrae. Beyond these axial structures and their intrinsic muscles, variation in morphology along the AP axis is a matter of different interactions between somitic and lateral plate mesoderm in the mediolateral dimension. These interactions result in primaxial and abaxial domains, separated by the lateral somitic frontier. We have examined the frontier in a wide range of vertebrates including chick, mouse, axolotl, shark and lamprey. We hypothesize that developmental patterning is independent on either side of the frontier, facilitating morphological evolution while maintaining integration between axial and appendicular systems.

SEG2-2 12:00 pm

Acquisition of serial patterning and the making of a 'segment' across the evolutionary origin of the vertebrate jaw.

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Abstract: A developing vertebrate head is a whole of many serial structures: hindbrain rhombomeres, neural crest streams, head cavities, pharyngeal arches and pouches, epibranchial placodes, and others. Although the traditional view of a unified segmentation scheme no longer holds, it remains a puzzle whether these serial structures originated at once or independently. A long-standing challenge to differentially test these alternative hypotheses is to identify more than one evolutionary event in which significant additions or modifications occurred to the serial patterns. I provide fossil and developmental evidence for such modifications in the pharyngeal apparatus at the origin of jawed vertebrates. Comparison between cyclostomes (hagfish and lampreys) and gnathostomes (jawed vertebrates) reveals that the mandibular region does not have a typical pharyngeal arch organization in cyclostomes. A diffuse boundary between "premandibular" and "mandibular" anlagen does not persist. In addition the "mandibular" ectomesenchyme occupy posterior positions in the head of cyclostomes that would only emerge as developmental defects in gnathostome embryos. Mapping of musculoskeletal elements in multiple extinct lineages of jawless vertebrates reveals similar patterns to cyclostomes in general, but also suggests that diffuse boundaries around the "mandibular" elements independently evolved in hyoid or hypobranchial positions in some lineages. A synthesis of the evidence indicates that the mandibular arch (typically labeled as PA I or BA I) acquired a pattern serial to the rest of the pharyngeal apparatus only at the origin of the jaw. This Mandibular Confinement Hypothesis leads to an emerging view that (a) in the last common ancestor of all living vertebrates, only hindbrain rhombomeres and pharyngeal pouches were truly segmented in the head; and (b) serial patterns in the living jawed vertebrate head gradually evolved through interdependent tissue interactions facilitated by multipotency of neural crest ectomesenchyme.

SEG2-3 12:15 pm

Serial homology of paired appendages and sexual organs: studies in early gnathostome fossils.

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Abstract: Among living early vertebrates, specialized copulatory organs resulting in internal fertilization occur in chondrichthyans (sharks) and osteichthyan (bony fish). For example, the claspers of sharks are a modification of the pelvic fin whereas in bony fishes the gonopodium is a modification of the anal fin. Specialized copulatory organs are absent in the jawless lampreys and hagfishes. This seems to imply that internal fertilization and viviparity are evolutionary novelties in these groups, and primitively absent in early jawed vertebrates. However, recent discoveries in placoderms (extinct armored fishes), currently resolved as a paraphyletic grade along the gnathostome stem, questions this interpretation. When first discovered, the copulatory organs in placoderms were predicted to be similar to sharks (i.e., part of the pelvic fin skeleton), but are now known to be completely independent of the pelvic girdle and fin. In addition, it is now apparent that the pectoral, pelvic, as well as the copulatory structures comprise dermal and perichondral bony elements suggesting that the claspers in placoderms represent a third set of paired appendages serially homologous with pectoral and pelvic fins. Within the fossils from the Gogo Formation in the Canning Basin (Devonian, Western Australia) soft anatomy is preserved in 3D as apatite, including specialized muscles associated with the paired appendages. A unique set of muscles in the abdominal region of placoderms appear morphologically more similar to squamate musculature than fishes and are interpreted as operating the paired copulatory organs. By comparison with other gnathostomes, these observations suggest that placoderms could be more informative regarding the acquisition of not only reproductive structures, but also paired appendages.

SEG2-4 12:30 pm

There may be more to the Hox Code than you thought. The "Distal Phase" HoxA/D expression pattern is an ancient module that is deployed in a variety of novel features in vertebrates.

Crow Karen *, San Francisco State University crow@sfsu.edu

Abstract: Fins and limbs are homologous structures patterned by a shared genetic repertoire of HoxA/D expression, or "the Hox limb building toolkit". A unique inversion of the HoxD expression pattern is associated with the most well characterized example of a novel fin/limb modification to date-the tetrapod autopod, where an inverted collinear HoxD expression pattern specifies digit identity and the origin of the thumb. This pattern also occurs in paddlefish pectoral fins and catshark paired fins, indicating that it arose in the common ancestor of jawed vertebrates. We refer to this pattern as "distal phase" (DP) expression because it occurs in distal structures and is regulated independently. We argue that it may be deployed in a modular fashion, suggesting a greater role in the evolution of morphological diversity in vertebrates than previously recognized. We demonstrated the first evidence for HoxD DP expression in a body plan feature beyond fins and limbs- the paddlefish barbel, and the first evidence for HoxA DP expression in the developing hindgut and vent of ray-finned fishes, suggesting that the limb-building program may have an expanded repertoire. Interestingly, HoxA DP expression is predicted by similar conformational properties between the HoxA/D cis-regulatory landscapes in zebrafish and mice, but has not been reported in vertebrate paired appendages. However, we found evidence suggesting that HoxA DP expression occurs in claspers-modified pelvic fin structures in male cartilaginous fishes. Taken together, these data support the modularity of DP Hox expression pattern, and a greater role for the Hox code in evolution of novel body plan features.

Symposium — Morphology & evolution of the Xenarthra (XEN)

Organizers: Susana Bargo, John Nyakatura

XEN1-1 9:30 am

Recent progress and future prospects in fossil xenarthran studies.

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Abstract: The ICVM meetings have become near-regular gatherings for us to present our latest findings and share our ideas and thoughts. It is appropriate that we occasionally reflect on our recent efforts, certainly to recognize and celebrate our successes but also to consider where we might do better and plot out a path for future endeavors. One highlight since our first Symposium (ICVM 6, Jena) is that there are more of us. The need for producing "intellectual descendants" is keenly felt and strong efforts have been made toward this end, but some of us, including fairly active members, have produced few, if any, students (mainly due to institutional restrictions). In such cases, it is important to promote more active participation of such members in student committees. Our field efforts to recover fossil xenarthrans have also increased, leading to further systematic work. Such activity continues in more traditionally worked areas, but efforts have increased in regions traditionally less well known, the northwestern and generally older deposits of South America. Certainly this has yielded much new information. However, perhaps the most fruitful efforts over the past 15 years are those focusing on functional morphology and paleobiology, which have produced a wealth of new understanding. Among these, the La Plata Museum-Duke University expeditions stand out for their recovery of numerous remains that have promoted paleobiological studies while also allowing reconsideration of long-standing systematic issues, thus combining the main thrusts of our research. One pressing issue is the continued need to recognize the importance of variation among fossil remains. We have learned much from recent studies of extant xenarthrans and the recovery of large fossil collections in this regard, but have yet to apply it more consistently to our systematic work. Closer integration of studies on fossil and living xenarthrans should prove fruitful in this regard and for functional morphology.

XEN1-2 10:00 am

Potential distribution of fossil xenarthrans during the late Pleistocene.

Varela L., Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay; Tambusso P.S., Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay; Di Giacomo M., Department of Art Conservation, University of Delaware, Delaware, USA; Patiño S.J., Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay; Fariña R.A.*, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay dogor@netgate.com.uy

Abstract: Species distribution models (SDMs) are helpful for understanding actual and potential biogeographical traits of organisms. SDMs for the last interglacial (LIG), the last glacial maximum (LGM) and the Holocene climatic optimum (HCO) were generated for 11 South American late Pleistocene xenarthrans; five Cingulata, *Glyptodon clavipes*, *Doedicurus clavicaudatus*, *Panochthus tuberculatus*, *Neosclerocalyptus paskoensis*, *Pampatherium humboldtii*, and six Pilosa, *Glossotherium robustum*, *Lestodon armatus*, *Myiodon darwini*, *Catonyx cuvieri*, *Megatherium americanum*, and *Eremotherium laurillardi*. Co-occurrence records were studied based on the overlap of their generated areas of potential distributions and compared with the available biome reconstructions of South America during the LGM to analyze species distribution patterns, ecological requirements and possible interactions. Our results suggest that sloths could have had a large co-occurrence area mainly in the Chaco-Paraná and the plains in the Río de la Plata regions, and a smaller area mainly in northeastern Brazil. At least two cases of possible competitive exclusion might have occurred in tropical South America, between *Megatherium* and *Eremotherium*, and possibly between *Glyptodon* and *Glyptotherium*. In both cases, potential distributions overlap but no co-occurrence is recorded. Areas of high suitability were observed for submerged parts of the continental shelf exposed during the LGM, showing an overall increase in potential habitat compared to the LIG and HCO. This, coupled with warmer conditions, suggests a drastic reduction in total available areas of preferred habitat at the end of the Pleistocene for most taxa. When all potential distributions are considered together, a northern latitudinal shift could be observed between the LGM and HCO both in Cingulata and Pilosa.

XEN1-3 10:15 am

Phylogeny and historical biology of sloths.

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Abstract: After 34 Ma of evolutionary history in South America, sloths reached North America during the GABI, were part of the impressive Pleistocene megafauna and only *Choloepus* and the basal *Bradypus* survived the Quaternary extinction. Here several recently described taxa were added to a previous morphological data matrix. Bayesian phylogenetic inference and Tip-Dating were applied to 57 genera to investigate their diversity, morphological disparity and biogeographical history. The obtained phylogeny supports the commonly recognized clades but some taxa, both traditional and recently described, are placed in different families. Our results give divergence time estimates for the major clades, which cannot be dated with molecular methods. Diversity increased early until Middle Miocene and then remained steady until the Quaternary extinction. Two diversity drops are observed, at the end of the Santacrucian and at the end of the Huayquerian. Phenotypic rates were initially high, with the diversification of superfamilies Mylodontoidea and Megatherioidea, but declined ca. 24 My ago, followed by a slow increase in rates as families diversified. Similarly, morphological disparity showed an early increase and a stable phase during much of the Miocene followed later by an increase associated with familial diversification. Southern South America was the most probable area of origin and of early diversification. Both megatheriid and nothrotheriid basal nodes were strongly correlated with Andean uplift events, while the complex, somewhat unresolved mylodontid early history showed an early occupation of the northern regions of South America. Quaternary South American megalonychids have North American forerunners while *Choloepus* have Antillean ancestors. After a complex ecomorphological and biogeographical history, the Quaternary extinction left only two living small genera, phylogenetically distant though very similar in general morphology and tree-dwelling habits.

XEN1-4 10:30 am

Osteoderms in ground sloths: plesiomorphic or apomorphic?

McDonald HG*, Bureau of Land Management hmcDonald@blm.gov

Abstract: Osteoderms occur in many tetrapods. In mammals osteoderms are only present in xenarthrans and for the Cingulata, armadillos, pampatheres and glyptodonts, form a distinctive feature, the carapace. The number of carapace osteoderms may exceed the number of bones of the skeleton and the earliest xenarthran records are based primarily on osteoderms, leading to the assumption that osteoderms are plesiomorphic in xenarthrans rather than a bias reflecting a common, easily preserved bone. If osteoderms are not considered but only the rest of the skeleton, the earliest records of both cingulates and pilosans occur at essentially the same time. In pilosans, osteoderms are only documented for a small number of mylodontine sloths and one species of megatherium and have

never been reported from megalonychids and nothrotheres. If osteoderms are pleisomorphic for xenarthrans they should be present in all the earliest sloth clades, and their absence should occur later in time with perhaps retention in only a few clades. This is not the case and all known osteoderm records in sloths occur later in time. It is proposed that osteoderms in a few closely related mylodontine sloths and a single megatheres are instead neomorphs, and not derived from an ancestral cingulate.

XEN1-5 10:45 am

When development and paleontology meet: novel developmental data shed new light on the evolutionary history of the Xenarthra.

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Abstract: Some mammalian clades are quite novel to morphologists (e.g., tenrec-golden mole-paenungulate; hippo-whale) and would not have been recognized without the recent analyses of molecular data. In contrast, the mammalian clade Xenarthra has a long history in comparative anatomy. The superorder includes the armadillos, anteaters, and tree sloths and is one of the four major lineages of placental mammals recently defined. Since the 19th century, biologists have been fascinated by their morphological peculiarities and have made some intriguing observations on their development. However, previous analyses rarely provided a comparative basis upon which to analyse possible homologies with the morphology of other mammals. Our past developmental studies have focused on the sequence of ossification events during growth in the skull and skeleton, and have shown that xenarthrans display heterochronic shifts as compared to other placental mammals. Here we extend our work by focusing on the development of specific anatomical features: xenarthrous vertebral articulations in armadillos and caniniform teeth in sloths. While the condition of xenarthrous vertebrae has been known to researchers since the first descriptions of xenarthrans, there is still uncertainty regarding the function and development of the involved articulations, and intermediate vertebral conditions remain unknown in the fossil record. Our study provides a novel developmental perspective on the evolution of xenarthrous morphology. In terms of tooth development, our developmental data directly supports the claim that the sloth lower caniniform teeth are not homologous to canines of other mammals and that upper caniniforms are not homologous between the two-toed and the three-toed sloths. Applied to the tooth row of all extinct sloths, these data support the interpretation that the dental morphology of the three-toed sloth is unusual and illuminate a potential ancestral dental formula for sloths.

XEN2-1 11:30 am

Expanded diagnosis of the ground sloth *Mylodon darwini* (Mammalia: Xenarthra: Pilosa) and the functional implications.

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Abstract: Although *Mylodon darwini* was initially described in the mid-1800s, present day characterization of the taxon has been restricted to diagnoses of only the skull, tibia, and astragalus. A partial skeleton assignable to *M. darwini* provides the opportunity to expand the diagnosis for this Lujanian-Ensenadan (late Pleistocene) ground sloth, primarily for the atlas (C1) and elements of the left forearm (radius, ulna, and some carpals and metacarpals). *M. darwini* is generally larger in size than contemporary mylodontids (i.e. *Catonyx*, *Glossotherium*, *Scelidotherium*) with the exception of *Lestodon*. Atlas vertebra of *M. darwini* bears distinct dorsal and ventral arch tuberosities suggesting well-developed rectus capitis ventralis and rectus capitis dorsalis minor muscles, which is in contrast to mylodontids with only one (e.g. dorsal) or no arch tuberosities. The occipital condyle articulations are very broad and triangular shaped, as in *Glossotherium*, and are not squared like *Scelidotherium*. These atlas characters together are adaptations for supporting a long and wide cranium. Radius lacks the distinct pronator flange seen in scelidotheres and *Lestodon*, and the dorsal margin of the ulna is straight and unbowed. The unciform and magnum each possess a third facet for articulation with the each other, and the lateral metacarpals exhibit a mediolateral thickening similar to that seen in other mylodontinae sloths. The combined forelimb features suggest *M. darwini* was primarily quadrupedal with the weight of the manus born by the lateral digits (IV and V) like that of other mylodontinae (e.g. *Glossotherium*, *Paramylodon*) in a horizontal position, as opposed to a vertical or "knuckle-walking" posture. Continued diagnosis of new elements (e.g. humerus, scapula) for *Mylodon* will further these functional inferences and relationships.

XEN2-2 11:45 am

Biomechanical study in claws of extinct sloths and extant xenarthrans.

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Abstract: The morphological variation in claws and ungual phalanges of vertebrates are associated to differences in the locomotor behavior of the species. These structures are the first to get in touch with the substrate and, consequently, they are adapted to the nature of that contact. This, in turn, depends on the characteristics of that

substrate and on the way in which the anatomical structures are applied to it. Here we analyze ungual phalanges of three extinct mylodontid sloths (*Lestodon armatus*, *Glossotherium robustum* and *Scelidotherium leptcephalum*) and claws of various groups of extant xenarthrans for actualistic comparison, aiming at testing hypotheses of substrate usage and locomotor behavior. For each species, the third digit was chosen because of its larger size and nearly perfect bilateral symmetry, which increases the possibilities of revealing functional differences between taxa. The inner and external curvature of the ungual phalanges and claws were measured and the mechanical advantage of its flexion in regard to the rest of the hand was calculated. In living species, it was observed that, as expected on mechanical grounds, in the curvature analyses all the digging species clustered together at lower values than those of non-diggers, which clustered separately. On the other hand, they all showed similar mechanical advantage values. The results obtained in this analysis indicates that the three genera of ground sloths were well adapted for strenuous activities, such as digging, in which force rather than velocity is optimized. The other two analyses allowed to identify the very large species *Lestodon armatus* and *Glossotherium robustum* as more able diggers than the relatively smaller *Scelidotherium leptcephalum*, although it cannot be ruled out that the less strong curvatures in the latter might have been due to a difference in the way the sediment was removed.

XEN2-3 12:00 pm

Early dietary, jaw shape and biomechanical performance differentiation in the evolution of armadillos (*Xenarthra*: *Cingulata*).

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Abstract: Armadillos are the most diverse group of extant xenarthrans, thus they are the most suited to investigate xenarthran evolutionary trends. Our aim was to explore the co-variation between some indicators of biomechanical performance, diet and the shape of the lower jaw in an evolutionary framework. We used Finite Element Analysis (FEA) to analyse the biomechanical performance of the lower jaw under equivalent loads. Mean values of stress were used as quantitative functional indicators. Also, we used geometric morphometrics to obtain shape variables for the lower jaw. 2D landmarks were digitalised on lateral pictures of jaws belonging to different species. Then, the first PC (explaining more than 80 % of variance) of a Principal Components Analysis (PCA) was used in some of the analyses as a single variable representing the main shape variability in our sample. We evaluated the covariation among jaw shape and jaw biomechanics using a Two-Block Partial Least Squares (PLS) analysis of the Phylogenetic Independent Contrasts (PICs). The influence of the diet on shape and biomechanics was evaluated with phylogenetic ANOVAs, and finally we applied maximum-likelihood evolutionary model to evaluate how shape and biomechanical performance evolved through the clade's history. Our results suggest that jaw morphology, diet and performance evolved slowly and differentiated mainly at the base of the tree. This translates into high within-lineage conservatism towards the present. Jaw shape and performance have a high covariance, indicating that they have coevolved. We also found a significant association of insectivory and omnivory with high and low performance values, respectively, in ordinary ANOVAs. However, when we controlled for phylogeny this relationship was not significant. This supports the scenario where the differentiation and this relationship arose early. Within closely related taxa, the relationship does not exist so it should not be considered a general rule.

XEN2-4 12:15 pm

Conceptual and methodological approaches for a paleobiological integration: the Santacrucian sloths (early Miocene of Patagonia) as a study case.

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Abstract: Paleobiological integration begins with the descriptive morphology and proceeds through a series of stages, finally reaching the paleosynecological reconstruction. This integration occurs through modeling of function, inference of faculties, performance and resource use to hypothesize the fundamental niche. Environmental information is then incorporated to speculate about biological roles and realized niche. The paleobiological integration of Santacrucian sloths is analyzed as a study case. These sloths comprise a diversity of eleven genera ranging from 40 to 120 kg in body mass; they are different morphologically from their living relatives. The realized niche of each taxon is reconstructed via integration of three paleoecological attributes: body size, dietary habits and substrate preference. An ecomorphological approach is applied, using Principal Components Analysis to explore the correlation between postcranial linear dimensions and substrate preference, together with functional indices. Integration of these results with previous studies indicates that the mid-sized genera *Hapalops*, *Peleciodon*, *Schismotherium* and *Analcimorphus* (stem Megatherioidea) and *Eucholoeops* (Megalonychidae) were members of the arboreal folivore paleoguild. The larger mylodonts *Analcitherium* and *Nematherium*, may have been semiarboreal consumers of leaves, fruits and tubers

thanks to their digging capabilities. *Prepothierium* (Megatheriidae), the largest and most terrestrial Santacrucian sloth, was also a folivore. Only the last three genera competed for trophic resources with other coexistent mammalian herbivores. The large body size and strength of the limbs with large claws made Santacrucian sloths only subject to predation by the largest Santacrucian carnivores, the borhyaenoids marsupials and phorusrhacoid birds. Finally, the absence of modern analogues to this heavy-sized arboreal and semiarboreal herbivore diversity is discussed.

XEN2-5 12:30 pm

Bend it like an armadillo: An investigation into the bending mechanics of the xenarthran vertebral column.

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Abstract: The xenarthran vertebral column is characterized by unique intervertebral articulations termed xenarthrae. These articulations are found between the posterior thoracic, lumbar, and first sacral vertebrae in all known xenarthrans, with the exception of glyptodonts and modern sloths. It is posited that xenarthrae stiffen the vertebral column, thereby serving as an adaptation to fossoriality in early xenarthrans. Here we investigate the implications of morphological regionalization of thoracolumbar vertebrae on the intervertebral bending mechanics of the nine-banded armadillo (*Dasypus novemcinctus*). We ran bending trials on excised "motion segments", consisting of two vertebrae and an intervertebral joint, in sagittal flexion and extension, and lateral flexion, in order to calculate compliance and range of angular motion across the region. A series of measurements were used to establish correlations between vertebral morphology and mechanics. We found a decrease in compliance in the post-diaphragmatic, xenarthrous vertebrae in all three measured directions, which was associated with a less substantial but notable increase in range of angular motion. Based on preliminary results, we predict that this decrease in compliance and increase in range of motion are indeed correlated with the morphological signatures of xenarthrous and post-diaphragmatic vertebrae. We therefore suggest that xenarthrous and post-diaphragmatic zygapophyseal articulations act in concert to passively stabilize the vertebral column, while allowing for greater mobility upon directed muscle activity. Xenarthrae can thus be considered as an extra layer of stability, precluding the need for additional exertion in these ancestrally digging mammals with particularly low metabolic rates.

XEN2-6 12:45 pm

Bone internal microstructure of the forelimb of xenarthrans (Mammalia) – functional implications.

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Abstract: The xenarthrans - sloths, anteaters, and armadillos and their extinct relatives - form an important group of placental mammals, today represented by taxa practicing several locomotor styles. While most armadillos are plantigrade, the tamanduas employ a highly peculiar stance, with the weight born on the lateral side of the hand. Additionally, giant anteaters utilise «pseudo knuckle-walking», the weight being born, for the hand, on the flexed ungual phalanges. Extinct xenarthrans, "ground sloths" in particular, were also reconstructed as practicing peculiar stances, mostly based on the gross morphology of their postcrania. Inner bone microstructure, and in particular the trabecular architecture, adapts to loadings applied to the bone throughout the whole life. The analysis of bone microstructural characteristics is hence a powerful tool that can potentially discriminate between different loading regimes withstood by the bone. Similarly, a previous analysis focused on bone compactness, was able to argue that the highly derived microstructure of one particular genus, was indicative of its aquatic habits. This past analysis also revealed that most xenarthrans, especially pilosans, depart from the mean mammalian condition in displaying rather compact bones. In the present preliminary analysis, we study the microstructural patterns of the forelimb bones of xenarthrans. With this new study, we aim at finding bone microstructural correlates to the various locomotor styles and modes of hand utilisation observed in extant xenarthrans. Ultimately, we endeavour to propose reconstructions of locomotor style in extinct taxa. EA is funded by the Alexander von Humboldt Foundation.

XEN3-1 2:30 pm

Architecture of dorsovertebral muscles corresponds with derived function of the vertebral column during suspensory locomotion in two toed sloths (Mammalia: Xenarthra).

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Abstract: Extant sloths are highly specialized in upside-down quadrupedal locomotion and completely lost the ability for asymmetrical gaits otherwise typical of terrestrial mammals. In order to study the consequences of the evolution of this derived locomotor mode on the morphofunction of the vertebral column we first analyzed *in vivo* intervertebral movements during locomotor trials of the sloths using x-ray motion analysis. To achieve this, sloths were trained to move on a motorized "tread-pole" in front of two perpendicular x-ray image intensifiers. When employing upside-down quadrupedal locomotion, dorsoventral flexion/extension of the sloth's spine is insignificant when compared to asymmetrical gaits of terrestrial mammals. Lateral bending and torsion of the spine, however, is as large as or even larger than what has been observed in right-side up terrestrial mammals. Subsequently, we tested whether this aberrant function of the vertebral column is also reflected in the muscle architectural properties of the dorsovertebral

muscles. We used layer-wise dissection of the transversospinal system, the longissimus, and the iliocostales to facilitate the 3D digitization of individual muscle fascicles. We determined fascicle length and orientation, the anatomical cross sectional area, muscle volume, and the moment arms to the intervertebral joints. These parameters were found to be in agreement with the previously observed kinematics: they favor extensive lateral bending and torsion, but are disadvantageous for powerful dorsal extension of the spine. The agreement of architectural properties with *in vivo* function documented in this study further characterizes the specific functional morphology of highly derived extant sloths.

XEN3-2 2:45 pm

Architectural specializations of the forelimb musculature of the three-toed sloth (*Xenarthra: Bradypus variegatus*).

Olson R*, Ohio University; Cliffe RN, Swansea University; Glenn ZD, Ohio University; Thomas DR, Youngstown State University; Kennedy SJ; Butcher MT, Youngstown State University ro603313@ohio.edu

Abstract: Sloths exhibit a range of arboreal locomotion that involves suspension by one or more limbs for extended periods of time. Despite these abilities that require great strength, their skeletal muscle mass is quite low; however, their overall limb form has been extremely modified for suspensory behaviors. The biomechanical functions of these modifications remain poorly understood due to the lack of available data on their limb morphology. To develop an initial understanding, we evaluated muscle architecture in the forelimb of (*Bradypus variegatus*) using measurements of moment arm (r_m), belly mass (MM), belly length (ML), fascicle length (LF), pennation angle (θ), and physiological cross-sectional area (PCSA). From these properties, estimates of isometric force, joint torque, and power were quantified. Our findings show that the limb retractors account for the greatest percentage of total forelimb muscle mass. Significant mass is also distributed to the limb adductors, elbow flexors, and digital flexors. Notably, the humeral medialis, radial, and ulnar heads of m. flexor digitorum profundus each have an isometric force capability similar to that of the massive and highly pennate m. subscapularis. Moreover, all of the antebrachial flexors have high PCSA:MM ratios indicating the substantial force production needed for prolonged suspension. No forelimb muscle has the capacity for high power, while numerous muscles have an architectural arrangement for applying large joint torque, and this capability is greatest among the limb retractors. The retractor and flexors muscles expected to exert large joint torque have low values for $FL:r_m$, and these are opposed by relatively high ratios for the limb protractors, and elbow and digital extensors. Collectively, these architectural specializations provide a means to compensate for the low muscle mass of sloths and suggest further modifications for sustained high force/joint torque.

XEN3-3 3:00 pm

Diagnostic imaging in Linnaeus's two-toed sloth (*Choloepus didactylus*)—pregnancy diagnosis and fetometry.

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Abstract: The knowledge of the reproductive physiology and biology of the two-toed sloth is fragmentary at best. So the data of the gestation period in the literature vary from 150 to 322 days. This study is intended to demonstrate the pregnancy diagnosis and the fetometry in the two-toed sloth with ultrasonography. The ultrasound investigations to visualize the genital system in this species can be performed transcutaneous or transrectal. Only the transcutaneous examinations can be performed without immobilization, if the animals are in medical training. The transcutaneous pregnancy examination is executed with a transducer frequency from 6 to 10 MHz. In total 23 pregnancies (n=10 animals) were diagnosed with certainty. The ultrasound investigations were also used to detect the fetal development (n=8 animals). The first indication of an existing pregnancy is the visualization of the gestational sac at the end of the first month of pregnancy. With the beginning of the second month of the gestation period, the embryo is detectable. In the same gestation month the cardiac activity can also be recognized. The crown-rump length of the fetus is only measurable in the third month. For the following months the fetal development is represented on the biparietal diameter (BPD) and the abdominal diameter (AD). The total gestation period in a two-toed sloth lasts 330 to 350 days. In a range from 294 to 316 days, the fetal development could be visualized with ultrasound (n=7 animals). A shorter fetal development of 265 days was registered in one female.

Workshop — Anatomical network analysis: A new tool to quantify morphological complexity, integration, and modularity in vertebrate evolution and development (AnNA)

Organizers: Borja Esteve-Altava, Diego Rasskin-Gutman, Rui Diogo

POSTER SESSIONS (POS1 & POS2)

Sensory Biology and Neuroscience (SBN)

POS1-1 7:30 pm

Structural changes in the olfactory organs of *Taricha granulosa*, the rough-skinned newt, between aquatic and terrestrial phases.

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Abstract: The olfactory organs and associated tissues in larval, aquatic adult phase, and terrestrial adult phase rough-skinned newts (*Taricha granulosa*) were examined by scanning electron microscopy and traditional histology. In adults of both aquatic and terrestrial phase newts the olfactory organs are paired, flattened sacs, extending from the external nares anteriorly to the internal nares posteriorly. The ventrolateral border of the main olfactory cavity (MOC) outpockets to form the lateral nasal groove. This runs longitudinally along the main olfactory chamber, and houses sensory cells of the vomeronasal organ (VNO). The nasolacrimal duct runs beneath the skin as a small canal, and joins the lateral nasal groove. The olfactory epithelium of the MOC is ridged, or striped, with strips of sensory and supporting cells set between raised ridges of respiratory epithelium. In aquatic adults, the respiratory epithelium is covered with long, presumably motile cilia. The olfactory epithelium has much shorter cilia. In contrast, terrestrial animals almost completely lack cilia on the ridges of non-sensory epithelium of the MOC, and the ridges are much more pronounced. The respiratory epithelium of the lateral nasal groove is ciliated in both aquatic and terrestrial forms, with long, thick, presumably motile cilia, while the vomeronasal epithelium has shorter, more slender cilia. Changes in epithelial characteristics between aquatic and terrestrial forms have also been reported in European newts (*Lissotriton*, *Triturus*) by Matthes (1926), and in Asian newts (*Cynops*) by Shibuya and Takagi (1963), though differing in detail from those in *Taricha*. This transition in morphology between media likely indicates a change both in olfactory mechanism and in sensitivity to chemical cues from conspecifics, as *T. granulosa* move between water and land as part of their annual reproductive cycle.

POS1-3 7:30 pm

Location specific protein expression and cell proliferation in the central nervous system following tail loss in the gecko (Reptilia: Squamata).

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Abstract: Reflexive tail loss, or caudal autotomy, is common to many species of lizards. Tail loss is typically followed by tail regeneration, a spontaneous morphogenetic program that gives rise to a replacement appendage. Although tail regeneration is a growing topic of biological and biomedical interest, less is known about the effects of tail loss on other tissues of the body. Here, we present new data demonstrating that populations of cells lining the ventricular system of the brain and spinal cord in the leopard gecko (*Eublepharis macularius*) respond differently to tail loss. Prior to autotomy, both ependymal cells of the spinal cord and periventricular cells lining the lateral ventricles of the brain are slow-cycling (bromodeoxyuridine label retaining) and express markers characteristic of neural stem/progenitor cells (NSPCs), including the transcription factor Sox2. However these two populations are distinct, with only periventricular cells expressing the neuronal markers HuC/D and NeuN prior to tail loss. Caudal autotomy ruptures the spinal cord and triggers changes in protein expression and proliferative activity. Among ependymal cells, tail loss initiates an increase in cell proliferation, changes in NSPC protein expression, and an up-regulation of HuC/D (but not NeuN). Conspicuously, proliferative activity of periventricular cells within the brain decreases during the same timeframe. Our data reveals location specific variation in the wound-mediated response of the central nervous system following tail loss. Grant sponsor Natural Sciences and Engineering Research Council (NSERC) Discovery Grant 400358 (MKV).

POS1-5 7:30 pm

Subterranean specialization of the ear morphology in *Eospalax fontanierii* (Rodentia: Spalacidae).

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Abstract: Acoustic conditions in the burrow systems of subterranean mammals are very special in comparison with the aboveground. The sound waves are spread only for short distances in the subterranean systems, best transmitted sounds are those of low frequencies. Moreover, there is high level of background noise. We can observe high level of specialization to the acoustic environment in mammals which inhabit this ecotone permanently. They are characterized by low hearing sensitivity and by shifting of their hearing range towards low frequencies. These adaptations are mirrored also in the ear morphology. Fossorial species, which are active also aboveground, are less specialized than strictly subterranean. Family Spalacidae is suitable taxon for studying of subterranean adaptations in the ear morphology, because it consists of species with different levels of specialization to this environment. It includes strictly subterranean species such as genus *Spalax* as well as species with large amount of aboveground activity such as genus *Rhizomys*. There are few studies on middle ear of this family which are focused on this topic,

but there is a lack of studies dealing with the inner ear. In our study we attend to middle and inner ear of plateau zokor (*Eospalax fontanieri*) and the level of its subterranean specialization. It is considered as subterranean species, but according to its appearance and the field observation we expect lower level of specialization than in subterranean blind mole rat (*Spalax fontanieri*).

POS1-7 7:30 pm

Vomeronasal organ development in the sand lizard (Reptilia: Squamata: Lacertidae: *Lacerta agilis*).

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Abstract: Olfactory system of tetrapods is anatomically and functionally divided into the main and accessory (vomeronasal) systems. There is no single opinion about the causes of vomeronasal system appearance. Earlier it was thought that it firstly appeared in tetrapods as an adaptation for terrestrial life. However, modern studies have shown that it appeared already in aquatic tetrapods. As the reptiles are the most primitive true land vertebrates, the developmental studies of vomeronasal system should shed light on its adaptation for the true terrestrial life. In the present study, we have investigated the development of the vomeronasal organ in the sand lizard. We have found that olfactory organ undergoes 4 stages of morphogenesis: 1) olfactory placode; 2) olfactory pit; 3) olfactory sac; 4) olfactory cavity. Division of the olfactory organ into two distinct parts starts with a medial invagination of the olfactory sacs, thus the rudiment of the vomeronasal organ appears. Later in ontogeny, vomeronasal organ becomes separated from the olfactory cavity and forms its own duct which opens into the oral cavity. At the same time, the medial and lateral edges of the olfactory sacs become fused in the middle part, thus olfactory sac receive two openings. The anterior opening represents nares and posterior one represents choanae. In comparison to amphibians, the early development of the vomeronasal organ in lizards is similar, however in lizards, at the later stages vomeronasal organ becomes completely separated from the main olfactory system. We assume that such anatomical differences could represent that in true terrestrial vertebrates vomeronasal organ received a new functional significance.

POS1-9 7:30 pm

Gross Anatomical Brain Region Approximation (GABRA): a new landmark-based approach for estimating brain regions in archosaurs.

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Abstract: Studying brain evolution in extinct taxa can be challenging due to a lack of close correspondence between the brain and the endocranial cavity. Cranial endocasts may be faithful brain proxies in certain groups (mammals, birds) due to relatively complete filling of the cavity with neural tissue in life. However, the brain does not fill the endocranial cavity in adult non-avian archosaurs, making their endocasts less reliable indicators of brain size and shape. As such, previous studies of relative brain size and evolution in archosaurs relied on untested assumptions about brain-endocast fidelity. We propose a new approach known as Gross Anatomical Brain Region Approximation (GABRA), which involves importing a digital endocast, derived from CT scanning and 3D visualization software, into modeling software (Maya). In Maya, brain regions underlying the endocast are modeled as 3D polygons, the limits of which are based on osteological correlates of soft-tissue structures that are 1) identified by comparison with extant taxa, and 2) visible reliably on endocasts. Discernible correlates for soft-tissue structures (e.g., neurovascular canals, dural sinuses, fossae formed by the brain itself) serve as landmarks that inform the location and size of general brain regions (e.g., cerebral hemispheres, cerebellum, optic lobes, olfactory bulbs). Together, landmarks form a set of explicit criteria used to assess endocasts and model brain regions. GABRA criteria and resulting brain models were validated in extant diapsids (lizards, snakes, alligators, birds) via literature review, gross dissection, CT scanning of iodine-stained specimens, and MRI studies. Therefore, GABRA models produced for extinct archosaurs are credible. Ultimately, GABRA permits moving beyond consideration of the cranial endocast as a singular entity to studying the evolution of the archosaur brain and its different parts, allowing hypotheses of brain-region evolution to be tested.

POS1-11 7:30 pm

The skull and endocranial anatomy of the extinct giant moa *Dinornis robustus* (Aves: Palaeognathae) and implications for the behavioral role of vision in moa.

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Abstract: Moa comprise a group of extinct flightless birds from New Zealand belonging to Palaeognathae, a basal neornithine group that includes both flighted (e.g., tinamous, lithornithids) and flightless members (e.g., ratites such as ostriches, etc.). The skull bones of a South Island giant moa (*Dinornis robustus*, FMNH PA 35) were CT scanned to study its skull structure and endocranial anatomy. Internal structures such as the brain endocast and inner-ear labyrinth were virtually reconstructed using Avizo. Similar analyses were done for all extant palaeognath clades, as

well as for *Lithornis*. Whereas much of the endocast of *D. robustus* is conservative, some apomorphies in its visual system may have implications for inferring sensory abilities. For example, the optic tectum, which is the major retinorecipient structure in the avian brain, shows marked reduction compared to that of other palaeognaths, and is located rostral to the trigeminal nerve trunk as opposed to dorsal to this structure as in other palaeognaths. Another surprising finding is that the floccular lobe of the cerebellum was absent, despite being moderately well-developed in other palaeognaths. The highly reduced flocculus in moa could have implications for their behavior, as this structure is intimately connected to the visual apparatus via the vestibulo-ocular reflex. Finally, the bony orbit itself is small relative to skull size compared to other palaeognaths, indicating a relatively small eyeball and potentially affirming reduced reliance on vision. However, previous authors failed to find a significant difference between moa and other palaeognaths in optic foramen and Wulst size, two characteristics that have been used as proxies for visual capabilities. Despite the apparent conservation of these two characters, the reduction in the suite of other neuroanatomical structures associated with vision strongly suggests a diminished importance of visually-driven behaviors in this clade.

POS1-13 7:30 pm

Neuroanatomy of the extinct terror birds (Aves: Phorusrhacidae): implications for a predatory mode of life.

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Abstract: Terror birds (Cariamiformes, Phorusrhacidae) are a completely extinct group of ground birds that comprise one of the most remarkable and diverse groups of the South American Cenozoic avifauna. Widely considered to have been apex predators, their basic habitus of being running predators has never been questioned for most of their species. Details about their predatory abilities, however, particularly with regard to prey detection behaviors, require more in-depth study. Here we present for the first time the morphology of the brain and vestibular apparatus of a diversity of terror birds based on high-resolution computed tomographic (CT) scans from which we constructed digital brain endocasts. Four taxa comprised the sample, including the mesembriornithine *Llallawavis scagliai*, the psilopterine *Psilotperus lemoinei*, the patagornithine *Patagornis marshi*, and the giant phorusrhacine *Kelenken guillermoi*. Comparison with other birds, such as extant raptorial and cursorial birds, sheds light on the adaptation to a terrestrial and cursorial predatory lifestyle. The enlarged Wulst (eminencia sagittalis, hyperpallium), the well-developed optic lobes, the large optic nerves, and large apparent eyeball size indicate that all terror birds were very visual birds, capable of handling large visual input. Moreover, the long and slender semicircular canals of the inner ear labyrinth suggest not only agility but also highly coordinated eye, head, and neck movements. The sense of smell, on the other hand, was not well developed in terror birds, as judged by the very small size of the olfactory bulb, which is consistent with a lifestyle as an active pursuit predator rather than as a more obligate scavenger. The consistent picture that emerges based on the neuroanatomical structure of these terror birds is that prey detection was based mainly on vision and during pursuit they were able to make agile, sudden, and fast movements to chase and subdue prey.

Locomotion (LOC)

POS1-15 7:30 pm

Muscle function in rainbow smelt, *Osmerus mordax*, during winter.

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Abstract: Rainbow smelt (*Osmerus mordax*) display an impressive ability to acclimate to very cold water temperatures. These fish express anti-freeze proteins, glycerol and additional osmolytes in their plasma, liver, muscle and other tissues to avoid freezing at sub-zero temperatures. In turn, smelt must feed actively in winter to maintain osmolyte levels. We explored smelt muscle function in winter through thermal acclimation studies on smelt swimming performance, muscle contractile properties and muscle protein expression. The thermal acclimation studies demonstrated a strong influence of cold acclimation on swimming performance, with cold acclimated fish able to swim at higher sustained swimming speeds but at perhaps higher energetic costs than warm acclimated fish. Cold-acclimated smelt had faster muscle contractile properties in both their fast- and slow-twitch myotomal muscle, with cold-acclimation associated with shorter relaxation times, faster maximum shortening velocity and increased power output. In addition, muscle from cold-acclimated fish displayed reduced thermal sensitivity to decreasing temperature in muscle mechanics experiments. Immunohistochemistry and dot blot analysis indicate shifts in muscle myosin heavy chain content. Quantitative PCR confirms a change in myosin gene expression with thermal acclimation. RNA-Seq suggests changes in the expression of genes for a variety of muscle proteins and for metabolic pathways associated with glycerol production. An integrative approach has revealed an impressive thermal acclimation by rainbow smelt that permits muscle function and active locomotion at sub-zero temperatures.

POS1-17 7:30 pm

Scaling of burial mechanics in the English sole, *Parophrys vetulus* (Actinopterygii: Pleuronectiformes).

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Abstract: The size of an organism influences its interactions with the environment, and the study of these interactions over a range of sizes (scaling) is key to understanding limits of performance in large and small fishes. Flatfishes (Pleuronectiformes) rapidly bury themselves under sediments using body undulations and fin movements. This burial behavior forces the fish to interact with both the fluid environment and a granular medium and is acutely affected by size of the organism. The fish must fluidize a volume of the substrate in a manner that distributes it over the entire surface of the body when it falls. We used the English Sole, *Parophrys vetulus*, as a model to explore the effects of scaling on burial. We recorded burial events from 15 fish across a size range (5 to 30 cm), keeping sand grain size consistent, using high speed video at 250 fps and determined undulation frequency, time to burial, and percent body coverage. We found that larger fishes bury more slowly and with a lower undulation frequency, but sediment coverage was not affected by the size of the fish. We then used 5 individual fish of the same size (5.7 – 8.1 cm) and changed the size of the sediment (125 – 710 microns) and found that grain size does not affect the undulation frequency or time to burial of small fish, but they do lose coverage on media of increased size relative to fish size. We propose that this is because the small fish cannot fluidize sand of larger grain sizes as effectively. Our results indicate that kinematics of flatfish burial are a function of fish size, and the success of the behavior is affected by the relative grain size of the sediment.

POS1-19 7:30 pm

How to modify a fin into a limb: Insights from anglerfish.

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Abstract: The evolution of tetrapod limbs from fish fins is one of the most-studied anatomical transitions in vertebrate evolution. However, tetrapods are not the only group of fish to have modified their fins into functional limbs. Various other vertebrate groups have adopted limb-like fins in order to navigate their environment, including epaulette sharks, mudskippers, and anglerfish. Of these groups, anglerfish (Lophiiformes), and particularly the charismatic frogfish (Antennariidae), have modified their pectoral fins into perhaps the closest functional analogue to a tetrapod limb – with joints that are similar to the shoulder, elbow, and wrist (including digit-like fin rays). Frogfish use these ‘limbs’ for station-holding and for active substrate-driven locomotion using one of two ‘gaits’. In the first, they move their pectoral fins in an alternating fashion, propelling themselves forward like a two-legged tetrapod, without use of the pelvic fins. Alternatively, they can progress with a slow gallop by moving their pectoral fins synchronously back and forth, transferring their weight to the pelvic fins during the swing phase of pectoral movement. Here we examine the musculoskeletal anatomy of the frogfish pectoral fin, compare it to the morphology of closely-related pelagic anglerfish, and isolate the underlying structural modifications which permit frogfish to use their fins as limbs. Hard and soft tissue anatomy was captured through contrast-enhanced μ CT scanning using Phosphomolybdic Acid (PMA) and the skeletal and muscular elements were virtually dissected to create high-resolution 3D musculoskeletal reconstructions. Through these 3D models, we trace the anatomical scaffolding underlying the frogfish pectoral fin and make correlations with its unique locomotor behaviors – thus providing a deeper understanding of this functionally convergent fin-limb complex.

POS1-21 7:30 pm

Simulating movement in early tetrapods: inputs from limb muscle physiology.

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Abstract: One of the great mysteries regarding the evolution of animals is how and when tetrapods achieved the ability to stand and move on solid ground. But, which pioneering tetrapod species could move on land and how well? Our past work inferred that the morphology of Devonian stem tetrapods could not have supported walking in a typical salamander-like fashion and that a mudskipper-like crutching gait was more likely to be employed. Such a hypothesis means we still know very little about the evolution of modern walking behaviours. To further our investigation, we aim to reconstruct dynamic motions in a series of early tetrapods bracketing the water-to-land transition using modern computer simulation techniques; however, such simulations depend on input data from relevant extant taxa. Here we present new measurements of the in vitro mechanical properties of isolated, intact forelimb (FL, n=10) and hindlimb (HL, n=14) muscles from adult fire salamanders (*Salamandra salamandra*), tested at 20°C under near maximal activation. Whole muscle cross-sectional area (CSA) ranged from 0.1–1.8 mm² across the two FL and three HL muscles tested. CSA-dependent maximal force (mN) was the same in FL ($y=240x$, $r^2=0.6$) and HL ($y=229x$, $r^2=0.56$) muscles. Similarly, peak power (μ W) was related to muscle volume (mm³) across the two muscle groups ($y=92x$, $r^2=0.4$). Mean (\pm SEM) maximal isometric stress (in kPa; 243 \pm 8 for FL and 234 \pm 6 for HL), peak power (in watts per litre; 93 \pm 3 for FL and 98 \pm 3 for HL) and Vmax (in muscle-lengths per second; 4.5 \pm 0.1 for FL and 5.5 \pm 0.1 for HL) were statistically indistinguishable for the two muscle groups. In addition, shortening speed at peak power (Vopt) was similar for FL and HL, being 27-28% of Vmax. Hence, a “generic” set of muscle properties are likely applicable to

biomechanical models of *S. salamandra* movements at 20°C, which helps inform future analyses of extinct tetrapod species.

POS1-23 7:30 pm

Why are long bones curved?

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Abstract: The presence of curvature in long bones has long puzzled scientists. The curvature would seem to make the bone less able to bear longitudinal loading. Recently, a novel hypothesis has been presented that suggests the bone is curved to resist its habitual loading. A striking example of a curved bone is the radioulna of obligate quadrupeds which has a caudal curvature (concave caudally). The radioulna in these species is a lever operated by the triceps muscle which tends to bend the bone in a cranial direction. The caudal curvature provides a mechanism whereby cranial bending strains induced by the action of triceps can be resisted by longitudinal and flexor muscle forces which produce caudal bending strains. This idea has been tested by comparing the performance of a curved radioulna with that of a straightened model of the same bone. This paper explores the generality of this idea by examining other curved long bones in vertebrates. In particular, arboreal species that use their (radio)ulna for prehension are considered. Here the habitual loading is provided by the brachialis muscle which introduces caudal bending strains, and it is predicted that, according to the novel hypothesis to explain curved bones presented here, these bones should have a cranial curvature – this is found to be the case and so, to be consistent with the predictions of the hypothesis. This begs the question of how bone curvatures develop. The hypothesis presented also leads to a possible explanation.

POS1-25 7:30 pm

Tendinous system in *Leptodactylus* (Amphibia, Anura, Leptodactylidae): Morphological diversity and its relation to habitat and locomotion.

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Abstract: Tendons can be characterized as fibrous connective tissue with the main function of connecting and transmitting force from muscles to bones, with a unique structure, physiology and developmental origin which allow their consideration as an independent system. Despite of their anatomical and functional singularities, a description of the tendinous system is still not available for anurans. Herein, we present a general categorization of the tendinous system of the most superficial surface of *Leptodactylus latinasus* using techniques of comparative anatomy. *Leptodactylus* encompasses species with gradual independence of water and different locomotor modes, so we test for the relation of these ecological features with morphometric data of tendons using comparative analysis, and optimize qualitative data. We compared the tendinous pattern of *L. latinasus* with 44 species of leptodactylid frogs. Morphometric and qualitative data were taken from the origin and insertion tendons of the following muscles: *longissimus dorsi*, *coccygeous sacralis*, *iliacus externus*, *iliofibularis*, *sternoradialis*, *triceps*, and *flexor digitorum communis*. The main tendinous areas were found on the girdle region and limb articulations. All log10-transformed variables showed highly significant phylogenetic signal ($p < 0.001$). Pagel's lambda values were equal or higher than 0.89, therefore the phylogenetic effect is high in this database. There was no significant relation between morphometric data and ecological characters, however the optimization of qualitative characters showed a relation between the shape of the origin tendon of the *iliacus externus* and species with digging locomotor modes.

POS1-27 7:30 pm

Does crocodilian ankle morphology relates ankle kinematics?

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Abstract: The functional morphology of the crocodilian ankle has been nearly neglected. The aim of this study is to clarify the relationship between ankle morphology and its kinematics in crocodiles. The ankle joint of crocodiles consist of two joints: i.e., a crurotarsal joint and a mesotarsal joint. These two joints produce the dorsiflexion/plantarflexion and the eversion/inversion movements. To investigate ankle joint mechanisms, seven crocodylids and four alligatorids were CT scanned in five positions ranging from maximum dorsiflexion to plantar flexion. This movement was performed along the sagittal plane on the 2nd metatarsal axis. In addition, bone specimens were measured from 11 crocodylids and 14 alligatorids. The averages of total ankle ROM at the tibia-1st metatarsal were 59.9°-136.4° in the crocodylids and 57.6°-152.0° in the alligatorids, respectively. While the averages of ROM at the tibia-4th metatarsal were 52.7°-147.6° and 60.3°-162.8°, respectively. In osteological characters, the crocodylids have a large fibular facet, and wide 1st metatarsal. The standardized width of the 1st metatarsal was significantly greater in crocodylids than in alligatorids ($p < 0.01$). The ROM analysis showed that the crocodylids are in eversion at dorsiflexion, while the alligatorids are almost in the neutral position. The crocodylids were considered to be mainly loaded on the first metatarsal because the crocodiles are in dorsiflexion at rest. This hypothesis is supported by the following osteological characters, i.e., a large fibular facet in the astragalus and a wide first metatarsal. In crocodylids, most of the load of the fibular side will be taken by the astragalus and first metatarsals, whereas that load will be taken more by the calcaneum in alligatorids. The present study suggested crocodylids and alligatorids evolved a different morphology of the ankle joint, and it has been associated with ankle movement.

POS1-29 7:30 pm

Investigating inter-limb evolutionary linkages in avian limb proportions.

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Abstract: Modern birds are the most diverse terrestrial vertebrates, displaying notably higher variability in ecology and locomotor behavior than their non-avian theropod relatives. It is hypothesized that a functional shift in the forelimb and hind limb during the early evolution of birds, with the forelimb co-opted for flight freeing the hind limb from functioning solely in terrestrial locomotion, played a role in facilitating this radiation. Specifically, differential evolution between these “locomotor modules” enabled a greater diversity of ecological and behavioral options for birds. A connection between these separate limb locomotor modules and ecomorphological diversity in birds is supported by greater diversity in forelimb and hind limb proportions in extant bird lineages relative to non-avian theropod dinosaurs. Evolution in one “module” will likely affect evolution in another due to functional tradeoffs related to properties of the whole organism such as ecology and behavior. Avian forelimb and hind limb proportions have been independently studied in relation to habitat, flight style, scaling, and intra-limb developmental integration, but little is known of how limb morphospace evolved through time in different avian lineages. Furthermore, potential functional tradeoffs inducing concomitant evolution in forelimb and hind limb proportions remain uncharacterized and uninvestigated across Aves. I report on the evolutionary tempo and mode of forelimb and hind limb proportions in 495 species of birds in a phylogenetic framework. I examine how limb proportions vary across clades when accounting for body size and relatedness. Additionally, I compare the evolution of forelimb and hind limb proportions and investigate whether or not shifts in the proportions of one set of limbs predictably result in modification to the other set, testing whether or not the nature of these potential evolutionary linkages can be correlated to factors such as ecology and locomotor behavior.

POS1-31 7:30 pm

Sciurormorph limb bones: morphological correlates to different locomotor behaviors.

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Abstract: Sciurormorph rodents are highly diverse in their habitat related locomotion, due to the varying extents and intermixture of aerial, arboreal, scansorial, cursorial and semi-fossorial lifestyles. We aim to find out, how sciurormorph locomotor behavior is correlated with morphology of the scapulae and femora, i.e. the limb elements whose motion has the biggest impact on propulsion during horizontal locomotion. Previous investigations suggest ecomorphological differences in attachment sites of internal and external retractor and abductor muscles. Climbing upside-down may demand for larger shoulder-extending protractor muscles and hence increased attachment sites in arboreal species. We use geometric morphometrics to analyze the complex shape of these limb elements. Bones from approximately 150 species are investigated, housed at various museum collections of Europe and North America. Detailed surface models are obtained using a surface laser-scanner or a μ CT to allow a three-dimensional analysis. Scapulae are photographed from different geometrically predefined perspectives for multiple two-dimensional analyses. A preliminary qualitative evaluation of photos and scans supports ecomorphological differences in muscle attachment sites. The scapula of arboreal species tends to have a relatively bigger attachment site for the teres major. Regarding the femur, arboreal species appear to have a relatively larger third trochanter, which serves as an attachment site for the gluteus maximus. These muscles may serve as whole limb or limb element retractors in agreement with increased demand for powerful retraction during vertical climbing against gravity. Yet, we observe exceptions to these observations indicating the need of a rigorous quantitative analysis.

POS1-33 7:30 pm

Kinematics of arboreal descent in primates.

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Abstract: Arboreal primates must often descend steep supports. Head-first descent gives an animal the advantage of being able to view its path ahead, but has the disadvantages of increasing load on the forelimbs and the risk of forward pitch. Previous research on primates shows that they mitigate increased force on the forelimb during declines through the use of protracted limbs, altered gait, and reduced speed. However, nothing is known about the mechanics of tail-first descent, or the influence of substrate orientation, body mass, and intermembral index (IMI) on descent posture. The present study tests the hypothesis that as steepness increases the proportion of head-first descents will decrease in favor of alternate means of travel (e.g. leaping, tail-first descent). Three strepsirrhine primate species, *Eulemur coronatus* (n = 4; species mean body mass (BM) = 1.6 kg; IMI = 69), *Varecia variegata* (n = 4, BM = 3.5 kg; IMI = 72), and *Nycticebus pygmaeus* (n = 2; BM = 0.3 kg; IMI = 88), were videorecorded moving between two platforms connected by a thin diameter, 1.8 m long support held at 0° (horizontal), 30°, 60°, and 90° (vertical). Frequency of descent methods, changes in speed, and limb angles were calculated and compared by angle of support orientation. Head-first descent was observed in all conditions, with a gradual decrease in use as slope increased in all species. During 90° descent, *E. coronatus* used head first descent in an average of 23.5% of cases, *V. variegata* in 69.5%, and *N. pygmaeus* in 62.5%. IMI appears to be a better predictor of head-first descent frequency than body mass; this relationship will be further studied with additional species. These results contribute to a better understanding of how tradeoffs in locomotor specializations and anatomy influence navigation of complex

arboreal environments by primates.

POS1-35 7:30 pm

Form-function relationships and the evolution of arboreal locomotion in mammals.

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Abstract: Almost all mammalian orders have arboreal representatives. The adaptation to life in a three-dimensional arboreal environment has been acquired independently in the different lineages. However, an arboreal lifestyle needs to be clearly distinguished from arboreal locomotion. The latter implies that the locomotor performance of the animal is challenged by the discontinuous nature and complexity of the arboreal substrates. Two eutherian lineages are exceptional in this regard because they evolve relatively large body sizes, display different mechanisms for arboreal locomotion, and have an excellent fossil record: Carnivora and Primates. Arboreal locomotion imposes selective pressures that may affect the anatomy of the appendicular skeleton as the limbs have to be mobile to reach across discontinuities yet at the same time need to be able to generate a firm grip. The present project aims at better understanding the relation between bone shape and the muscular anatomy of the appendicular skeleton in the context of arboreal locomotion. The functional properties of the forelimb muscles in carnivores and primates will be described and related to quantitative analyses of limb bone morphology using PLS analyses. This comparative study will shed light on the functional adaptations of the forelimb associated with arboreal locomotion. The results will provide better insights into the functional link between limb structure and locomotion mechanics and will improve our inferences of function and behavior in fossils.

POS1-37 7:30 pm

Functional implications of manual grasping strength in marmosets (Primates: *Callithrix jacchus*) and squirrel monkeys (Primates: *Saimiri boliviensis*).

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Abstract: Grasping supports via the powerful flexion, adduction and opposition of the autopodial digits is a critical performance demand for many arboreal tetrapods, from tree frogs to primates. Functionally, grasping appendages are thought to permit arboreal animals to maintain purchase and exert torques around the support, thereby promoting stability. In this study, we test the association between grasping performance and narrow-branch arboreality by quantifying grasping strength and digit robusticity in two closely-related New World monkeys - marmosets (*Callithrix jacchus*) and squirrel monkeys (*Saimiri boliviensis*). Whereas squirrel monkeys typically feed and travel quadrupedally in a fine-branch niche, marmosets are devoted gummivores that primarily forage on vertical tree trunks. We therefore predicted grasping forces and digital robusticity should be significantly greater in *Saimiri*. We used a custom-constructed grip force transducer to measure hand grasping strength (*Saimiri*: 48 trials; (*Callithrix*: 82 trials; n = 2 individuals per species), quantifying the maximum and average grip force exerted during each trial as a percentage of body weight (% BW). To test for a morphological correlate of grasping strength variation, we also quantified metacarpal cross-sectional section moduli (scaled to bone length) in museum samples. Maximum within-trial grasping forces were significantly greater in *Saimiri* (74% BW) than in *Callithrix* (59% BW) (p<0.001), as were average grasping forces (*Saimiri*: 46% BW; *Callithrix*: 27% BW; p<0.001). Correspondingly, *Saimiri* had stronger post-axial metacarpals (i.e., digits 3-5) than did *Callithrix*. Both stronger manual grasping forces and more robust post-axial digits likely facilitate safe and efficient locomotion when squirrel monkeys travel and forage above narrow-diameter branches. Supported by NSF (BCS-0959438, BCS-1126790, BCS-1317047), NEOMED, and USC.

POS1-39 7:30 pm

Functional anatomy of the nasal muscles in Japanese badger *Meles anakuma* (Mammalia: Mustelidae).

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Abstract: The infraorbital foramen in badgers is considerably larger than that in other Carnivora of similar body size. The morphology of the infraorbital foramen is an important characteristic for identification of badgers. Generally, the infraorbital foramen is a passage for the infraorbital nerve and vessels, and the surface of the infraorbital foramen is the origin of lip and nose muscles in many mammals. However, no anatomical studies have reported on the infraorbital foramen in badgers. Here we describe the nasal muscles around the infraorbital foramen and the infraorbital nerve and vessels, and we report on the function of the nasal muscles in the Japanese badger. The superficial muscle of levator nasolabialis muscle arises in the frontal region between the anterior surface of the orbit and the lateral surface of the maxillary bone. It inserts on the lateral side of the nasal and superior lip. The well-developed levator rostri muscle arises from the inside wall of the inferior orbital foramen and inserts on the subcutaneous tissue at the dorsal midline of the rhinarium. The levator rostri muscle is situated on the deep to the levator nasolabialis muscle. The distal part of the levator rostri muscle is tendinous. The infraorbital nerve and vessels are situated on the deep to the levator rostri muscle and reach the tip of the nose. The large infraorbital foramen in the Japanese badger is suitable for providing the origin for the well-developed the levator rostri muscle. Although the levator rostri muscle of the Japanese badger is an important muscle that elevate the nose, similar to that of other

mammals, the morphology of the levator rostri muscle that arises from the inside wall of the infraorbital foramen showed a specific form in the Japanese badger.

POS1-41 7:30 pm

Thoracic strengths a new indicator of life reconstruction in extinct secondary aquatic mammals.

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Abstract: Habitat-shifts from land to water have occurred independently in several mammal lineages. However, reliable life reconstructions of each extinct taxon remain difficult due to our little knowledge about the relationship between skeletal morphology and its function, and therefore, the timing of the shifts in their locomotor strategies and habitats are yet to be fully understood. We estimated the strengths of rib cages against vertical compression in approximately 30 extant and 4 extinct mammal specimens of three lineages of mammals (cetartiodactyls, paenungulates, and carnivorans) which include terrestrial-quadrupedal, semi-aquatic, and obligate aquatic taxa. Our analyses in the extant taxa showed that the strengths were high among terrestrial-quadrupedal/semi-aquatic taxa, whose rib cages are subjected to vertical compression during the support on land, whereas the strengths were low among obligate aquatic taxa, whose rib cages are not subjected to antigravity force in the water. We therefore propose the rib cage strength as a new index to estimate the ability of the terrestrial support by either the forelimbs or thoraces. Among the extinct taxa, the rib cage strengths of a basal cetacean (Cetartiodactyla: *Ambulocetus*) and two desmostylians (Paenungulata: *Paleoparadoxia* and *Neoparadoxia*) were as low as those of the extant obligate aquatic taxa. Based on our new index, these extinct mammals were not likely to move actively on land, though they have retained all four limbs. Further study on the rib cage strengths in extant/extinct semi-aquatic taxa may help understanding of the processes of ecological shifts in these groups.

Paleontology (PAL)

POS1-43 7:30 pm

Anatomy and diversity of the earliest fossil vertebrates (Chengjiang Biota, Cambrian, China): new evidence from experimental taphonomy.

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Abstract: The oldest fossil vertebrates are from the Lower Cambrian Chengjiang biota of China, which contains four genera of fish-like, primitive vertebrates: *Haikouichthys*, *Mylokunmingia*, *Zhongjianichthys* and *Zhongxiniscus*. These fossils play key roles in calibrating molecular clocks and informing our view of the anatomy of animals close to the origin of vertebrates, potentially including transitional forms between vertebrates and their nearest relatives. Despite the evident importance of these fossils, the degree to which taphonomic processes have affected their anatomical completeness has not been investigated. For example, some or all might have been affected by stemward slippage – the pattern observed in experimental decay of non-biomineralised chordates in which preferential decay of synapomorphies and retention of plesiomorphic characters would cause fossil taxa to erroneously occupy more basal positions than they should. This hypothesis is based on experimental data derived from decay of non-biomineralised chordates under laboratory conditions. We have expanded this analysis to include a broader range of potentially significant environmental variables; we have also compared and combined the results of experiments from several taxa to identify general patterns of chordate decay. Examination of the Chengjiang vertebrates in the light of these results demonstrates that, contrary to some assertions, experimentally derived models of phylogenetic bias are applicable to fossils. Anatomical and phylogenetic interpretations of early vertebrates that do not take taphonomic biases into account risk overestimating diversity and the evolutionary significance of differences between fossil specimens.

POS1-45 7:30 pm

Morphology of two early fossils aligned with the specialized deep-sea predatory fish groups Gempylidae and Trichiuridae assessed using micro-computed tomography.

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Abstract: Gempylids (snake mackerels) and trichiurids (cutlassfishes) are pelagic fishes characterized by slender to eel-like bodies, deep-sea predatory ecologies, and large fang-like teeth. Several hypotheses of relationships between these groups have been proposed, but a consensus remains elusive. Fossils attributed to gempylids and trichiurids consist almost exclusively of highly compressed body fossils and isolated teeth and otoliths. Two three-dimensional crania from the London Clay of England join these remains. Identified as *Eutrichurides* and *Progempylus*, these taxa are 53 million years old and represent some of the oldest fossils aligned with Gempylidae and Trichiuridae. We applied computed tomography in order to clarify structure in these potentially critical taxa. *Eutrichurides* bears large premaxillary fangs, found in trichiurids, gempylids, and scombrolabrbrids. Apart from the jaws and hyoid arch, this specimen is highly fragmented. However, features of the vomer apparent in CT data but not visible externally suggest a closer relationship with trichiurids. By contrast, *Progempylus* preserves a braincase, gill skeleton, suspensorium,

and lower jaw, but lacks the upper jaws. It shows a mosaic of apparently derived features with a restricted distribution among gempylids (e.g., a single or pair of teeth on vomer) or trichiurids (e.g., short posterodorsal process of quadrate), and its placement remains unclear. Uncertainties relating to the phylogenetic positions of these critical early taxa reflect conflicting hypotheses for the relationships of modern species. Trichiurids are reliably resolved as a clade, but gempylids are more problematic. Most analyses report gempylid paraphyly, either with respect to trichiurids or a set of lineages classically identified as 'scombroids'. Ongoing assessment of the relationships of extant gempylids, trichiurids and related families aims to identify the placement of these fossils among living groups.

POS1-47 7:30 pm

Early Permian amphibamid *Pasawioops* (Amphibamidae, Dissorophoidea): An ontogenetic series.

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Abstract: Amphibamids (Temnospondyli: Dissorophoidea) were small, amphibian taxa that were mostly present during the Early Permian (~270 to 300 Mya). These taxa are generally considered to be close relatives of modern amphibians (lissamphibians). Thus, detailed analysis of their morphology and phylogenetic relationships sheds light on the evolution of lissamphibians and the origin of several unique traits. Amphibamids are additionally interesting because for some taxa larval, juvenile and adult specimens have been found, allowing researchers to discern the ontogenetic progression of morphological traits. However, because many amphibamids have a more juvenile appearance than other amphibians (e.g. comparatively large orbits and small body size), distinguishing between ontogeny dependent traits and diagnostic traits of taxa is of utmost importance. The goal of the present research is to first document the detailed morphology of the skull of the recently described amphibamid *Pasawioops* (OMNH 73019) using novel CT data, and to second explore the nature of ontogeny dependent traits in this taxon through comparison with a recently referred specimen of *Pasawioops* (MCZ 1415). We found the smaller OMNH 73019 specimen differs from MCZ 1415 in the following traits: the skull bones are not as tightly sutured, the anterior skull has a more rounded appearance, and the jaw articulations do not extend as far posteriorly beyond the occiput. Together, these data indicate that OMNH 73019 likely represents a more juvenile specimen of *Pasawioops* and the observed differences between specimens are consistent with previously posited juvenile traits in amphibamids. This suggests the nature of ontogeny dependent traits may be more conserved across Amphibamidae than previous thought.

POS1-49 7:30 pm

Phylogeny, ecology, and time: 2D outline analysis of anuran skulls from the Early Cretaceous to Recent.

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Abstract: Anura have a long fossil record spanning from the early Jurassic to Recent. However, even the best-preserved specimens are often severely flattened, limiting their inclusion in quantitative analyses of anuran morphological evolution. Here we perform a 2D morphometric analysis of anuran skull outlines obtained from the published literature, incorporating 42 Early Cretaceous to Miocene species, as well as 93 extant species in 32 families. Outlines were traced in tpsDig2 and analysed with elliptical Fourier analysis in the R package 'Momocs'. Fourier coefficients were used as high dimensional variables in MANOVAs and disparity analyses across multiple ecological and life history groupings, such as region, habitat, and developmental strategy. As skull outlines showed significant phylogenetic signal ($k=0.53$, $p=0.006$), phylogenetic MANOVAs, using composite phylogenetic trees from recent published analyses, were also conducted. The Neotropical realm shows higher disparity than the Australian, Palearctic and Oriental realms ($p=0.007$, 0.013 , 0.038 , respectively), suggesting concordance of disparity and diversity. Developmental strategy had a weak effect on skull shape ($R^2=0.02$, $p=0.039$), and disparity was similar in metamorphosing and direct developing frogs. Ecological niche was a significant discriminator of skull shape ($F=1.44$, $p=0.004$), but not after phylogenetic correction. Body size is strongly associated with differences in skull shape in fossil frogs ($R^2=0.44$, $p=0.017$), and to a lesser extent, in extant taxa, ($R^2=0.10$, $p=0.049$), and this effect is only partly due to allometry, which is weak but significant in both fossil ($R^2=0.11$, $p=0.002$) and extant frogs ($R^2=0.09$, $p=0.001$). Finally, morphospace occupation of anuran skull outlines has changed over time, as skulls binned in 5-million year bins based on first occurrence date showed significant differences in morphospace position ($F=2.42$, $p=2.2e^{-16}$).

POS1-51 7:30 pm

New skull material of the Early Permian *Eryops* from Brushy Creek (Wichita Group, Texas) showing the morphological variability of foramina and canals in the quadratojugal of basal tetrapods.

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Abstract: *Eryops* is an important representative of Permo-Carboniferous basal tetrapods and one of the best-known large temnospondyl amphibians of this period. This taxon forms a significant component of the Early Permian tetrapod fauna of Texas and New Mexico and here we report on a new undescribed record from Brushy Creek in Texas (Petrolia Formation, Wichita Group; Lower Permian - lower Artinskian). Our material, found in 2015, consists of

a partial left mandible, a left nasal, a jaw fragment (premaxilla or maxilla), and left quadratojugal fragments. We used computed tomography methods (CT) for imaging both internal and external structures, for the first time for *Eryops*. The quadratojugal presented here is exceptional compared to all known basal tetrapods in having four different internal foramina. CT data have shown that these foramina are interconnected by canals within the bone. This indicates that the morphology of the foramina and the course of the canals in the quadratojugal of basal tetrapods is more variable than hitherto thought.

POS1-53 7:30 pm

The description of the axial osteology of a juvenile plesiosaur, and revision of polycotyloid systematics.

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Abstract: The polycotyloid's were a clade of plesiosaurs that proliferated during the Cretaceous period of the Mesozoic. The clade became very speciose during the late Cretaceous, and there is speculation that the high species diversity is a relic of the lack of information on ontogeny and intraspecific variation within the polycotyloids, since most species are only represented by one fossil specimen. To answer the question of whether the late Cretaceous polycotyloids featured high species diversity, ontogeny must be accounted for within the polycotyloid clade. The presence of juvenile plesiosaurs in the fossil record are rare, and ontogenetic growth series for plesiosaur taxa remain speculative. The axial osteology of the juvenile polycotyloid from the Wallace Ranch was described, and a reconstruction of its skull has been made. The juvenile Wallace Ranch skull provides insight into the cranial development of an immature plesiosaur, and from this specimen, allometric growth patterns of the cranial bones for polycotyloids will be evaluated. The juvenile and the adult specimen, along with all the other polycotyloid species were evaluated via a phylogenetic analysis, in an attempt to illuminate the relationships between the taxa. The adult and juvenile specimens formed a clade, indicating that the two specimens were of the same species. However, a more comprehensive phylogenetic analysis of all polycotyloid specimens is needed before the Wallace Ranch specimens are elevated to their own species.

POS1-55 7:30 pm

Body size evolution in glyptosaurine lizards (Squamata: Anguidae) accurately models paleoclimates for the interior of North America.

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Abstract: Poikilothermic vertebrates such as lizards offer viable proxies for terrestrial climate based on the metabolically-scaled relationship between ambient temperature and body size. Ambient temperature constrains maximum body size in extant lizards, but this relationship has not been tested in extinct forms through geologic time. In this study, we estimate mean annual paleotemperature (MAPT) of the North American Interior during the Paleogene from body size in glyptosaurine lizards. We modeled the relationship between skull length and snout-vent length (SVL) for extant anguimorphs and used these models to estimate SVL in glyptosaurines based on fossil cranial material. We then applied the model relationship between mass-specific metabolic rate, maximum SVL and minimum mean annual temperature for extant *Heloderma*, the largest North American anguimorph, to body size estimates of glyptosaurines to estimate paleotemperatures through time. We find that maximum body size remained approximately constant among the largest glyptosaurines through the Eocene, with estimated MAPT of about 19 – 21°C in the Great Plains and Western Interior during this interval. Our estimates indicate that maximum body sizes of Oligocene glyptosaurines were less than half of those of the largest Eocene glyptosaurines, corresponding to a significant cooling period in the same region. Our results are consistent with other local proxies for the Paleogene of North America, indicating that body size in fossil poikilothermic vertebrates is a useful proxy for estimating terrestrial paleotemperatures over geologic timescales.

POS1-57 7:30 pm

Constraints in crocodylomorph body size evolution.

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Abstract: Evolutionary studies aiming to quantify patterns of morphological radiation in clades that include fossils are mostly temporally limited (i.e. to timescales shorter than 100 Ma), restricted to the origins of modern groups (e.g. birds and mammals), and based on discrete characters. Therefore, more comprehensive analyses are fundamental to understand patterns of phenotypic evolution on long timescales, and not only in successful modern clades, but also in groups that have lower diversity today than in the geological past. We present here a detailed analysis of body size evolution in Crocodylomorpha, a c. 240 Ma-old archosaurian clade that includes modern crocodylians. Body size is strongly related to many aspects of animal physiology and ecology, but has not previously been examined extensively in analyses of phenotypic evolution in crocodylomorphs. Total body lengths for 53 crocodylomorphs were obtained using a formula derived from the regression of body length on dorsal cranial length in modern crocodylians. The estimates were log transformed, so that they represent proportional changes in body size. A time calibrated phylogeny was generated, based on a modified version of a recent crocodylomorph supertree and fossil age data from literature and the Paleobiology Database. Four maximum-likelihood models of trait evolution were fitted using

the R package GEIGER: Brownian motion (BM), Ornstein-Uhlenbeck (OU), Early-burst (EB), and trend. The comparison between the AICc weights obtained for each model demonstrates that the OU model provided the best fit. The OU is a process that has a constant pull toward an optimum value, indicating a constrained pattern of body size evolution around a trait 'optimum'. This suggests constraints within long-term patterns of crocodylomorph body size evolution, consistent with the range of estimated body sizes [most taxa range from 1 to 5 meters] seen in living and fossil taxa, which is narrow compared to that seen in birds and mammals.

POS1-59 7:30 pm

Predicting skull size in Breviostres using cranial pit depth.

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Abstract: Crocodylians are frequently represented in the fossil record by fragmentary cranial elements which are often disregarded in studies. Here we explored the utility of these elements in determining overall skull size. Because most of the cranial bones of crocodylians develop pits on their external surfaces, we sought to determine whether a relationship was present between pit depth and skull dimensions. We measured average pit depth on 13 cranial bones from 13 modern and extinct taxa from which complete specimens are known in Breviostres. Pit depth, skull length, skull width, and jaw length were all measured using a MicroScribe 3D digitizer. We then ran ordinary least squares regressions between the pit depth of each cranial bone and the skull length, skull width, or jaw length for representatives of Breviostres and six subclades. Among these 273 regressions, we considered all bones with an r^2 value = 0.70 as having a strong predictive power for either skull length, skull width, or jaw length. We found the squamosal, quadratojugal, and maxilla had the strongest relationships to all skull dimensions for nearly every clade but those within Crocodylidae. Caimaninae had the strongest relationship to all skull measurements, with every bone producing an r^2 value above 0.80. We suggest using regression equations for bones with r^2 values = 0.70 and 95% confidence intervals for the line equation to predict cranial sizes of fragmentary individuals in the fossil record. We applied both of these standards to partial specimens of Alligator found at the 4.5–7 million year old Gray Fossil Site in northeastern Tennessee. The 5 partial specimens were predicted to be similar in size to the adult specimen found at the site and suggests a bias toward preservation of adults. This could indicate the site was dominated by adults, juveniles did not have as high a mortality rate as modern Alligator, or preservation of smaller individuals is not favored at the site.

POS1-61 7:30 pm

The mechanical origin and morphology of the labial (horizontal) shelf in Leptoceratopsia demonstrates it is now a synapomorphy of Neoceratopsia (Dinosauria: Ornithischia).

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Abstract: The labial shelf of non-ceratopsid neoceratopsians is a ledge that extends laterally from the basal edge of mandibular teeth, and formed via differential wear as upper and lower dentitions slide incompletely past each other. Previous descriptions of this shelf have referred to it as horizontal, and limited its distribution to members of Leptoceratopsidae. However, the shelf displays a variety of shapes from the recognized horizontal to rostrally or caudally sloping surfaces, as well as a delta configuration. These shapes are a consequence of the number of maxillary teeth that intersect a single dentary tooth during mastication. Given this fuller understanding of the morphology and genesis of the shelf, a re-examination of Neoceratopsia reveals that this character is not limited to leptoceratopsids but present in a number of other neoceratopsians, including the most basal neoceratopsian *Liaoceratops*, as well as more derived protoceratopsians. Previous phylogenetic analyses recovered the labial shelf as a diagnostic synapomorphy of Leptoceratopsidae. Recent work has not reformulated the character in light of our current understanding of its shape and formation. In order to test the effects of this new understanding on tree topology, the labial shelf was redefined to include the delta configuration and the relevant taxa were recoded. Using several recently published matrices, we found that the labial shelf shifted from being a synapomorphy of Leptoceratopsidae to a synapomorphy for all neoceratopsians. Overall tree topologies remained stable, partly due to characters added to matrices since 2010. The most notable changes include the exclusion of *Cerasinops* from Leptoceratopsidae, and the recovery of *Aquilops* as the most basal member of Neoceratopsia in some trees. This new distribution of the "labial shelf" emphasizes the need to more carefully examine the distribution of dental characters and changes in jaw mechanics at the base of Neoceratopsia.

POS1-63 7:30 pm

The visual apparatus of archosaurs: correlates of orbital anatomy, eye size, and behavior.

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Abstract: Like their avian descendants, extinct dinosaurs were visually oriented animals. Reconstructing orbital soft tissues has received little attention and, if not taken into account, the eyeballs of dinosaurs may be mis-sized or positioned inaccurately, leading to poor reconstructions of visual fields and spurious conclusions about behavior and ecology. High-resolution, iodine-enhanced microCT scans were taken of intact heads of a diversity of avian,

crocodilian, and squamate specimens. High-resolution microCT scans without contrast enhancement were taken of intact heads of several dozen additional avian specimens. Orbits of key specimens were dissected to identify bony signatures of ocular adnexa and to validate the CT-based analyses. Soft tissues were segmented in Avizo and modeled in Maya. Osteological correlates were identified for orbital soft tissues, including the extraocular muscles, cranial nerves, Harderian gland, lacrimal gland, nasal gland, eyelids, supraorbital membrane, subocular ligament, and nasolacrimal duct. Eyeball size was measured directly and compared with estimates using regressions from the literature. Eyeballs of maximum, average, and minimum size estimates were modeled in Maya for each sample taxon. These eyeball models were subsequently re-inserted along with accessory orbital soft tissues into the digitized skulls. If eyeball models, accessory soft tissues, and/or bones overlapped, the model was rejected as an overestimation. The results indicate that reconstructing accessory soft tissues in the orbits of extant diapsids can provide upper limits on estimates of eyeball diameter and axial length. Thus, optical parameters including focal length and monocular visual field, which depend in part on eyeball size, shape and position, may be modeled based on these constraints. Models of visual fields based on optical parameters will subsequently inform reconstructions of dinosaur visual abilities in a later phase of this project.

POS1-65 7:30 pm

A novel method to estimate cranial muscle strain in fossil and extant vertebrates using digital modelling and visualisation.

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Abstract: Muscles form an integral part of an animal's anatomy and play a fundamental role in feeding, locomotion and other physiological activities. In particular the anatomy, size and arrangement of the cranial musculature are important factors for an animal's capability for vocalization, social signalling and food acquisition. In extinct animals, these parameters are often difficult to determine and numerous studies have focussed on the reconstruction of various parts of the musculature in fossils. Inferences on the biology, behaviour and ecology of extinct vertebrates, however, rely considerably on the accuracy of these reconstructions. Although the advent of digital reconstruction techniques has facilitated the creation and testing of musculoskeletal hypotheses in recent years, muscle strain capabilities have rarely been considered. However, muscles can only stretch a certain amount before they tear and, muscular performance is closely related to the extension of muscle fibres. Detailed information on these factors can, therefore, provide a better understanding on the feeding behaviour of extinct organisms. Here, a digital modelling approach using the freely available visualization and animation software Blender is applied to estimate cranial muscle length changes and optimal and maximal possible gape in different vertebrates. Two case studies are presented here using this approach: (i) Investigating different feeding behaviour and dietary specializations of theropod dinosaurs. (ii) Testing of musculoskeletal hypothesis in cynodonts and mammaliaform taxa. Both studies use extant taxa in a phylogenetically bracketed framework and demonstrate that this novel method can be used in a versatile approach to study different anatomical and palaeobiological aspects. Although focussed on the cranial musculature, there is scope for the integration of this method into studies of other musculoskeletal systems.

POS1-67 7:30 pm

The morphology of motion: sub-surface foot trajectories and fossil tracks.

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Abstract: Dinosaur footprints are extremely common in the fossil record. Relative to pedal disparity, the morphological diversity of tracks is inflated by two key factors. First, variation in substrate depth and consistency can cause animals to sink and move differently from step to step. Second, track surfaces can be exposed on bedding planes at any depth within the disturbed volume. To understand these factors, we need to know more about movement below the surface. Even in living animals, however, documenting foot motion within the substrate is difficult because the distal limb is hidden by opaque sediment. We used X-ray Reconstruction of Moving Morphology (XROMM) to visualize and measure sub-surface kinematics in Helmeted Guineafowl (*Numida meleagris*). In order to image the feet, we walked birds through radiolucent artificial substrates created to mimic dry sand (poppy seeds) and wet, cohesive muds (glass bubbles, clay, water). Undistorted and calibrated biplanar x-ray videos (250 Hz) synchronized with two standard light videos imaged the feet both above and below ground. Our initial efforts have focused on tracing the tip of digit III, a highly identifiable landmark in many dinosaur tracks. Guineafowl display a surprisingly wide range of toe trajectories, even within a single individual. Comparison among and within substrates is hampered by a lack of obvious landmarks. Unlike the discrete stance-swing phases of strides on solid ground, birds on deformable materials appear to transition from air to substrate and back again more gradually. We have identified a number of kinematic events that may be homologous across all substrates that allow paths to be aligned and compared quantitatively. Results suggest that entry and exit motions are decoupled within a single track. Our goal is to use the diversity of guinea fowl toe trajectories to provide context for fossil specimens, and to begin to unlock the ancient locomotion preserved within them. (US NSF EAR 1452119 and IOS 0925077)

POS1-69 7:30 pm

One foot, many footprints: the origin of track morphological diversity.

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Abstract: Fossil tracks offer unrivaled evidence of behavior in long extinct species. Although complementary to skeletal remains, footprints differ in being purely sedimentary structures. Tracks are neither organism nor environment, but emergent features documenting their dynamic, coupled interaction. Track morphologies vary widely. Some disparity is attributable to differences among species, individuals, limbs, and behaviors, but substrate plays a less explored role. We recorded tracks made by Helmeted Guineafowl (*Numida meleagris*) traversing dry grains (poppy seeds) and a series of wet, cohesive muds (glass bubbles, clay, water). Photogrammetric surface reconstructions record a wide range of morphological variation. Shallow prints can resemble molds of plantar anatomy, but most tracks involve more complex entry and exit patterns arising from foot penetration and sediment collapse. A paleontologist trying to interpret such a spectrum could be easily misled about not only trackmaker identity, but also behavior, ecological interactions, and environment. Such errors can snowball into even more serious miscalculations of taxonomic range, geographic distribution, stratigraphic correlation, and faunal composition. Unlike modern examples, fossil footprints present a critical depth dimension as well. Track surfaces are frequently exposed at bedding planes below the original air-substrate interface. The morphological diversity of Early Jurassic tracks from the Connecticut River valley led workers like Hitchcock in the mid 1800's to infer the presence of dozens of species of trackmaker. We believe that very few taxa were responsible; most variation can be explained by substrate-induced changes in sub-surface foot motion combined with sampling at different depths. A better understanding of the mechanisms of track formation will help resolve the "one-to-many" conundrum and foster more reliable interpretation of the fossil record. (US NSF EAR 1452119 and IOS 0925077)

POS1-71 7:30 pm

A total-evidence, time-calibrated phylogeny of the 'waterbird' assemblage (Tetrapoda, Aves).

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Abstract: Although the evolutionary relationships of major neoavian groups have remained notoriously difficult to resolve, consensus is emerging across studies in support of a large "waterbird" clade. This diverse assemblage of aquatic and semi-aquatic birds includes most members of the traditional Pelecaniformes (pelicans, frigatebirds, gannets, boobies, darters, cormorants), Ciconiiformes (storks, herons, ibises, shoebill, hammerkop), Procellariiformes (tube-nosed seabirds), Sphenisciformes (penguins), and Gaviiformes (loons). However, phylogenetic hypotheses for the group vary substantially across analyses that differ in data type (molecular, morphological) and density of taxon sampling, hindering analyses of trait evolution in this highly diverse group. For the first time, I apply Bayesian phylogenetic methods that incorporate fossils as terminal taxa to a combined matrix of 551 morphological characters and 6,683 basepairs from five genes for 156 taxa (106 extant, 50 fossils). Importantly, I assess the affinities of the Plotopteridae, an extinct lineage of wing-propelled diving birds often interpreted as convergent with penguins, in a matrix that includes a dense sampling of stem and crown penguins. The total evidence Bayesian analysis did not converge after an initial run of 10 million generations and is ongoing. Calibrated morphology analysis weakly supports the divergence of plotopterids from the penguin stem 62.4 Ma (95% HPD = 56.7-69.3 Ma), a topology also supported by parsimony. Uncalibrated Bayesian morphology analysis pulls the plotopterid-penguin clade into a sister group relationship with anhingas and cormorants, reflecting several aspects of cranial and pectoral morphology shared by plotopterids and pelecaniforms and highlighting the potential importance of temporal information in phylogenetics. Recovery of Plotopteridae near the base of Sphenisciformes suggests that early specializations for wing-propelled diving were independently elaborated in each group.

POS1-73 7:30 pm

Dental microwear and macrowear morphology of the Japanese dormice (Mammals: Gliridae *Glirulus japonicus*).

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Abstract: Japanese dormice (*Glirulus japonicus*) are endemic to Japan and are thought to be the most primitive species in the Gliridae family. Fossils of this species have been uncovered from the Pleistocene mammal fauna in Japan. However, there is also uncertainty regarding the form of the molars, as there is less morphological information available for comparison with fossils. Using the skull of extant species, with a focus on wear facets and microwear, premolar and molar teeth were studied and compared with other Japanese rodents (*Sciurus lis*, *Microtus montebelli*, *Myocastor coypus*, *Rattus norvegicus*, and *Mus musculus*). In addition, wear facets was also identified. Many variations in the microwear patterns were confirmed for Japanese dormice as compared with those for any other rodents. It is possible that chewing patterns and diet are more diverse for this species than for other rodents. This observation is considered to be useful for fossil, function and ecological studies. In the future, there is a need for comparison with Gliridae species in Europe and Asia (fossil and extant).

POS1-75 7:30 pm

Occipital condyle width predicts body mass in proboscideans.

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Abstract: Body mass is one of the most important traits of an organism, and has been widely studied in mammalian paleobiology. Many studies have demonstrated significant relationships between dental and skeletal measurements

of extant mammals and their body masses. These regression equations have been used to determine the mass of extinct species. A commonly used estimator is the area of the first molar, and this relationship has been found to be robust across many orders of mammals. Proboscideans are the exception. Due to complex replacement patterns and the highly derived structure of extant proboscidean teeth, dental dimensions are not useful in predicting the body mass of extant and extinct species. However, studies have demonstrated the use of shoulder height, limb bone dimensions and volumetric measures in estimating body mass. The problem with the fossil record is that one rarely finds complete skeletons that can be used to estimate shoulder height or volume, and some species are identifiable from cranial remains alone. Therefore, the goal of this study is to determine whether cranial measurements can be used to estimate body mass for proboscideans. Occipital condyle width is a reliable estimator of body mass in sirenians, the sister group to proboscideans, and I hypothesize that it will be a useful estimator of body mass in proboscideans as well. I used two extant species, *Elephas maximus* and *Loxodonta africana* to determine whether occipital condyle width correlates with limb bone dimensions which have been shown to predict body mass in both extinct and extant taxa. Preliminary data from two *E. maximus* and three *L. africana* show a strong correlation between occipital condyle width and humerus and femur circumference, and humerus and femur length. An analysis of more specimens will be used to verify this trend and generate a predictive equation for limb bone measurements, which will then be used to determine the body mass of extinct species.

POS1-77 7:30 pm

A complete description and phylogenetic analysis of *Puijila darwini*, (Mammalia: Carnivora) and inferences on the plesiomorphic swimming condition of pinnipeds.

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Abstract: Whereas the land-to-sea transition is well-documented in many secondarily aquatic mammals, the fossil record of stem pinnipeds is relatively sparse, offering few well-preserved transitional fossils. Due to this paucity of transitional pinniped forms, it remains unclear how the divergent locomotory modes of modern pinnipeds (i.e. forelimb vs hindlimb swimming) and associated morphologies evolved within pinnipeds. In 2009, Rybczynski et al. reported the discovery of *Puijila darwini*, a putative stem pinniped from the Miocene of Canada's High Arctic. A brief description was complemented with a preliminary phylogenetic analysis uniting *Puijila* in a clade with *Enaliarctos* (previously the oldest known pinniped), *Potamotherium* (previously considered a stem lutrine) and *Amphicticeps*. The present study offers a complete description of *Puijila*, and identifies new potentially taxonomically informative traits shared by *Puijila*, and other proposed stem pinnipeds. Such traits include reduced, lingually-located M2s and m2s, a posteriorly expanded and shallowly excavated basioccipital, presence of a fossa muscularis anteromedially to the circular infraorbital foramen, confluence of the foramen ovale and caudal alar foramen, and the absence of a postglenoid foramen, among others. To infer the locomotor habits of *Puijila*, a PCA was performed, following Gingerich (2003), who examined the relationship between osteology and swimming behaviour across a variety of mammalian taxa. PC scores for PC2 (level of aquatic adaptation) and PC3 (preference for forelimb or hindlimb powered propulsion) were calculated for *Puijila*, plotting it as adapted to aquatic environments (PC2) and as a forelimb-dominated swimmer (PC3). Such results may indicate forelimb powered propulsion evolved before pinnipeds became specialized for marine environments. A phylogenetic analysis will determine if forelimb swimming arose multiple times within pinnipeds.

POS1-79 7:30 pm

Macroevolutionary responses to invasion in terrestrial carnivorans from the early Miocene of North America.

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Abstract: The macroevolutionary effects of species invasion in vertebrates have been well documented in island settings, but remain relatively unexplored with respect to large-scale continental migrations. Taxonomic diversification rates through time indicate that competitive interactions between endemic and migratory fauna on continents may have been an important factor in shaping community composition. Patterns in ecological diversity, or morphological trait evolution, have the potential to offer more detailed information about these interactions, and the fossil record presents an opportunity to study them on macroevolutionary timescales. Here I focus on whether it is possible to detect long-term patterns in the morphological evolution of terrestrial carnivorans that can be attributed to the influence of invasion. The study period comprises around 10 million years of the early Miocene, from 23.03-13.6 Mya. This represents a comparatively well constrained system, when North America experienced repeated migrations of taxa across the Bering land bridge from Eurasia. I analyse a dataset of continuous and discrete cranio-dental characters for over 50 carnivoran taxa, under a phylogenetic framework. I test three hypotheses; 1) character displacement allows maintenance of a phylogenetically even body size distribution following invasion, 2) phylomorphospace occupation distinguishes successful invaders from other taxa and 3) a geographically constrained phylogenetic model of competition-mediated evolution is the best fit to trait change through time. To ensure validity of results I use a model based simulation approach to test the sensitivity of these methods with respect to trait variance and uncertainty derived from an incomplete and time averaged fossil record.

POS1-81 7:30 pm

A well-preserved malleus in a juvenile specimen of the extinct family Nimravidae.

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Abstract: The auditory ossicles are an amplification system that evolved in terrestrial vertebrates as a way to adapt to hearing out of the water. The number of ossicles is variable among the vertebrate groups, however the presence of three auditory ossicles (malleus, incus, and stapes) is one of the defining characteristics of the Class Mammalia. There is considerable variability in ossicle morphology across the orders of mammals, and in extant and some extinct taxa they can have taxonomic utility. These small bones are only occasionally discovered as fossils, due to their small size, fragility and that they are usually inside the auditory bullae where matrix may be covering them. This project examines the presence of well-preserved auditory ossicles in a specimen of juvenile *Nimravus brachyops* (F:AM 99259) from the White River chronofauna. In other mammals it is shown that the auditory ossicles are close to adult size and shape at birth, so even though this fossil is a juvenile, the morphology should be very similar to that of adult Nimravids. As the ossicles are preserved in situ and are held in place by matrix, the malleus, as the lateral-most ossicle, is the one that was uncovered most easily. The presence of the incus and stapes cannot be determined at this time. Based upon the morphology of the muscular process, the lateral process, and the head of the malleus, this specimen most closely resembles the malleus of modern felids and canids and is less similar to other members of the modern Carnivora.

Morphological Integration & Modularity (MIM)

POS1-83 7:30 pm

Histological analysis of morphological integration and development in the Weberian apparatus of the zebrafish.

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Abstract: The Weberian apparatus is a complex morphological structure unique to Otophysi, a diverse clade that includes several large teleost orders (Cypriniformes, Characiformes, Siluriformes, and Gymnotiformes). Considered a key innovation for otophysan fishes, the Weberian apparatus produces dramatically increased hearing sensitivity via transforming and amplifying far-field sound (pressure) captured by the swim bladder into a near-field input transmitted to the inner ear via modified vertebral elements. While the skeletal contributions to the apparatus, the Weberian ossicles (claustrum, scaphium, intercalarium, tripus, and os suspensorium), have been described in several species, few studies have focused on their ontogenetic development. Even fewer studies have addressed the development of soft tissue components, or how these elements are integrated within the apparatus. In this study, a detailed histological analysis of the development of the Weberian apparatus in the zebrafish, *Danio rerio*, is presented, including elements from the vertebrae, ear, swim bladder, ligaments, and other soft tissue components. Preliminary data suggest a strong relationship in developmental timing between the vertebral, auditory, and swim bladder components of the Weberian apparatus, indicating strong functional constraint on development of the apparatus as a unit. The significant morphological and developmental integration are likely required for the Weberian apparatus to become functional quickly during late larval/early juvenile stages.

POS1-85 7:30 pm

A refined system of vertebral column subdivision in Chinook salmon, *Oncorhynchus tshawytscha* (Actinopterygii: Salmonidae).

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Abstract: Teleost vertebral bodies are often similar in size and shape, but neural arches, haemal arches and ribs show regional differences. Here it is asked if the presence and characters of vertebral body appendages can be used to refine the system of vertebral column subdivision in juvenile Chinook salmon. Animals raised at 8 and 12°C were studied at 1400 and 1530 days post hatching. Anatomy and the skeletal tissue composition of the vertebral column were studied using Alizarin red S whole mount staining and histological serial sections. Based on the presence of neural arches, parapophyses, ribs, haemal arches and caudal fin endoskeletal elements, six regional types of vertebrae are recognised: (1) postcranial, (2) abdominal, (3) transitional, (4) caudal, (5) preural and (6) ural. Postcranial vertebrae (1) carry vestigial parapophyses and lack ribs. In abdominal vertebrae (2) ribs articulate with parapophyses fused to basiventrals. Elastic- and fibrohyaline cartilaginous joints and Sharpey's fibres connect the bone of the parapophyses and ribs. Neural arches of postcranial and abdominal vertebrae are fused to the basidorsals. In the transitional region (3) the parapophyses gradually transform into haemal arches. The neural and haemal arches fuse to the vertebral bodies. Ribs decrease in size, anterior to posterior. Vestigial ribs remain attached to the haemal arches with Sharpey's fibres. In caudal vertebrae (4) basidorsals and basiventrals are small and

internalized into the bone of the vertebral centrum. Preural vertebrae (5) carry neural and haemal arches that also support the caudal fin. Two ural vertebrae (6) carry hypurals and epurals that represent modified haemal and neural arches respectively. The postcranial and transitional vertebrae and their respective characters are usually not recognised but should be considered for subdividing the vertebral column into distinctive regions.

POS1-87 7:30 pm

Chemical manipulation of axolotl regeneration and angiogenesis.

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Abstract: In mammals, tissue repair requires angiogenesis, and angiogenesis requires the VEGF, Notch, and TGF- β signaling systems. The dependence of epimorphic regeneration on the formation of new blood vessels and these signaling pathways is less well known. We used small molecule inhibitors and/or activators of these signaling pathways and assessed their effect on tail regeneration and regenerative angiogenesis in the axolotl tail following amputation. Larval and juvenile salamanders were treated daily with drug or vehicle control. Each animal's regenerative outgrowth and vascular density was quantified using ImageJ over the period of regeneration. Vascular density and regenerative outgrowth were not strongly correlated: a decrease in vascular density did not predict poor regenerative ability, and poor regenerative ability was not necessarily coupled to low vessel density. The results are consistent with there being fundamental differences in mammalian tissue repair versus ectotherm regeneration. This work provides a first step towards developing a system for the manipulation of regeneration.

POS1-89 7:30 pm

Ontogenetic integration and modularity in the dermatocranium of the Greater Short-horned lizard, *Phrynosoma hernandesi*.

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Abstract: Ontogenetic change in dermatocranial form in a series of 79 *Phrynosoma hernandesi* (54 F: 25 M) was examined, using geometric morphometric analytical techniques. Multivariate regression of Procrustes residuals on $\ln(\text{centroid size})$ indicated that allometry accounts for ~53% of the total sample variance in landmark configuration, and suggests no sexual shape dimorphism. Groupings of multivariate regression coefficients by magnitude and sign suggest regions of localized allometric integration of the dermatocranium, principally the posterior regions of the parietal, the squamosals, and the posterior region of the frontal, all of which bear horns throughout the genus. A principal component analysis of the variance-covariance matrix generated from the residuals of the multivariate regression yielded a first principal component which describes shape variance concentrated in the posterolateral and posterior regions of the dermatocranium. Hypotheses of modularity for the dermatocranium based upon observations of geographic variation in external head shape, and groupings of the PC1 coefficients by magnitude and sign, were tested with multi-set RV coefficients. We failed to reject an hypothesis based upon PC1 groupings, dividing the dermatocranium among six modules. Three of these encompass the dermatocranial horn suite of *P. hernandesi*. We hypothesize that adult dermatocranial shape in *P. hernandesi* results from the interaction of this modularity and localized allometric integration. Dermatocranial shape and horn morphology display great disparity among the species of *Phrynosoma*, and our findings for *P. hernandesi* suggest that evolvability in the dermatocranium may result from greater independence in variation and response to selection among its parts.

Evo-Devo (EVD)

POS1-91 7:30 pm

Comparative study of hexose transporters in ostrich small intestine.

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Abstract: Background and aim of the study. As there are notes in literature about high mortality of ostrich chicken in farms especially until 30 days after hatching (mortality rate about 46 %) and there are relatively few data about scientific research on organ systems, including the gastrointestinal system, at early periods of ontogenesis of ostrich chicken, more detailed scientific research is necessary to carry out in this field. As carbohydrates are the main energy source of food, but up to now there is few information about the localization of hexose transporters in ostriches gastrointestinal tract the aim of the present study was to localize glucose transporters-2 and -5 in ostriches small intestine in their first postnatal month. Methods. Material from duodenum and terminal zone of ileum was collected from eight female ostriches (*Struthio camelus* var. *domesticus*): three chicken after hatching, three 7 and three 30 days old ostriches. Material was fixed with 10% formalin, embedded into paraffin, slices 7 μm thick were cut followed by immunohistochemical staining with polyclonal primary antibodies Rabbit anti-GLUT-2 and Rabbit anti-GLUT-5 carried out according to the manufacturer's guidelines (IHC kit, Abcam, UK). Results and conclusion. The results showed that the staining for both antibodies was weaker of ostriches after hatching compared to 7 and 30 days old ostriches showing that the small intestine of ostriches immediately after hatching is not entirely able for transportation of carbohydrates. The results of our study may indicate to the possibility of close relationship between feeding and ability to transport sugars in gastrointestinal tract.

POS1-93 7:30 pm Fetal membrane morphology in oviparous lampropeltine snakes (Colubridae). Kim YK*, Trinity College; Blackburn DG, Trinity College young.kim@trincoll.edu

Abstract: In oviparous reptiles, fetal membranes line the eggshell and maintain the developing embryo by regulating gas exchange and the uptake of water and calcium. Unfortunately, the scarcity of morphological studies hinders an understanding of their functional specializations and evolution. We have used scanning electron microscopy to study fetal membrane morphology in two oviparous snakes, the Pueblan milksnake, *Lampropeltis triangulum campbelli*, and the kingsnake, *Lampropeltis getula*. In both species, two major fetal membranes, the chorioallantois and yolk sac omphalopleure, are present. The chorioallantois in early development is characterized by enlarged chorionic and allantoic epithelia and avascular connective tissue. As the chorioallantois matures, vascularization increases and the chorionic epithelium thins to facilitate gas exchange. The yolk sac omphalopleure is initially an avascular structure which is transformed into an omphalallantois upon vascularization by the allantoic capillaries. As the isolated yolk mass regresses and the epithelia thin, the omphalallantois is transformed into a chorioallantois, enhancing the growing embryo's potential for gas exchange. In early development, the chorionic epithelium exhibits microvilli that increase surface area for water uptake. The allantoic epithelial cells may produce allantois fluid involved in water uptake and storage. Our findings are consistent with a previous study on the corn snake, *Pantherophis guttatus*, but offer novel morphological observations and functional hypothesis. Comparisons of fetal membranes to those of other squamate species may contribute to a reconstruction of ancestral characteristics for snakes.

POS1-95 7:30 pm

Placental morphology in viviparous North American water snakes (Colubridae).

Blackburn D. G.*, Trinity College; Johnson A.R., Trinity College; Anderson K.E., Cornell University; Marquez E.C., Boston University; Callard I.P., Boston University daniel.blackburn@trincoll.edu

Abstract: In viviparous snakes and lizards, placentas maintain developing embryos in the maternal uterus through transfer of respiratory gases, water, and nutrients. As part of a long-term survey of reptile placentation, we used light microscopy, SEM, and TEM to study placental membranes in the water snake *Nerodia sipedon* (Colubridae). The chorioallantois and adjacent uterine lining are highly vascularized with thin epithelia, features that enhance gas exchange. The yolk sac placenta shows evidence of histotrophic nutrient transfer. Scanning EM reveals elaborate networks of capillaries in fetal and maternal components of both placentas. The chorioallantoic placenta replaces the yolk sac placenta during development to meet growing embryonic needs for gas exchange. In late development, earlier functions of the fetal yolk sac placenta are evident in residual yolk droplets and absorptive cells. Placentation in *Nerodia* is similar to that of other thamnophiine snakes and has converged evolutionarily on viviparous lizards and eutherian mammals.

POS1-97 7:30 pm

A novel pattern of yolk mobilization in developing squamate reptiles.

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Abstract: Corn snakes (*Pantherophis guttatus*) serve as a valuable model for developmental studies. Unlike birds, which employ a well-vascularized yolk sac to transport nutrients to the embryo, corn snakes use an elaborate network of blood vessels that penetrate into the yolk mass itself. In this study, we have used light microscopy and SEM to image yolk samples from eggs of mid to late developmental stages. Our observations have revealed how the large yolk mass is vascularized, cellularized, and mobilized for embryonic use. As the endodermal cells proliferate, they form elongated cords of interconnected cells that are filled with yolk platelets. During angiogenesis, the vitelline blood vessels become encased in these cells, allowing them to transport the products of yolk digestion back to the developing embryo. Our lab has found that this unusual mechanism of yolk cellularization and mobilization occurs in other snakes as well as lizards and may be ancestral for squamate reptiles. Studies of this developmental mechanism offer information on patterns from which viviparity has evolved and contribute to an understanding of reptilian evolutionary history.

POS1-99 7:30 pm

Endocrine control of limb development in the direct-developing frog *Eleutherodactylus coqui* (Anura: Eleutherodactylidae).

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Abstract: Direct development has evolved independently in at least a dozen anuran lineages. Direct-developing frogs, including the Puerto Rican coquí, *Eleutherodactylus coqui*, hatch from terrestrial eggs as miniature adults. Their embryonic development is characterized by precocious formation of adult morphology, including limbs. In metamorphosing frogs, formation of limbs at metamorphosis is mediated by thyroid hormone (TH). Changes in temporal or spatial expression of the nuclear thyroid receptor - (TR) or thyroid receptor - (TR) in the limb could facilitate their early development in *E. coqui*. qRT-PCR analysis shows that *TR* and *TR* are indeed expressed at every stage of limb development. Moreover, these TRs may be functional... T3 treatment, for example, appears to alter expression of some candidate T3-response genes in the brain. These data suggest that the *E. coqui* limb is competent to respond to TH and that TH-mediated development may begin very early in embryonic development.

However, the TR dual-function model suggests that both T3-bound and unbound TRs play important developmental roles. Thus, quantification of native THs in the developing embryo is needed to more precisely determine T3 availability and the role of the receptor. Liquid-chromatography mass-spectrometry (LC-MS) is an accurate and sensitive method to measure THs. LC-MS detects both T4 and T3 at the initial stage of limb development in *E. coqui* embryos (TS5), well before embryonic TH synthesis begins at TS9. Thus, maternally derived TH likely plays an important role in precocious limb formation. This work is an important first step in describing the physiological mechanisms that underlie direct development and will serve as a comparison to examine the evolution of this life history strategy in other amphibian groups.

POS1-101 7:30 pm

A survey of morphological and heterochronal variations during early ontogeny in six families of Leptodactyliformes (Anura: Hyloides).

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Abstract: The early ontogeny in anurans includes the occurrence of transient, exclusively embryonic structures, plus the initial stages of development of larval features. We compared developmental series of 13 species belonging to six families of the clade Leptodactyliformes, in order to record morphological and heterochronal changes among them. Tailbud embryos of *Telmatobius oxycephalus* (Telmatobiidae), *Limnomedusa macroglossa* (Alsodidae), and ceratophryid *Ceratophrys cranwelli*, *C. ornata*, and *Chacophrys pierotti* are well-pigmented and have no dorsal curvature. Conversely, *Batrachyla leptopus* (Batrachylidae) and six species of Odontophrynidae have pigmented but kyphotic embryos. Embryos of *Cycloramphus brasiliensis* (Cycloramphidae) lack pigmentation completely. Three different adhesive gland types occur: type A in Ceratophryidae and *L. macroglossa*, type C in Odontophrynidae and *B. leptopus*, and type B in *T. oxycephalus*, this latter being typical of unrelated bufonids. The adhesive glands are absent in *C. brasiliensis*. Regarding gills, two pairs occur in Odontophrynidae, *L. macroglossa*, and *C. brasiliensis*, and a third pair develops in Ceratophryidae, *T. oxycephalus*, and *B. leptopus*, in this latter case poorly developed. Ontogeny of the oral disc is similar in all species with labial tooth row formula 2/3, whereas *Ceratophrys* spp. differ in development of supernumerary tooth rows. Some patterns will likely be proven diagnostic of some clades (e.g., type B adhesive glands in *Telmatobius*, three gill pairs in ceratophryids). On the other hand, the unusual set of features of the exotrophic, semiterrestrial *C. brasiliensis* specimens (large yolk provision, and lack of pigmentation and of adhesive glands) are typical of endotrophic embryos, and possibly conserved within the genus.

POS1-103 7:30 pm

Evolutionary and developmental mechanisms underlying craniofacial variation in Neotropical bats.

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Abstract: Parallelism between individual development and the pattern of organismal evolution has been discussed for almost 200 years, but examples of the connection between these fundamental biological phenomena have been isolated and phylogenetically disparate. The New World leaf-nosed bats (Phyllostomidae), arguably the most ecologically diverse clade of mammals, have evolved extraordinarily diverse faces and skulls adapted for many different food types, such as insects, fruit, nectar, other vertebrates, and blood. To understand the processes that generated this diversity, we employ a phylogenetically informed geometric morphometric approach analyzing the variability of 3D skull landmarks from developmental and adult data across several lineages. Our results demonstrate widespread peramorphosis in phyllostomid skull morphologies and reveal that their distinctive ecomorphologies are largely achieved through “terminal addition” as the evolutionarily more recent features in cranial morphology emerge later in bat development. Phyllostomids, thus, provide a real-world example of “ontogeny recapitulates phylogeny” with important implications for understanding the evolution of adaptive morphological diversity in vertebrate body form.

POS1-105 7:30 pm

Hoxa11 and Hoxd11 loss-of-function mutations alter pisiform growth plate organization.

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Abstract: Mammalian pisiforms are typically elongated and develop from two centers of ossification with a single organized growth plate on the palmar end; however human pisiforms are unique among mammals because they are short, develop from a single ossification center, and lack a growth plate. *Hox* genes provide crucial developmental patterning information, and are thought to influence growth plate formation. *Hoxa11* and *Hoxd11* are expressed around the developing pisiform in mice, and mutations to these genes result in abnormal shortening of the pisiform. This study seeks to determine if *Hoxa11* and *Hoxd11* loss-of-function mutations influence pisiform growth plate formation and chondrocyte organization, resulting in the observed pisiform shortening compared to wild type. Histological analyses of *Hoxa11* and *Hoxd11* mutant mouse pisiforms indicate that abnormal chondrocyte

organization occurs in heterozygotes and homozygotes for either deletion. Severity of organizational abnormalities is dosage dependent for both genes. *Hoxa11* mutants lack a distinct hypertrophic zone and exhibit a reduced columnar zone. All chondrocytic zones appear reduced in *Hoxd11* heterozygotes, with more marked disorganization in homozygotes. *Hoxd11* mutants also have irregular progression of the ossification front. These results support the role of *Hox* genes in pisiform growth plate formation and overall pisiform length in *Hoxa11* and *Hoxd11* mutant mice. Understanding the influence of *Hox* genes on chondrocyte organization may also help to explain developmental processes responsible for growth plate loss in the unique human pisiform. This research is funded by the Hill Fellowship (Department of Anthropology, Penn State) and NSF BCS-1540418.

POS1-107 7:30 pm

Evolution of fetal skeletogenesis in mammals: patterns, diversity, and modularity.

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Abstract: The multiple skeletal components of the body originate asynchronously, and their developmental schedule varies across mammals. It has been assumed that simple alterations in the onset, duration, and tempo of development are regarded as causes of profound morphological changes. Until recently, however, most heterochronic studies on mammals have focused on postnatal life, and our knowledge of fetal development has largely been restricted to model organisms. The critical stages for examination of skeletogenesis are fetal or around the time of birth, and thus non-model organisms are rarely available and difficult to sample. Gathering more than thousand fetal and neonatal specimens from museum collections and adopting nondestructive microtomographic imaging technique, we described the sequence of skeletogenesis of more than 100 mammalian species. Mapping this comprehensive dataset to the reported molecular phylogeny enabled us to reconstruct the ossification sequence for the common ancestor of Mammalia and to identify evolutionary shifts of ossification sequence at all nodes. Timing of limb development appears to be strongly related to the modes of newborn lifestyle, most clearly exemplified in bats. Compared to other amniotes, timing of the neurocranium development was considerably accelerated during the origin of mammals. Furthermore, association between developmental timing of the supraoccipital and relative brain size was confirmed among mammals. We also highlight that skull bones form two separate modules, one consisting explicitly of dermal bones and the other of endochondral bones. However, neither mesoderm vs. neural crest origin nor phenotypic modularity identified based on adult metric traits appear to be related to cranial ossification heterochrony. We suggest that the mode of ossification (dermal or endochondral) imposes evolutionary bias on cranial heterochrony.

POS1-109 7:30 pm

Linking morphometrics with 3D analysis of gene expression patterns of early limb development in an Apert syndrome mouse model.

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Abstract: Understanding how gene networks coordinate organogenesis remains one of the key questions of developmental biology. An important step has been the development of new techniques to visualize gene expression patterns within developing structures in a three-dimensional (3D) framework, such as Optical projection tomography (OPT). However, there have been few attempts to quantitatively analyze the shapes of gene expression domains. Here we combined OPT with Geometric Morphometrics (GM) for embryonic phenotyping of the developing limbs of the *Fgfr2*+/*P253R* Apert syndrome mouse, a model for a congenital disorder characterized by cranial, neural, and limb malformations such as syndactyly. We explored early limb morphogenesis to assess whether the *P253R* mutation in the *Fgfr2* gene induces changes in the expression pattern of *Dusp6*, a downstream target of the FGF/FGFR signaling pathway, and whether these genetic changes can be associated with limb malformations in mutant mice. GM analyses of 3D landmark-based data recorded on OPT images of 11.5 embryonic day (E11.5) embryos labeled for *Dusp6* expression using whole-mount in situ hybridization revealed differences in limb size and shape between mutant and unaffected littermates. At E11.5, the limbs of mutant mice were significantly smaller; and the shapes of the limbs and of the 3D expression pattern of *Dusp6* were also affected, especially of hind limbs. This suggests that altered FGF/FGFR signaling has direct consequences on target genes that contribute to limb malformations as early as E11.5. Precise embryonic phenotyping of Apert syndrome mice with more time points and genes is ongoing and will help us identify the origins of abnormal limb morphogenesis. By combining OPT and GM, our method is a potentially useful tool to compare normal and disease-altered patterns of variation and to reveal how the genotype translates into the phenotype. Grant support: FP7-PEOPLE-2012-IIF 327382, SEV-2012-0208.

POS1-111 7:30 pm

Expression of a set of cranial neural crest regulatory genes in the dental mesenchyme during mouse tooth development.

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Abstract: During mammalian embryonic development, cranial neural crest cells are specified in the dorsal neural tube by a set of regulatory genes that distinguish these cells from adjacent non-migratory cells of the neural tube and the non-neural ectoderm. Cells derived from the cranial neural crest contribute to the mesenchymal tissue in the branchial arches that form the head, including the dental mesenchyme in developing teeth. Tooth development has been studied extensively in mice (*Mus musculus*) and the expression patterns of many genes necessary for proper tooth development are well documented. However, similarities in the genetic regulation of cranial neural crest development and tooth development have not been explored in depth, despite the fact that cranial neural crest-derived cells comprise much of the dental mesenchymal tissue in developing teeth. This study documents the spatial expression patterns of a set of cranial neural crest regulatory genes in developing mouse teeth to test the hypothesis that a gene regulatory network that is initiated in embryonic development in the cranial neural crest is later re-activated during dental development. In situ mRNA localization analyses were used to examine spatial expression patterns of these genes at three key stages in dental development: bud (E12.5), cap (E14.5), and bell (E16.5-17.5) stages. Preliminary results suggest that at least some of these genes are expressed in both the cranial neural crest cells and the dental mesenchyme. Additional in situ assays to detect expression of other genes associated with the cranial neural crest will demonstrate whether the expression of this entire set of regulatory genes is held in common between cranial neural crest cells and their derivatives in the dental mesenchyme, or alternatively, if only part of this gene network is re-activated during tooth development.

POS1-113 7:30 pm

Fetal growth in mysticete and odontocete skulls: the developmental origins of the highly divergent skulls of cetaceans .

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Abstract: Cetaceans (whales, dolphins, porpoises) have highly divergent skulls, but how the mammalian skull groundplan became modified for aquatic life and how that morphology arises in ontogeny is still not well understood. The arrangement of the skull differs significantly in the two sub-clades of crown cetaceans: toothed whales (odontocetes) and baleen whales (mysticetes). Miller (1923) coined the term “telescoping” to describe a major aspect of cetacean skull morphology, wherein the cetacean skull bones overlap to a much greater extent than is the case in overlapping or squamous sutures observed in other mammals; these changes occurred concomitant with the nares moving posterodorsad to form a blowhole. In order to elucidate the developmental mechanisms that generate telescoped skull morphology, we documented and compared the ontogeny of cetacean skulls using measurements from CT scans of ontogenetic series of cetacean fetuses representing the two crown cetacean sub-clades. Preliminary findings suggest, in contrast to previous reports, that change in skull length relative to total body length is indistinguishable from isometry during the early portion of the fetal period. Additionally, *Balaenoptera physalus* (mysticete) and *Stenella attenuata* (odontocete) differ in positive allometry of several skull features relative to skull length during fetal growth, which contribute to the development of the two adult telescoped conditions. This study on the ontogeny of the extremely divergent morphologies of cetacean skulls allows us to examine how changes in development shape the limits of morphological variation.

POS1-115 7:30 pm

Testing a model of scute patterning in cheloniid sea turtles.

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Abstract: A recent model suggested that placodal signaling centers in primordial carapace are likely to act as developmental modules that are responsible for the evolution of scutes in turtles. Further, the regulation of these centers has allowed for the diversification of turtle shell's scute patterns. Scute anomalies occur during embryogenesis and may be connected with environmental conditions during incubation. Environmental factors have been hypothesized to contribute to the development of scute anomalies; some factors may be related, such as mechanical stresses that occur with desiccation. Here we quantify and compare scute pattern anomalies in cheloniid sea turtles that were incubated under natural conditions, but during normal and hotter-than-normal years. Three types of scute anomalies were found: supernumerary scutes, atypically shaped scutes, and absence of some regular scutes. As has been noted in other turtle species, these types of anomalies may occur separately or together in the same individual. By comparing the scutes of hatchlings sampled from in situ nests, we test the hypothesis that abnormal growth or a shift in reaction-diffusion dynamics may be a consequence of the combined thermal and hydric environments. When scute asymmetries occur under extreme thermal conditions, the relative distances of the forming scute primordia resulting in “vacant” areas where supernumerary primordia could have a thermal basis.

POS1-117 7:30 pm

Functional characterization of enhancer variants driving human evolution.

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Abstract: The genetic changes underlying the myriad differences between humans and other primates are largely

unknown, although it is clear that gene regulatory changes play an important role. Whole-genome comparisons show that protein-coding sequences do not vary greatly between humans and other primates. Rather, the vast majority of inter-species genetic differences lie in non-coding regions of the genome, namely enhancers. Enhancers are regulatory sequences that determine when, where, and how much a protein-coding gene is expressed in every animal tissue. Even though enhancers tend to be evolutionarily conserved, they evolve faster than coding regions, suggesting that changes in regulatory DNA play an important role in evolution. Many authors, starting with the seminal work of King and Wilson, have suggested that the majority of the changes that distinguish humans from other hominoids are to be found in the 98.5% of the genome that is non-coding. As our knowledge of the regulatory code progresses, the closer we are to understanding the molecular basis for human evolution, development, and disease. To identify human-specific regulatory elements, several groups have developed computational approaches to scan mammalian genomes for evolutionarily conserved sequences that have changed significantly and uniquely in humans. The Pollard group has previously identified 721 human accelerated regions (HARs) using a method based on likelihood ratio tests for accelerated sequence divergence on the human lineage. 92% of these HARs are non-coding, further underscoring the likely importance of regulatory sequences in recent human evolution. Although a subset of HARs has been shown to act as enhancers in vivo, the vast majority of the HARs remain to be functionally characterized. Here, I present my work on functionally characterizing these HARs en masse, and identify human-specific nucleotide variants driving divergence in human and chimpanzee gene regulation during development.

Hard-tissue Biology (HRD)

POS1-119 7:30 pm

Evidence of hyperostosis in the oarfish (*Actinopterygii: Regalecus russellii*).

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Abstract: Hyperostosis, extra bone growth, has evolved independently in at least 22 families of fishes most of which are tropical or subtropical marine species. While the presence of hyperostosis is well documented in fishes, the mechanism driving the development of the extra bone growth is unclear. We documented regular, repeating hyperostosis along the dorsal pterygiophores in mature Oarfish, *Regalecus russellii*; e.g. those with total lengths greater than 3m. In oarfish, the majority of the skeleton contains low mineralized, acellular bones with localized areas of stiffened, cellular bony growths near the distal edge of the pterygiophores. We propose these additional skeletal elements help to provide a stiffened lever structure for dorsal fin undulation. Oarfish lack a swim bladder so they must continuously beat their bi-directional dorsal fin to maintain position within the water column and while engaged in locomotory behavior. It is therefore not surprising that these fishes have areas of localized, hyperostotic skeletal elements that are capable of withstanding higher mechanical pressures and that undergo bone remodeling.

POS1-121 7:30 pm

Bone growth and bone morphology in Atlantic salmon under conditions of severe phosphorus deficiency: The uncoupling of bone formation and bone mineralisation.

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Abstract: Teleosts, can obtain calcium (Ca) from the water to mineralise their bones. Contrary to tetrapods teleosts do not suffer from dietary calcium deficiency, but depend on dietary phosphorus (P) intake to mineralise the bones. To understand the effect of low dietary P intake on the morphology of the vertebral column a P deficiency was induced in post-smolts (early seawater phase) of Atlantic salmon *Salmo salar*. The P content of the diet was reduced by 50% for 10 weeks. The vertebral column morphology was subsequently evaluated using X-rays, histology and histochemical (detection of minerals) analyses. Bones and scales were chemically analysed for the Ca and P content. In animals that received a P deficient diet the bone and scale mineral content decreased by c. 50%. The X-rays of the deficient animals exhibited undersized vertebral bodies and enlarged intervertebral spaces. Contrary to the X-ray-based diagnosis, histology revealed that vertebral bodies had a regular size and regular internal bone structures (trabeculae); the intervertebral spaces were not enlarged. Bone matrix formation continued uninterrupted, albeit without traces of minerals in the bone matrix. Likewise scale growth continued with newly formed non-mineralised annuli that retain the regular spacing. The experiment generated a homogeneous osteomalacia of vertebral bodies but no skeletal malformations and demonstrates (a) the dependency of Atlantic salmon on dietary P and (b) bone formation and bone mineralization are, to a large degree, independent. The finding that a severe deficit in mineralization did not alter the structure or growth of vertebral bodies was unexpected and is counter to the accepted paradigm in both teleosts and tetrapods. The fact that large individuals of other osteichthyan groups such as Sturgeons, Lungfish and Coelacanth maintain a non-mineralised vertebral column raises fundamental questions about the primary function of vertebral body mineralization.

POS1-123 7:30 pm

Ligaments that push and cartilage that bends: Diverse connective tissue morphology in teleost fishes is

associated with diverse functions.

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Abstract: Teleost fishes provide a classic example of cranial kinesis, where bones of the head move relative to each other especially during feeding. Functional morphological studies on fish feeding have focused on bone movement and the muscles behind it, but the links among bones are an important component. While mammals possess distinct connective tissue (CT) morphologies (e.g., ligaments made of dense regular CT with few cells and parallel fibers), teleosts exhibit diverse morphologies of CTs linking the bones, to which less attention has been paid in a functional context. Two case studies here show that the CTs linking teleostean cranial bones are of equal importance to the functional unit. For example, cypriniform fishes (carps, zebrafish) have a network of ligaments involved with jaw protrusion. The ligament connecting the premaxilla to the kinethmoid (and ultimately the rest of the head) is highly cellular and not fibrous. Functional experiments have shown that the kinethmoid begins rotating prior to jaw protrusion, evidence that the kinethmoid – and its ligament – are pushing the jaw forward. Some teleostean CTs are assumed to be composed of hyaline cartilage because they stain with Alcian blue in whole mount preparations, but often these tissues do not have the same cellular morphology and/or function as mammalian cartilage. In poeciliid fishes (mollies, guppies), a rod of cartilage (Meckel's) linking the dentary to the anguloarticular undergoes >90 degrees of bending during feeding. Histology reveals that the articulation points of the Meckel's cartilage resemble mammalian hyaline cartilage with cells trapped in a hyaline-like matrix; however, in the middle of the rod of cartilage, presumably where jaw bending occurs, the tissue is more cellular and has much less extracellular matrix. This work demonstrates that the cellular morphology of biomechanical linkages in fishes deserves closer attention, especially when studying the overall function of a cranial unit.

POS1-125 7:30 pm

High-resolution study of salamander braincase morphology using micro-CT reveals novel phylogenetic information.

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Abstract: The prevalence of neotenic taxa, animals that retain juvenile features as adults, has introduced numerous complications to morphological phylogenetic analyses of salamanders. One potential solution is the study of the braincase: in salamanders it undergoes most of its development pre-metamorphosis, but variation amongst families has yet to be documented. We scanned 28 species of salamander, including metamorphic and neotenic representatives of all 10 families, using micro-CT to visualize changes in braincase morphology across the group. We present variation in a number of braincase features that were previously thought to be generalized across salamanders, including: the bony boundaries of the brain and nerves, the afferent vascularization, and the morphology of the sensory capsules. Furthermore, features that were considered paedomorphic, and therefore phylogenetically uninformative, such as vomerine dentition, are here shown to differ amongst adults of different families. The inclusion of this novel variation may help to elucidate the morphology-based phylogenetic relationships of salamanders and may help to resolve many of the outstanding questions of salamander evolution and radiation.

POS1-127 7:30 pm

The overlooked cranial sesamoids of squamate reptiles.

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Abstract: Sesamoid bones are elements embedded within a tendon or a muscle. Although these bones have been reported frequently in the postcranium of vertebrates, cranial sesamoids have been reported almost exclusively in fishes. The only tetrapod cranial sesamoid reported until now has been the transiliens cartilage of crocodiles and turtles, located in the bodenaponeurosis of the adductor muscles of the jaw. Here we report the presence of cranial sesamoids in two different positions in the skull of several squamate species. One sesamoid is attached to the cephalic condyle of the quadrate of *Ophiodes intermedius* (Anguidae), which is embedded in the bodenaponeurosis and the jaw adductor muscles. This sesamoid seems to have a function related to the protection and movement of the adductor tendons, and might play a role in streptostyly of the quadrate. The other sesamoid is consistently found at the base of the cranium, capping the sphenoccipital tubercle (basal tubera), on the lateral side of the basioccipital – basisphenoid suture. This bone has previously been reported as “element-X” in amphisbaenians, and we here reinterpret it as a sesamoid, as it is associated with tendons of the cranio-cervical muscles (m. longus colli). This bone is also embedded in cartilage, at least earlier during the development, and seems to have the function of resisting tension-compression forces generated by the muscle during flexion the head. We have confirmed the presence of similar structures in three families *Calaptommatus leioplepis* (Gymnophthalmidae), *Chondrodactylus bibronii*, *Chondrodactylus angulifer* (Gekkonidae), and *Paradelma orientalis* (Pygopodidae). This new interpretation changes our understanding of the head skeleton in squamates, and suggests that these elements might be more widespread, at least in squamate reptiles.

POS1-129 7:30 pm

Integration of histology and morphology to assess the skeletal maturity of early-diverging dinosauiromorphs.

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Abstract: The Upper Triassic sediments of North America record the evolution of many extant vertebrate groups, including Dinosauromorphs; however, growth patterns of early dinosauromorphs are relatively unexplored because of a lack of well-preserved growth series. Additionally, our knowledge of the relationship between histological and external morphological ontogenetic changes in this clade is lacking. *Dromomeron romeri*, an early-diverging dinosauromorph from the Late Triassic of New Mexico, is reported to lack ossified bone scars in the proximal portion of the femur that are present in other archosaurs. Bone scars are important phylogenetic characters, and increase in number and size during ontogeny in many extant reptiles. In this study, we tested whether this absence of scarring is indicative of the skeletal immaturity of the reported specimens, or if this lack is an evolutionary novelty. Morphological data from a growth series of six femora of *D. romeri* (96.9 mm – 136.6 mm long) and samples of bone tissue of one femur and one tibia were taken. The histology of the sampled femur showed characteristics of a skeletally immature individual, with a vascularized bone surface and one double annual line of arrested growth (LAG); however, this LAG may indicate the cessation of growth. The sampled tibia is from an individual with the largest femur in the growth series, but this tibia did not possess LAGs, suggesting that size is not strictly correlated with ontogenetic age in this taxon. *D. romeri* does not deposit ossified femoral muscle scars during ontogeny, and histology serves as the only method of assessing maturity. Whereas muscle scarring can be an additional sign of skeletal maturity, lack of scarring does not necessarily indicate skeletal immaturity. Ontogenetic changes may not be conserved across Archosauriformes, and implementing both histological and morphological data is essential to correctly understand ontogenetic patterns in this clade.

POS1-131 7:30 pm

Body mass estimation of juvenile individuals: towards a better understanding of extinct animal growth.

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Abstract: Growth curves can provide important insights into animal physiology and ecology and are of interest to paleobiology. Growth curves of extinct animals, however, rely entirely on three estimated parameters: 1) age of individual; 2) adult body mass; and 3) juvenile body mass. Recent studies have developed elaborate age retrocalculation methods to estimate the number of ontogenetically-obiterated growth marks and accurate body mass estimation methods of adults from intraspecific limb scaling. For mass estimation of juveniles, a previous study noted that intraspecific scaling patterns need not follow interspecific ones, and proposed a simple geometric scaling ($\text{length} \propto \text{mass}^3$) method, called Developmental Mass Extrapolation (DME), for estimating the mass of juveniles. Despite its merits, DME has not been empirically tested thoroughly, which questions the accuracy of growth curve reconstructions in extinct tetrapods. In order to assess DME, juvenile masses of four extant model taxa (*Alligator mississippiensis*, *Iguana iguana*, *Procyon lotor*, and *Struthio camelus*) are estimated using DME and an interspecific limb scaling equation. Estimated and actual masses are compared using mean percent prediction errors (PPEs). Mass estimates are based on a dataset of linear limb measurements (femur circumference and total length) and body mass. The results reveal lower PPE values when DME is used compared to the interspecific equation. These indicate that 1) intraspecific scaling approximates geometrically similarity, and 2) supports the use of DME to estimate the mass of juveniles in various tetrapod taxa. However, bivariate plots show systemic biases in DME (e.g., *Procyon lotor*) that are attenuated by using femoral circumference, rather than the total length. This study reveals critical insights into the uncertainty surrounding growth curve reconstructions in extinct forms with implications for understanding the biology of extinct animals.

POS1-133 7:30 pm

The calcar: a novel hindlimb structure in bats.

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Abstract: The evolution of the mammalian skeleton is a fascinating story of adaptation and specialization. Mammalian bones have often been co-opted for new and divergent purposes, resulting in significant morphological diversity. In several clades, the number of bones has been reduced, allowing for increased locomotor performance. Here we describe a rare case of skeletal addition in mammals—the calcar, an ancestral hindlimb feature of Chiroptera that is often used in taxonomic classification but is poorly understood in terms of its anatomy and function. Bats use their hindlimbs for many tasks, including flight, roosting, and prey capture. These functions vary extensively across bat species. We hypothesize that the bat calcar is a novel skeletal feature in mammals, and that its tissue and morphological structure correspond with specialized function and ecology. We explore this hypothesis with comparative histology and 3D morphological descriptions of the calcar and tarsals across several species. Consistent with previous research, the calcar is often a mineralized cartilaginous element that projects medially from the calcaneum into the hindlimb membrane. However, we found evidence of calcar ossification in at least one bat species, *Noctilio leporinus*, which raises questions about the homology of the calcar among mammalian tarsals. We also describe a surprisingly high morphological diversity among bats in both calcars and calcanea that might be associated with differences in hindlimb function.

POS1-135 7:30 pm

Compressive behavior of vertebral bodies in cetaceans (*Delphinidae*) and Sirenians (*Trichechidae*).

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Abstract: The axial skeleton of fully aquatic mammals is a key anatomical feature powering locomotion. Body deformation is mediated by the mechanical properties of the vertebral column and surrounding non-osseous tissues, force production of swimming muscles, and the interaction of the body with water. Vertebral column stiffness, the ability to resist bending, varies regionally and increases rostro-caudally. We are investigating mechanical properties of vertebral bodies in two groups of marine mammals, cetaceans and sirenians, to understand how bones respond to force. The goals of the present study are to (1) assess yield strengths (stress at the elastic to plastic transition) and elastic moduli (resistance to compression) in the rostro-caudal plane of vertebral bodies; (2) compare yield strength and elastic moduli by functional location and vertebra anatomy, and (3) measure apparent density in the rostro-caudal plane of vertebral bodies to estimate microarchitecture. Vertebrae from the thoracic, lumbar, and caudal regions were sampled from the Florida manatee (*Trichechus manatus latirostris*; Sirenia) and melon-headed whale (*Peponocephala electra*; Cetacea). Soft tissue and bony projections from the vertebral body were removed with a bone saw and sander to isolate the vertebral body. Vertebral bodies were tested under a compressive load at a displacement rate of 0.05 in/min until the sample transitioned from the elastic to plastic region of deformation. The yield strength of the thoracic vertebra of the melon-headed whale was nearly double that of the Florida manatee. The melon-headed whale thoracic vertebral body was more than four times stiffer than the Florida manatee. However, the apparent density of the Florida manatee was double that of the melon-headed whale. These values indicate that bone in the melon-headed whale has structurally adapted to withstand higher forces in locomotion.

POS1-137 7:30 pm

Bone architecture in the rabbit (*Oryctolagus cuniculus*) mandible as a function of load and age.

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Abstract: Although the vertebrate head skeleton is not loaded by body weight, the jaws are subject to large forces from contraction of masticatory muscles and occlusion of teeth. Presumably loading influences architecture in these bones as it does the postcranial skeleton. We reduced mandibular loading in 5.5-month-old adult female rabbits by injecting one masseter with botulinum neurotoxin A (BoNT/A) once (endpoints 4 weeks or 12 weeks after injection) or three times with a 12-week recovery after each (total 36 weeks). Control animals received saline. The mandibles were examined histologically and with microCT. Bone loss was seen on both sides of the mandibular body and more dramatically at the condyle of the BoNT/A-injected side at 4 weeks. At 12 weeks, when muscle activity and force were near normal, partial bone recovery had occurred. The mandibular body no longer showed statistically significant differences between BoNT/A and saline rabbits, but after 3 injection-recovery cycles, the loss was again clear ($p < 0.02$). A similar but more extreme pattern was seen for the BoNT/A-side condyle, which lost more bone and recovered more slowly, showing a slight additive effect in the 36-week group. Interestingly, the control as well as the BoNT/A mandibles had lower bone density in the 36-week animals than in the 4- and 12-week animals. Indeed, the internal architecture of the condyles after the 36-week experiment was quite different than after the shorter experiments. There was far less trabecular bone, and the condylar cartilage was underlain by compact rather than spongy bone. We interpret these observations as age effects. The 36-week rabbits were 6-8 months older than those of the 4- and 12-week experiments. Although the transition of trabecular bone to cortical bone may indicate maturation rather than senescence, the generalized decrease in bone density suggests senescence. Thus both loading and age affect bone quality in the rabbit mandible. Funded by NIH DE018142.

POS1-139 7:30 pm

Bone microstructure of *Bathyergus suillus* (Rodentia: Bathyergidae): cortical bone thickening and sexual dimorphism.

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Abstract: Given that patterns of bone development in mammals are mostly known for cursorial animals, there is a considerable gap in our understanding of how other lifestyles affect bone growth. In addition, scarce research has been done on wild mammal populations, and these often include few individuals and incomplete ontogenetic series. This study examines the limb bone microstructure of a feral population of *Bathyergus suillus* ($n=49$), an endemic and solitary subterranean rodent from the Western Cape of South Africa. Undecalcified cross sections from the diaphysis of femur, humerus, tibia-fibula, ulna and radius through ontogeny were studied, and additional histomorphometric analyses were performed. Cortical bone thickening occurs mainly by periosteal apposition of zonal bone (fibrolamellar, parallel fibered and lamellar bone tissues) and limited endosteal resorption was observed. Midcortical areas with woven and compact coarse cancellous bone tissues also contributed to the cortical thickening. Mid-diaphyses were well vascularized during ontogeny, especially in juvenile stages, although secondary reconstruction was minor. Thickening of the compacta is evident from larger juveniles, although it is unclear if these changes are

coupled with the attainment of sexual maturity and/or dispersion from nest. Histomorphometric analysis showed sexual dimorphism in femoral and humeral cortical porosity, with females having higher levels of intracortical resorption. The shape and size of resorption cavities also indicates sexual differences in mineral homeostasis. These findings contrast with the generally high levels of resorption and remodeling documented in cursorial vertebrates. This study provides much insight into sexual differences of *B. suillus*, and provides fresh insight into how the subterranean lifestyle impacted on bone growth and development.

POS1-141 7:30 pm

Effects of selection for high wheel running on femoral nutrient foramen dimensions.

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Abstract: Genetic composition is the blueprint from which bone is built, affecting over 50% of overall bone mineral content in adult mammals. However, stress from mechanical loading causes micro-fractures in bones, triggering dynamic bone remodeling by shifting the balance of absorption and formation to net formation. This remodeling is limited by supply of blood through the nutrient artery, which supplies 50-70% of total blood volume in long bones. The nutrient artery is limited in size by the nutrient foramen that it penetrates. Because genetic and environmental factors can independently affect the structure of bone, we used mice from lines that have been selectively bred for high levels of voluntary wheel running (High Runner, or HR lines) to determine whether a difference in nutrient foramen size in long bones was present in mice selectively bred for increased voluntary running (11th and 72nd generations). Femoral foramen, cortical thickness of the diaphysis, length, volume, moment of inertia, and polar moment were measured via micro-computed tomography. We use the data to test the effects of selection (HR vs control), exercise (wheel access vs sedentary), and potential interactions between them (HR vs control with wheel access).

POS1-143 7:30 pm

Comparison of impact loading and wheel running on femoral cross-section morphology in young outbred mice.

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Abstract: The mechanostat hypothesis holds that long bones adapt to loading by increasing cortical thickness in areas that experience high strain and resorbing bone that experiences little strain, thus optimizing strength and weight. While exercises such as jogging or jumping are known to alter the cross-sectional dimensions of limb bones in vertebrates, we do not fully understand the relative contributions of ground reaction force (GRF) and muscle force in producing strains that lead to increased bone deposition with exercise. To examine the influence of loading environment on bone cross-sectional geometry, we exposed 4-week old, outbred ICR mice to one of three loading regimes for 21 days (n = 10 per group): impact loading to increase GRF to 6-10 body masses by dropping from a height of 25cm 10x per day, voluntary wheel running to increase both GRF and muscle-induced loading, or controls left undisturbed in their home cages. Undecalcified femoral mid-diaphyseal cross-sections were mounted, polished, photographed, and digitally silhouetted for analysis of cross-sectional properties. Standardized major axis regression against body mass demonstrates that the impact loading group had significantly greater cross-sectional areas, moments of inertia, and polar moments of inertia than control mice, while the running group showed no increase in cross-sectional dimensions relative to controls. Anteroposterior and mediolateral diameters and sectional moduli did not significantly differ between treatment groups. These results demonstrate that daily impact loading is more effective at altering bone cross-sectional properties than moderate to high levels of voluntary running. We conclude that further investigation is needed regarding the roles of GRF and muscle-induced forces in long bone modeling and the upper threshold of exercise duration effective for altering cross-sectional geometry, particularly in the context of voluntary locomotion.

POS1-145 7:30 pm

Effects of disrupting the dental lamina and mandibular nerve on tooth replacement in the green iguana (*Squamata: Iguana iguana*): A reanalysis of historic radiograph data.

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Abstract: The use of reptiles as amniote model organisms in the study of tooth development has become more common in recent years. The usefulness of the reptile model for studies of tooth replacement was developed in the 1960s by A.G. Edmund of the Royal Ontario Museum, Canada. In a series of prescient studies on tooth development, Edmund performed several surgeries on individuals of *Iguana iguana* to examine the effect of tooth removal and injury to soft tissues on tooth replacement patterns. Results of these experiments were never published, although mention was made that damage and wear do not affect the rate and pattern of tooth replacement. Combinations of surgeries included tooth extraction, removing small portions of the mandibular nerve with and without tooth extraction, and removal of portions of the dental lamina with and without tooth extraction. Surgeries were performed on one or two quadrants of the mouth and were monitored for up to six months post-surgery through bi-monthly radiographs (n = 8). When only tooth removal was carried out, successional teeth erupted normally after six months. In individuals where only the mandibular nerve was severed, tooth replacement rates and patterns also appeared to be unaffected.

Interestingly, in individuals where teeth were removed and the mandibular nerve was severed, teeth were continuing to be replaced, although with abnormal timing and patterning. Complete cessation of tooth replacement occurred when the dental lamina was damaged or removed. These results suggest that there is an interaction between the mandibular nerve and the tooth replacement process. However, tooth replacement cycles are very long in the iguana and the brevity of data collection may have missed a later phenotype. Hence, experiments will be repeated in the leopard gecko (Squamata: *Eublepharis macularis*) over longer time periods to determine whether there is role for the mandibular nerve in tooth replacement in reptiles.

POS1-147 7:30 pm

Comparative assessment of enamel tufts.

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Abstract: Teeth have the ability to adapt to diet through variation in shape, size, enamel thickness, prism decussation, and through the potential protective mechanism provided by enamel tufts. Tufts are hypocalcified, protein-filled fissures with a wavy-like appearance that extend outward from the enamel-dentine junction (EDJ) and between the organic sheaths that define enamel prisms. Initially, tufts were believed to be the undesirable byproducts of tooth development with no real function or value to the tooth. However, tufts are now believed to help protect teeth from catastrophic tooth failure through the mechanism of stress-shielding. Through this proposed mechanism, tufts absorb tensile stresses that build up along the EDJ during loading of the enamel and help protect teeth from large-scale fracture. If true, one would expect to find tufts primarily in animals that eat hard foods and/or apply high stresses to their teeth. However, almost nothing is known about the phylogenetic distribution of tufts in non-humans. We examined more than 25 species of carnivorans, primates, and suoids (pigs and peccaries) to determine tuft presence/absence. When tufts were present, we collected data on their distribution, density, length, and angle relative to the occlusal surface. Only humans, sea otters, and suoids featured tufts. The hypothesis that tufts are solely related to high tooth stresses is challenged by the absence of tufts in animals like wolverines and hyenas. Likewise, phylogenetic determinism does not explain the presence of tufts in sea otters but no other carnivorans. It appears that tufts are only present in animals that experience high tooth stresses and have a bunodont tooth form. Other notable findings include an inverse relationship between tuft length and density, and a different spatial arrangement of tufts in suoids compared to humans and sea otters.

POS1-149 7:30 pm

Enamel decussation patterns in carnivorans.

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Abstract: Mammalian tooth enamel is comprised of large numbers of elongate crystalline prisms running from the enamel-dentine junction (EDJ) to the outer enamel surface (OES). In some species, these prisms run in a straight line, but in others they wave, so much so that prisms appear to crisscross ('decussate'). The changing orientation of enamel prisms across the tooth crown results in an optical illusion of varying light and dark bands known as Hunter-Schreger Bands (HSB). The larger the number of HSBs in a given region of the enamel, the more intense is the decussation. High HSB packing densities have been proposed as a crack-stopping mechanism to prevent catastrophic fracture of the tooth crown. If decussation is influenced by natural selection, then we hypothesize that species with harder diets would feature greater HSB packing densities than those with softer diets. We tested this in premolar and molar teeth from nineteen carnivoran species ranging in body mass and diet. Teeth were sectioned buccolingually through the most mesial cusps and polished for microscopic observation. HSB packing densities were determined in longitudinal section by counting the number of HSB bands per millimeter parallel to the EDJ. HSBs also differ qualitatively in form, being either undulating, acute-angled, or with a zig-zag. We also examined the relationship of this with diet. Our results indicate no trend between HSB packing density and diet. Instead, HSB packing density correlates predominately to species body mass, with smaller species showing greater packing density. This is in contrast to several earlier studies on non-carnivorans that suggested larger-bodied species show greater decussation due to the increased bite forces they can produce. However, we did confirm the results of other earlier studies that showed that HSB type correlates with diet, with increasing degrees of prism waviness associated with harder diets.

POS1-151 7:30 pm

The role of enamel thickness in carnivoran dietary adaptation.

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Abstract: Thick tooth enamel has been argued to protect against both fracture and wear of the tooth crown. Hard foods can cause tooth fracture because they are loaded with high axial forces perpendicular to the occlusal surface. Tough foods require shear to break down and tend to result in the loss of enamel through wear. Given the reportedly high incidence of tooth fracture among members of the Order Carnivora, and the purported relationship between tooth fracture and hard foods, we examined several carnivoran species to see whether they vary in enamel thickness, and if so, whether that variation is primarily a reflection of their need to prevent tooth fracture. We compared enamel

thickness among a sample of twenty carnivorous species ranging in diet and body size. We hypothesized that species with harder foods in their diets will have both absolutely and relatively thicker tooth enamel. Average enamel thickness was digitally recorded from buccolingual sections made at primary cusps of minimally-worn premolars. We found that absolute measures of average enamel thickness do correlate with the presence of hard foods in the diet. Sea otters (*Enhydra lutris*) and spotted hyenas (*Crocuta crocuta*) had thicker enamel than any other carnivore included in this study, reflective of their regular consumption of hard-shelled invertebrates and mammalian bone, respectively. Sea otter enamel was more than four and a half times as thick as that of the closely related river otter (*Lontra canadensis*), while hyena enamel was 65% thicker than that of larger-bodied lions that hunt similar prey. Sea otter and hyena enamel thicknesses remain relatively high when corrected for body mass. The small-bodied Asian mongoose, which consumes hard-shelled crustaceans and mollusks, was also found to have relatively thicker enamel than the other carnivores in our study.

Geometric Morphometrics (GMM)

POS2-2 4:30 pm

Geometric Morphometrics reveals morphospaces for early and late shark embryos (Chondrichthyes, Elasmobranchii).

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Abstract: Modern sharks can be divided into two clades. The Squalomorphii, comprising five orders such as the Squaliformes and the Galeomorphii, including orders such as the Orectolobiformes or the Carcharhiniformes. There is little known about the embryonic development in modern sharks, as these relatively large predators are often migratory and can hardly be held and bred in captivity. Geometric Morphometrics (GM) is an appropriate tool for investigating specimens of different sizes and ontogenetic stages, respectively. Here various developmental stages of three different shark species, *Chiloscyllium punctatum*, *Galeocerdo cuvier* and *Chlamydoselachus anguineus* were investigated using GM. Previous studies showed that the overall adult morphology is already established in stage 30 when approximately 37% of the embryonic development are completed. All specimens at this stage or older occupy three different morphospaces, revealed by a principal component analysis based on 15 homologous landmarks. The bottom dwelling bamboo sharks have a relatively ample morphospace, which indicates a high variability in their developmental trajectories. The tiger sharks display the very commonly known torpedo-like body shape, whereas the frilled sharks exhibit a more eel-like morphology. Both exhibit a very narrow morphospace, which portends a rather directional developmental trajectory. Early embryonic stages, conversely, seemingly occupy different morphospaces, demonstrating massive shape changes through which all the species go during their development. This indicates that two morphospaces for each species exist, one for the early and one for the late embryos. It was not possible to identify a phylotypic period, indicating that development in these three species might diverge very early. Further studies, however, incorporating additional species, specimens, and also metric measurements are necessary for support of this assumption.

POS2-4 4:30 pm

Phylogenies from shapes: using shell landmarks to infer the phylogeny of geoemydid turtles.

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Abstract: Morphology is an important source of phylogenetic markers, but the complex nature of phenotypes creates major methodological challenges for estimating phylogenies. The field of geometric morphometrics has had great success in the analysis of biological form based on landmark coordinates to address problems of intra- and interspecific variation. However, the use of landmark data for phylogenetic inference has been limited and historically contentious. A series of recent studies has succeeded in finding significant phylogenetic signal in landmark coordinate data, allowing for a more optimistic outlook. Here, I explore the use of this kind of data for the inference of the phylogeny of geoemydids, a species-rich clade of cryptodiran turtles. The relationships between the species of this group have proven particularly difficult to estimate with both molecular sequences and matrices of traditional discrete-state morphological characters. The meshes formed by the sutures and the scute sulci on the bony carapace of turtles are particularly convenient for the placement of type I landmarks. I defined 76 such landmarks for each side of the shell, and digitised them in a 3D space with a microscribe. The sample includes over 130 specimens, representing over 57 percent of all the geoemydid species plus testudinid and emydid species as outgroups. In the present contribution, I assess the potential of these data for phylogenetic analysis by comparing the results and performance under alternative methods, and I discuss some general challenges.

POS2-6 4:30 pm

Sources of shape change in the testudine skull: A 3D geometric morphometric analysis.

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Abstract: The breadth and diversity of testudine head shapes are hypothesized to reflect aspects of ecology and behavior. In order to investigate the evolutionary and functional links between feeding behavior and the morphology of the feeding apparatus of testudines, we performed the first landmark-based 3D geometric morphometric analysis of testudine crania. Virtual 3D models were produced from CT scans of 24 species representing the breadth of families, diets, and feeding modes present in turtles and tortoises. Landmark data were collected using the auto3dgm package in the statistical program R and analysis was performed in Geomorph. Species in the principal components (PC) analyses were labeled with their dietary, feeding mode, habitat, or phylogenetic affinities to assess potential associations with patterns of shape change. The only variable that produced a clear pattern was diet. Nearly all species with a carnivorous diet plotted on the positive side of PC1 (explaining 30% of the variation), while herbivorous and omnivorous species were grouped on the negative end of PC1. No clear dietary pattern is associated with PC2 (22%) or PC3 (13%) in this sample. Shape change towards the positive extreme of PC1 primarily involves an increase in head width relative to head length, but there are also conspicuous rotations in the aspects of the mandibular condyle (to face more medially) and the trochlear process (to face more laterally). PC2 appears to increase the ratio of head height to head length toward the positive extreme, while the positive extreme of PC3 reflects an increase in the depth of the supraoccipital crest and a relative anterior-posterior shortening of the adductor chamber. In addition to confirming previous findings that overall head width and head height vary predictably with diet, this study has also uncovered new sources of variation in anatomical details that were previously unexamined.

POS2-8 4:30 pm

The influence of phylogeny and diet in the skull morphology of representatives of Dipsadidae (Squamata: Serpentes).

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Abstract: Body form can be attributed to adaptation to the environment by natural selection, but can also be a result of strong phylogenetic inertia. Skull morphology in snakes provides critical information on the evolution of some morphological complexes. The family Dipsadidae includes representatives with a large diversity of forms, habits, and diet. We aim to explore the evolution of skull morphology within the family Dipsadidae through geometric morphometrics (GM) and to verify the existence of skull forms with morphological syndromes associated to certain diets. We performed GM analyses using the dorsal view of 70 species of the family and 37 landmarks. The PCA showed discrimination between the subfamilies Xenodontinae and Dipsadinae, despite having some overlap; some tribes were recovered, although showing a large overlap of patterns, except for Dipsadini and Elapomorphini (well discriminated); all diet categories were weakly discriminated. PC1 reflects mostly the width of the skull and proportion of the bones. PC2 reflects mainly width and length of the skull and length/position of supratemporals. The CVA concerning the tribes showed the groups well discriminated, with an overlap of patterns between Xenodontini, Philodryadini and taxa considered as incertae sedis—CV1 reflects mostly the proportion of braincase bones while CV2 reflects mostly the width of the skull. CVA concerning diet also showed well discriminated groups, with a complete overlap related only to species which feed on lizards and anurans—CV1 shows changes in the width of skull and proportion of braincase bones; CV2 reflects the width and length of skull and proportions of all bones, except for supratemporals. Snakes feeding on a wide variety of vertebrates have wider skulls, corroborating previous works. These results indicate that both phylogeny and diet are reflected in the skull morphology of such snakes, showing the importance of feeding habits in the evolution of the skull.

POS2-10 4:30 pm

Beak shape is a poor predictor of trophic ecology in extant birds.

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Abstract: Beak shape is a textbook example of trophic adaptation in bird biology and of diversification in evolutionary theory. In spite of numerous qualitative studies linking beak shape and trophic ecology, a quantitative, phylogenetically-comprehensive study of beak ecomorphology is still lacking. Using geometric morphometrics, we digitized beak shape of a 176 extant birds (38 orders, 96 families) in lateral view and statistically tested the association between beak morphology and trophic ecology. On the same sample we calculated the mechanical advantage (MA) of the main adductor muscles of the skull for each species. Surprisingly, we found that neither beak shape nor MA are good predictors of trophic ecology in birds. 80% of the studied species show low MA values within a narrow range, implying that in most birds the beak is employed as a fast gape/low force mechanism. Clades utilizing pre-swallowing mechanical processing of food items are best categorized by the interplay between shape and MA, showing two very morphofunctional solutions; cracking/biting herbivorous birds, particularly parrots, exhibit deep and curved beaks along with the highest values of MA (enhanced bite force/slow gape speed), exploring more than the upper half of the total range of values. By contrast, the three main clades of raptorial birds exhibit deep, curved beaks with relatively low MA values. The absence of an enhanced bite force in these avian clades is surprising, and implies that more research is necessary to understand if and how birds rely on alternative strategies

for feeding. Given the extreme multifunctional nature of the avian beak, it is plausible that non-trophic selective pressures might be underlying in its macroevolution, thus impeding a finer match between trophic ecology, bill shape, and mechanical performance in birds.

POS2-12 4:30 pm

Growth orientations of rhamphothecae in extant beaked animals with implications to the reconstruction of the beaks in extinct taxa.

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Abstract: The beaked rostra evolved in many lineages of tetrapods, including turtles (Testudinata) and birds (Aves), accompanied by the loss of their teeth. The beaks of these extinct taxa were possibly covered by keratinous rhamphothecae in those of the extant turtles and birds. To reveal the evolution of the designs and functions of the jaw apparatus among tetrapods, more accurate reconstruction of the entire shape of the beak is required for each extinct taxon. However, reconstruction of the shape of the rhamphotheca, which is rarely preserved in fossils, remains difficult because the relationship between the shape of the rostral bone and the thickness/growth orientation of the overlying rhamphotheca is yet to be understood. We CT-scanned upper jaws of more than 70 extant beaked tetrapod specimens (Aves: 41 genera, 28 families; Testudinata: 16 genera, 10 families), and compared the shape of the rostral bone and the overlying rhamphotheca. The rhamphotheca occupied 16.6–71.6% of the entire volume of the beak, and did not cover the rostral bone uniformly in thickness. The results imply that estimation of the rhamphotheca volume or the thickness in fossil specimens remains a challenging topic. However, the following features were found for the rhamphotheca growth orientations among the studied specimens, regardless of the beak shape. (1) The thickness of the rhamphotheca was emphasized distal to the distal-most local maximum point of the width or depth of the rostral bone. (2) The rhamphotheca grew distally along the distal-most curvature of the culmen margin of the rostral bone. The abovementioned morphological relationship between the bone and the rhamphotheca will be one of proxies for reconstructing the entire shape of the beak in extinct taxa.

POS2-14 4:30 pm

Novel analyses estimating evolutionary rates using ancestral state reconstruction suggest recent stasis in the cranium of the dwarf lemur *Cheirogaleus* (Primates: Cheirogaleidae).

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Abstract: The Darwin is a rate unit of evolutionary change. Application to the fossil record requires a relatively complete stratigraphic column to infer ancestor/descendant relationships, however. In lieu of direct information on ancestral species, there are now methodologies for estimating character state values at the internal nodes of a lineage using values from tip taxa and a phylogenetic tree. We utilize ancestral state reconstruction in the calculation of rates in Darwins and propose this novel protocol as a means of investigating evolutionary pattern in recently diverging taxa. We obtained craniodental measures and genetic samples from 42 individuals of *Cheirogaleus* from an earlier study. Craniodental measures were regressed against geometric mean and the residuals reduced to three principle components. A population tree was inferred using mitochondrial sequences. ML ancestral state reconstructions were performed using each PC and the geomean as continuous traits. Darwins were calculated as the log difference between the values at each node or tip and its adjacent, ancestral node, divided by the intervening branch length. Under directional evolution, the best-fit line relating Darwins to branch length should have a slope of 0. Under stasis, it should have a slope of -1. Intermediate values fit the null expectation of a random-walk. Slopes of Darwins against branch lengths were tested for significant difference from slopes of 0 and -1 using a 0.95 confidence interval. PC1, PC2, and PC3 of the genus; PC1, PC2, and the geomean of *C. medius*; and PC1, PC2, and PC3 of *C. major* show slopes significantly different from 0 and not from -1. PC2 of *C. crossleyi* shows a slope significantly different from -1 but not from 0. All other slopes were consistent with a random walk. This suggests a preponderance of stasis in the recent evolution of the cranium of dwarf lemurs except in *C. crossleyi*, which shows some evidence of directional evolution.

POS2-16 4:30 pm

Comparative shape analysis of koalas and wombats.

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Abstract: Extant vombatiform marsupials (koalas and wombats) are the only survivors of an extensive radiation of mostly terrestrial vombatiforms dating back to the late Oligocene. This mammalian “megafauna” ranged in size from the ~6 kg koalas alive today to the 3000 kg *Diprotodon optatum* and exhibited a wide variety of skull shapes and sizes to exploit different ecological niches. Extant wombats and koalas are highly adapted for either grazing or browsing, respectively. Within wombats, the northern hairy-nosed wombat (NHNW) and common wombat live in moister habitats and vegetation than the southern hairy-nosed wombat (SHNW), which is confined to an arid environment. Nearly all extinct vombatiforms are expected to have been fallen along the dietary spectrum delimited by the koala and wombat. This study defined the morphological change along this spectrum, and looked for finer cranial adaptations among wombats, using Procrustes-based three-dimensional geometric morphometrics. Principal components analysis of 54 landmarks on skull shapes of koalas (n=10), northern (n=30)/southern (n=12) hairy-nosed wombats, and common wombat (n=6) showed that most of the variation in the dataset (PC1; 65%) relates to wombat/koala differences. As expected for a browser, 3D warp visualizations show that koalas have shorter, pincer-like snouts, and less procumbent teeth, than wombats. Wombats mostly differ from each other along PC2; surprisingly, SHNWs are intermediate between NHNWs and common wombats. This is unexpected because NHNW and common wombats are more similar both in range and, at least historically, in having a moister habitat and higher water-content in their diet. It is possible that phylogenetic signal outweighs ecological adaptation in the wombat species, with the common wombat closer to the ancestral state; extrapolations of feeding type might therefore be best restricted to the grazer/browser dichotomy between koalas and wombats. Funding: The Wombat Foundation, Australia

POS2-18 4:30 pm

Analyzing the association between platyrrhine locomotor mode percentages and talar shape.

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Abstract: Locomotor mode percentages (LMPs) (i.e. the time percentage a species spend performing a certain locomotor behavior) and talar morphology were assessed to investigate if there is a relationship between locomotor behavior and talar shape. The LMPs of 31 platyrrhine species were obtained from the literature. These values were log-transformed to perform a PCA in order to visualize locomotor affinities (explained variance: PC1 54.27% and PC2 25.23%). Furthermore, the 3D surface models of 22 platyrrhine species downloaded from online databases were analyzed using geometric morphometrics to understand morphological affinities. A principal component analysis (PCA) of the Procrustes coordinates was carried out and a phylogeny was projected onto the two first dimensions to display most of the morphological variation (explained variance: PC1 30.98% and PC2 13.03%), while showing the evolutionary relationships between the analyzed taxa. A partial least squares analysis was performed to examine the association between shape variables and log-transformed LMPs in 15 species present in both datasets. The obtained results show that there is a significant association between talar morphology and the time percentage that different species spend performing dissimilar locomotor behaviors (RV-coefficient: 0.63; p-value: <0.0001; 10,000 permutations). These results contribute to understand the relationship between talar morphology and LMPs, thus providing an important tool to reconstruct the possible locomotor repertoires of extinct species and to appreciate the locomotor diversity observed in extant platyrrhines. Grant sponsor: Becas Chile Scholarship Program, CONICYT, Chile.

POS2-20 4:30 pm

Musculoskeletal Fitness in Small Mammals: Are captive-bred individuals fit for the wild?

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Abstract: Many attempts at reintroducing captive-bred mammals, with the aim of preserving biodiversity, are unsuccessful with causes being attributable to cognitive inability to recognise predators, lack of normal social behaviours and failure to thrive due to poor ability to find food, water and shelter. Animals for reintroduction are typically reared under spatially constrictive conditions compared with their wild counterparts yet very few studies have tested musculoskeletal fitness as a factor for reintroduction to the wild. The European hare (*Lepus europeaus*) provides a sensitive model for such a study as its survival is dependent on its extreme athleticism in the wild to escape predation by the fox (*Vulpes vulpes*). Due to the finely balanced sensitive nature of predator-prey relationships, this study assumed that any changes in morphology in captive-reared animals that deviate even slightly from wild-type would have diminished survival probability. The aim being to determine whether rearing animals in spatially restrictive environments had a significant impact upon the musculoskeletal system of the animal which could ultimately diminish survival probability. Two populations of hares (wild-caught (N=21) and captive-bred (N=24) were sampled. The proximal femur was chosen for shape change analysis due to its importance in providing anchorage for major locomotor musculature. Landmarks were selected and measured in three dimensions and analysed using geometric morphometrics. Hares raised under confined conditions showed marked shape changes in the proximal

femur (notably a proximal shift in the lesser trochanter and quadratus femoris attachment site; a shorter femoral head/neck; a reduced greater trochanter). These changes occurred at sites of major musculature attachment resulting in reduced stride length and hind limb manoeuvrability whilst running. Therefore, these animals lacked the musculoskeletal fitness for release into the wild.

POS2-22 4:30 pm

Reconstruction of muscle fascicle architecture from digital images: a combined texture mapping and streamline approach.

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Abstract: Skeletal muscle models are used for a better understanding of movement and force generation in both biological and bioengineering research. Yet, they often lack a realistic representation of the muscle's internal architecture, which is primarily composed of muscle fibre bundles, known as fascicles. Here, we present a reconstruction method of the fascicular spatial arrangement and geometry of an exemplary facial muscle, based on a combination of pattern recognition and streamline computation. From our preprocessed μ CT-data and based on a pattern recognition algorithm, which represents the fascicle directions, a vector field was created. The pattern recognition algorithm uses the different statistical gray value distributions along or across the fascicles to find their main direction. After this, the resulting vector field was transformed into a realistic muscle fascicle representation based on a streamline approach. We conclude that the presented approach allows for implementing realistic fascicle information into finite element models of skeletal muscles for a better understanding of the function of the musculoskeletal system. Additionally, it can be used to analyse intraspecific or interspecific muscle architectures.

Feeding (FED)

POS2-24 4:30 pm

Measuring bite force in the domestic dog (*Canis lupus f. familiaris*): A novel experimental approach for recording predatory bites *in vivo*.

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Abstract: Bite force is an important ecological variable that is related to vertebrate feeding and social behavior. Although bite force is known to change with behavior (e.g. prey capture, ingestion.), it is difficult to gain accurate measurements for these different behaviors. Here we present *in-vivo* bite force data taken with a new measurement system designed for domestic dogs, which are an ideal model for studying biting performance given their large diversity in body size and skull form. To this end, load cells were integrated into a protection biting sleeve and so changes in bite force over time were recorded. We gathered bite force data from 14 mixed sex, adult, trained German shepherd dogs ranging in age from 0.7 - 9 years. Body mass and wither height were collected to determine if either was correlated to bite force. We measured bite force for two predatory behaviors (short distance biting from a seated position and biting after running a distance of 10 meters) using the sensorized biting sleeve worn by a dog handler. Values were estimated in a 5 second window after biting began. Results yielded a maximum bite force (MBF) of 905 ± 249 for the seated bite and 967 ± 231 N for the running bite. Dogs tended to reach their MBF within the first 2 seconds of biting followed by a decrease over time. Bite forces showed an oscillatory pattern, indicating no constant bite force was reached. This could be due to the dogs' training, or an instinctive predatory behavior. Contrary to previous studies, neither sex nor body mass was correlated to MBF ($p < 0.05$), although there was a trend towards increasing MBF with increasing body mass and wither height. Following this promising pilot study we now aim to apply this measurement system to a larger range of dog breeds.

POS2-26 4:30 pm

Biting mechanics of raccoons (*Carnivora: Procyon lotor*) and skunks (*Carnivora: Mephitis mephitis*): exploring the link between cranial morphology and infectious disease control.

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Abstract: Oral rabies vaccination (ORV) programs in North America have historically been effective in controlling the spread of rabies in carnivorous populations. This is accomplished by distributing baits filled with the rabies vaccine that are located and consumed by wild animals. This has been most effective in raccoon populations which show significantly reduced rabies infections. However, despite also being a major rabies vector, the striped skunk has a significantly lower inoculation rate in wild populations although the vaccine has been shown to be effective in captive studies. Here, we aim to elucidate biomechanical differences between skunks and raccoons that may contribute to differences in oral immunization success. 3D biomechanical models incorporating data from the jaw muscles were developed to estimate bite forces and muscle moments at different gapes for the two species. Results demonstrate differences that might impact their ability to break down the baits to access the vaccine. Data from this project may be used to improve bait design and manufacturing.

POS2-28 4:30 pm

The evolution of insectivory in freshwater stingrays.

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Abstract: Stingrays have diversified to fill numerous trophic niches across freshwater, estuarine, and marine habitats, despite lacking the suite of feeding mechanisms (i.e. pharyngeal jaws) that underlie similar ecomorphological plasticity in teleosts. Notable among examples of such diversity are the freshwater rays of South America. From an estuarine, dietary generalist ancestor, these rays have evolved to specialize on prey such as mollusks, fishes, crustaceans, and even insects – the only extant insectivorous elasmobranchs. We analyzed data characterizing prey processing in an insectivorous freshwater ray (*Potamotrygon motoro*) presented with prey of increasing toughness proportional to the amount of chitin in its exoskeleton. Asymmetrical jaw protrusion and symphyseal flexion of the jaws are typical of feeding on tougher prey items like insects. Insectivorous rays can behaviorally reorient their teeth from flattened occlusion to occluding cusps when feeding on tough prey, as the dental ligament is contracted. Despite a deceptively simple jaw architecture these fishes accomplish impressive post-capture prey manipulation and processing by combining hydrodynamic forces with complex movements of the jaws.

POS2-30 4:30 pm

Strange from the start: Ontogeny of the filtering mechanism in Silver Carp.

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Abstract: Highly invasive Asian carp are destroying ecosystems throughout the United States by outcompeting native species. With populations growing at an alarming rate, these fish have proven difficult to control. Their ability to thrive within eutrophic environments is due to their very efficient filter-feeding mechanism. Here we present data from an ontogenetic series of Silver Carp ranging in size from 15-400mm SL detailing how this unique filtering structure is built. Like many filter-feeding species, Silver carp possess an incredibly large epibranchial organ that occupies the majority of the dorsal buccal cavity. Branchial arches 1-4 have greatly modified gill rakers that span both the ceratobranchial ventrally and the epibranchial as it curves into the body of the epibranchial organ. From the earliest ontogenetic stage examined individual gill rakers already show a modified shape as compared to the basal character state for Cypriniformes. As development proceeds the structure of these gill rakers becomes increasingly complex. By early juvenile stages secondary growth of bone stitches together the primary gill rakers, forming a screen-like mesh upon which future elaborations of the filtering structures are built. As development proceeds the original shape of the gill rakers is modified, regressing in height only later to become scaffolding for more complex filtering structures. Gill rakers involved in filtering undergo significant architectural changes during development, while those curling into the epibranchial organ remain largely unchanged from earlier ontogenetic stages. Comparisons with the Bighead carp, a congeneric, suggest that the basal cypriniform morphology is retained within Bigheads.

POS2-32 4:30 pm

The role of the chondrocranium and sutures in a biomechanical model of *Tupinambis* (Lepidosauria).

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Abstract: Lizards and tuatara are ideal taxa for investigating the evolution of skull mechanics as they exhibit a wide range of skull shapes, feeding behaviours and lifestyles. Due to recent advances in visualization and modelling software, such research can now be undertaken using complex computer-based simulations. However, the role of soft-tissue structures such as cranial sutures, which are known to vary considerably in structure amongst lepidosaurs, remain poorly understood. To date, biomechanical models of *Uromastix* and *Sphenodon* suggest that cranial sutures redistribute strain rather than simply dampening it, but wider comparisons are necessary. We investigate lepidosaur sutures in the South American tegu lizard (*Tupinambis*) and for the first time include another 'soft-tissue' component, the chondrocranium: the cartilaginous part of the braincase that lies along the mid-sagittal plane between the rostrum and ossified posterior braincase. Micro-computed X-ray tomography (microCT) was used to build an accurate 3D model of the skull with sutures, and a representation of the chondrocranium. Detailed dissection was used to construct a representation of the muscles and multi-body dynamics analysis (MDA) was used to predict the forces acting on the skull during various biting conditions. Finally, finite element analysis was used to reveal the resultant strain distributions through the skull and the influence of the soft tissue structures. Our analyses show that including the cranial sutures has a far greater effect on strain distribution than inclusion of the chondrocranium. As in previous studies, the presence of the sutures increases overall skull strain but reduces areas of peak strain. This result is consistent with an even-strain distribution necessary for appropriate growth and bone turnover. By contrast, the chondrocranium made little difference to the strain within the cranial bones despite various adjustments to its shape and material properties.

POS2-34 4:30 pm

Functional aspects of the interpterygoid vacuities in the palate of early tetrapods and a reconstruction of the associated cranial muscles.

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Abstract: A diagnostic feature of temnospondyls is the presence of an open palate with large interpterygoid vacuities, unlike the closed palate of most other early tetrapods and their fish-like relatives, in which the vacuities are either slit-like or completely absent. Attachment sites on neurocranium and palatal bones in temnospondyls allow the reconstruction of a powerful m. retractor bulbi and a large, sheet-like m. levator bulbi that formed the elastic floor of the orbit. This muscle arrangement indicates that temnospondyls were able to retract the eyeballs through the interpterygoid vacuities into the buccal cavity, like extant frogs and salamanders. In contrast, attachment sites on palate and neurocranium suggest a rather sauropsid-like arrangement of these eye muscles in stem-tetrapods and stem-amniotes. However, the anteriorly enlarged, huge interpterygoid vacuities of long-snouted stereospondyls suggest that eye retraction was not the only function of the vacuities here, since the eye-muscles filled only the posterior part of the interpterygoid vacuities. We propose an association of the vacuities in stereospondyls with a long, preorbital part of the m. adductor mandibulae internus (AMla). The trochlea-like, anterior edge of the adductor chamber suggests that a tendon the AMla was redirected in an anteromedial direction in the preorbital skull and dorsal to the pterygoids. This tendon then unfolded into a wide aponeurosis bearing the flattened AMla that filled almost the complete interpterygoid vacuities anterior to the orbits and was medially and laterally attached to the margins of the interpterygoid vacuities and dorsally to the skull roof. To test the possibility that the interpterygoid vacuities served for stress distribution during contraction of the AMla, we conducted different Finite Element Analyses in which an original stereospondyl skull and different theoretical models were considered in which the vacuities differ in size or are completely absent.

POS2-36 4:30 pm

Inferring the diets of pterosaurs and extant analogues using quantitative 3D textural analysis of tooth microwear.

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Abstract: Pterosaurs were a successful group of flying reptiles, dominating the air for 150 million years during the Mesozoic. The ecology of pterosaurs has been widely debated, and a range of hypotheses concerning diet have been proposed, including insectivory, piscivory, carnivory and/or durophagy. Many of these hypotheses are based on comparisons between the shapes and structures of their teeth with those of extant organisms. This approach however is generally qualitative, and assumes that tooth form and function are closely linked and correlated with diet. A more robust method involves quantitative analysis of the 3D sub-micron scale textures of worn tooth surfaces—dental microwear texture analysis. Microwear is produced during feeding as abrading food items alter tooth surface textures. Material properties of food create different microwear characteristics; in general harder items create rougher surfaces. 3D textural analysis of microwear has proven useful in elucidating the properties of food for several extinct taxa, including early stem mammals, fishes and early whales, but the technique has never been applied to pterosaurs. This study tests the hypothesis that microwear patterns can be detected in non-occluding pterosaur teeth, and that microwear textures differ between pterosaur taxa with different diets. An important step in addressing these hypotheses is to validate pterosaur microwear analysis by examining microwear textures of extant organisms with known diets to provide a comparative data set. This has been achieved through analysis of non-occlusal microwear textures in extant bats and crocodilians, clades within which species exhibit a range of insectivorous, piscivorous and carnivorous dietary ecologies. Our results—the first test of the hypothesis that non-occlusal microwear textures in these extant organisms vary with known dietary differences—provide the context for the first robust quantitative tests of dietary ecology in pterosaurs.

POS2-38 4:30 pm

Morphology of the pterygoid musculature in pleurodire turtles.

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Abstract: Among sauropsids, at least three parts of the jaw adductor musculature can be identified. The musculus (m.) adductor mandibulae externus is the most prominent jaw adductor in turtles. Its fibers originate on the walls of the upper temporal fossa and insert to the coronoid process of the lower jaw mostly by the coronar aponeurosis. They are directed in rostral and ventral direction, exerting an adduction component when closing the jaw. M. adductor mandibulae posterior originates on the rostral surface of the quadrate on the otic chamber, runs ventrad, and inserts to the surangular of the lower jaw. This unit is closely associated to m. adductor mandibulae internus, although clearly separated from it by the mandibular ramus of the trigeminal nerve. The internal adductor is commonly separated into Partes pseudotemporalis et pterygoidei. The former originates on the vertical wall of the

parietal and inserts to the articular of the lower jaw. The pterygoideus portion can be separated into three heads, the pterygoideus dorsalis et ventralis, whose fibres run caudad and ventrad from their origin on the dorsal and ventral surface of the pterygoid, and the pterygoideus posterior, which originates on the basisphenoid and on the ventral surface of the caudal part of the pterygoid. The pterygoideus fibers insert close to the jaw joint (articular-quadrate) and exert a protraction component on the movement of the lower jaw. In pleurodires, there are three specific skull structures affecting the unique arrangement of the pterygoideus structures, namely the processus trochlearis pterygoideus, the septum orbitotemporale, and, in Podocnemididae, the cavum pterygoideum. We focus on two taxa, *Podocnemis unifilis* and *Phrynosoma geoffroanus*, to reanalyze and compare the different arrangements of the pterygoideus structures in Pleurodira and their subsequent force components to protract and retract the lower jaw in detail. [Funding: FAPESP 2014/25379-5 to GSF]

General Morphology (GEN)

POS2-40 4:30 pm

Domestication effect on skull morphology and biting performance in rats.

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Abstract: Domestication of wild animals has been a key factor in the development of human civilizations. It enabled the development of more suitable food resources, modes of transportation, companionship and even enhanced group defense against potential threats. This practice has resulted in a wide variety of breeding lines differentiated by their differences in morphology, physiology, gene expression and behavior. Here, *in vivo* incisor biting performance and skull morphology were tested in 4 months old male and female gray rats *Rattus norvegicus*, originating from two wild derived breeding lines selected for aggressive and tame behavior, respectively, towards humans for over 70 generations. We focused on the aggressive and intercross (aggressive*tame) lines, totaling 39 individuals. Body size, head length and mandibular width all showed clear sexual dimorphism, with males always being larger than equivalent females. Considering inter-line comparisons, no significant difference was found in any size measurement in either males or females, except for aggressive males having larger heads than intercross males. Contrary to the morphological data, within breeding lines females produced stronger bites than males, whilst aggressive females bit harder than the intercross females. However, no inter-line differences were found in males. Once the body size effect was removed, bite force was (poorly) predicted by mandibular width, and only in aggressive males. Thus, beyond their behavior, genetics and physiology, the long-term domestication process resulted in smaller head size in the least aggressive rats while overall body size remained relatively similar. Yet, our results on biting performance cannot be attributed to differences in body or head size. They might offer additional evidence of the dimorphic aggressive behavior in female rats associated with maternal care and social structure, which has been observed in gregarious wild rodents.

POS2-42 4:30 pm

Finite element analysis of maxillary alveolar bone in rats under dental occlusal changes.

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Abstract: The dental occlusal plane can be changed during dentistry procedures. Premature contacts can result in changes in morphology alveolar bone, and consequently stimulate bone remodeling. The aim of this study was evaluated the equivalent von Mises strain at the interradicular septum of the upper first molar of rats under dental occlusal changes by finite element analysis. To develop the finite element model, the geometry condition were based on an experimental model, where the occlusal surface of molars in rats was changed by resin cementation. The rat head was scanned in microCT, in which the images presented thickness of sections (pixel size) of 30 µm. From these images, the 3D geometry was composed by skull and mandible structures, periodontal ligament and the teeth. In this step were obtained two geometries, one with normal dental occlusion (control) and one with a resin block bonded on the upper molars occlusal surface. The finite element analysis configuration was defined according the rat molar chewing. The mechanical properties values were assigned as linear elastic and isotropic. The mechanical properties used were to bone teeth (Young modulus: teeth (Young modulus: 19920 MPa/ Poisson coefficient: 0.3), teeth (Young modulus: 30000 MPa/ Poisson coefficient: 0.3) and periodontal ligament (Young modulus: 50 MPa/ Poisson coefficient: 0.4). To simulate the molar chewing, the masticatory force was 20 N. The force was applied in the long axis of each tooth. We evaluated the same side of the experimental condition. The results showed that the interradicular septum presented high micro-strain values in control model compared to the model with occlusal change. We concluded that the occlusal strain caused minor micro-strain in alveolar bone crest of the upper first molar.

POS2-44 4:30 pm

Feeding in Testudines: A finite element and parametric analysis of a tortoise skull.

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Abstract: In turtles, the adductor musculature in the skull is partly attached to the supraoccipital crest and, consequently, the latter plays a potential role in feeding behavior that largely remains unexplored. We performed a CT scan of an adult skull of an African spurred tortoise (*Centrochelys sulcata*) and, on its basis, we performed a 3D Finite Element Analysis (FEA), to test the biomechanical capabilities of this taxon during mastication and to understand its feeding ecology. We also performed a parametrical analysis of the length of the supraoccipital crest, enlarging and reducing its size. We generated several cases to test the efficiency of this structure under different feeding behaviors, so as to better understand its function as well as to determine the most likely selection pressures that determined its evolution. Our results show that, during loadings, most of the skull roof experiences no significant values of stress (particularly on the nasal area) or only low levels (around the orbital region). The highest values of stress are located in the anterior part of the crest and near the occipital condyles. Regarding the palate, significant stresses are mainly found near the posterior palatine foramen, while moderate stresses are found in the palate. Our parametric results reveal that enlarging the supraoccipital crest length increases of the stresses in the whole skull, but the potential bite force is only slightly increased and the mechanical advantage of enlarging this structure decreases. In contrast, if the crest is reduced or removed, the amount of stress mainly decreases, the bite force is almost equal to that in the original model, and the mechanical advantage increases. Overall, these results suggest that there should be a selection pressure toward maintaining (or even slightly decreasing) the length of the crest, whereas a further enlargement would not produce any obvious selective advantage from a biomechanical viewpoint.

POS2-46 4:30 pm

The utility of polymorphic characters in reconstructing the phylogeny of geoemydid turtles.

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Abstract: Geoemydidae is a speciose clade of turtles with 69 species currently distributed in the tropical to temperate regions of Asia, Europe, North America, and South America. Although there have been several attempts to resolve the phylogeny of the group using morphology – the only method to reliably assess the completely unresolved fossil record of the group – unusually high levels of polymorphism and homoplasy have hindered this process, particularly as polymorphic characters were readily omitted thereby eliminating potentially useful phylogenetic information. A number of methods have been developed that allow coding polymorphic characters in phylogenetic reconstructions and it is our goal to explore the performance of these methods in tackling the phylogeny of geoemydids. The methods selected here to treat polymorphic characters after scoring were the 'majority method', 'frequency coding' and 'missing'. These methods were chosen because they recover a high phylogenetic signal and similar topology regardless of sample size. Of the 72 morphological characters analyzed for 307 specimens (representing 61 extant species of Geoemydidae), 70 characters were observed to be polymorphic and 24 show more than two character states. We expect that the use of polymorphic characters for reconstructing the phylogeny of geoemydid turtles will yield good results as previous studies have already shown that polymorphic characters can be an important source of phylogenetic information.

POS2-48 4:30 pm

Evolutionary associations between body shape and climate in tree frogs (Amphibia: Anura: Hylidae).

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Abstract: Variation of body size and shape can influence several aspects of individual's morphology, physiology and ecology. Changes in size and/or shape are expected to affect surface-to-volume ratios (SVR) and, particularly for ectotherms, it can potentially affect thermal and water dynamics between the organism and its surrounding environment. The sensibility to environmental conditions might determine the distribution and diversity of these animals along different environments. Therefore, body shape can be a powerful predictor for detecting associations between species distribution patterns over different climates. This relationship can be investigated in a model with broad geographic distribution and morphological diversity, such as Hylidae treefrogs. SVR has been scarcely accessed, and discussions regarding species distribution usually do not incorporate this parameter and generalizes consequences about variation in size. As such, this work aimed to investigate patterns of variations in body shape in order to detect possible evolutionary associations with climate. Body shape was taken by conventional morphometrics and stereological SVR estimations and climatic parameters were extracted from WorldClim.org (Hijmans et al., 2005). Analyses were conducted in R under a phylogenetic approach. Our results suggest that thinner smaller body shapes as well as increased SVR are associated with warmer climates. Additionally, species with increased SVR present relative narrow thermal niche width. Precipitation variables had no effects on body shape. As mostly anuran species are nocturnal and thermoregulatory behavior might be costly due to temperature effects on performance, temperature seems to play major role setting limits in body shape. Thus, increased SVR coupled with thinner and smaller body shape might contribute in cooling down process in warmer climates, whereas low SVR

combined with robustness shapes can represent a conservative shape for species distributed in colder climates.
Funding: CAPES and FAPESP.

POS2-50 4:30 pm

Musculoskeletal development of the only matrotrophic viviparous anuran, *Nimbaphrynoides occidentalis* (Amphibia: Anura: Bufonidae).

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Abstract: Viviparity is exceedingly rare in anuran amphibians. So far, only about 15 species (out of a total of over 6600) are known to be viviparous. Of these, only the West African toad *Nimbaphrynoides occidentalis* has a matrotrophic form of viviparity (the remaining species are ovoviviparous). Previous research indicated that fetuses of *N. occidentalis* start feeding from a very young age on, which necessitates a functioning musculocranial system, among other things. The extent as to which the foetal morphology differs from that of free-living aquatic tadpole larvae has been unclear though and we examined and described the morphology of the chondrocranium, branchial apparatus and associated musculature. A series of fetuses at different stages were investigated using clearing and staining, histology and synchrotron micro CT scanning and subsequent computer aided 3D reconstruction. Overall, the structural organisation of the chondrocranium, lower jaw and the branchial apparatus of *N. occidentalis* does not differ substantially from that of free-swimming bufonid tadpoles. However, there are marked differences in the orientation and proportions of these structures. There are furthermore some reductions or fusions of several muscles. Because of the compression of the chondrocranium and the resulting shortening of the arcus subocularis and the processus ascendens, the origin and insertion of various muscles are reduced and the force produced for opening and closing the jaw is presumably somewhat decreased. All of these differences with free-swimming tadpoles are apparently related to the intrauterine feeding in *N. occidentalis*. Fetuses ingest an intrauterine secretion produced by the mother and keratinized jaws typical of tadpole larvae are missing.

POS2-52 4:30 pm

Diversification of pectoral girdle muscles within frogs (Amphibia: Anura).

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Abstract: Frogs evolved a broad diversity of locomotor modes and uses of their forelimbs compared to their nearest relatives (caudates). Therefore, it appears more likely that adaptation of existing and development of new pectoral girdle muscles occurred in anurans, rather than a secondary simplification in the Caudata. The pectoral girdle muscles of basal and higher anuran and one caudate species (*Hynobius tokyoensis*) were compared using contrast-stained microCT-scanning, episcopic microscopy, virtual three-dimensional reconstructions, and dissections. Differences were coded in characters and character states and a mapping on a phylogenetic tree allowed for the reconstruction of ancestral states. The absence of girdle and girdle musculature in the immediate outgroup (caecilians) posed a conceptual problem in inferring ancestral character states. In the frogs examined, depending on the respective species, 27 to 34 muscles and muscle heads with connection to the pectoral girdle skeleton were identified, compared to 19 in *H. tokyoensis*. A number of muscles were present as one muscle belly in caudates but as two or more heads or portions at the base of or within anurans, and additional muscles occurred in anurans. We found interspecific differences in more than 50 muscle characters suggesting considerable variation in character states within Anura. The character mapping revealed potential apomorphies for nearly all clades among the frogs examined. Despite our data covering the basal branches, several ancestral character states and inter-order homologies remain uncertain for basal nodes in Batrachia and Anura, mostly due to the lack of shoulder girdles in caecilians; studies on anuran muscle ontogeny might help determine polarity.

POS2-54 4:30 pm

Tipping the scale: Muscle mass distribution and its effect on center of mass position in the wild and modern domestic turkey.

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Abstract: The poultry industry has artificially selected for increased body size in the domestic turkey, resulting in dramatic changes over short evolutionary time scales. These animals provide the opportunity to study the evolution of morphological traits that have accompanied this change in body size. In this study we seek to determine: (1) if muscle groups of the modern domestic turkey have experienced the same proportional increase in size compared to wild turkeys; and (2) where the center of mass (CoM) position is located for comparison between the two strains. We dissected and measured muscle masses in 6 adult turkeys per strain. We grouped muscles by anatomical location (distal hindlimb, proximal hindlimb, trunk and forelimb) and calculated a ratio of muscle mass to total body mass. Only the trunk had significantly greater mass in the domestic turkey ($P = 0.004$). The sole muscle responsible for this increased proportional mass was *M. pectoralis* ($P = 0.002$), which is strongly selected for breast meat in the poultry industry. In addition, the physiological cross-sectional area of the lateral gastrocnemius scaled with body mass^{0.73} in

the wild turkey, but only body mass^{0.56} in the domestic turkey, indicating this leg muscle becomes relatively weaker as the birds grow. We measured the CoM position using a force plate and biplanar x-rays for accurate 3D measurements. The domestic turkeys' CoM position is further anterior, in agreement with a prior study (Abourachid, 1993, Br. Poult. Sci.). These results have implications not only for posture and effective mechanical advantage, but also, in conjunction with previously collected ontogenetic skeletal measurements, tell us how the musculoskeletal system evolves to deal with increased body mass.

POS2-56 4:30 pm

Three-dimensional analysis of rib kinematics during lung ventilation in the Argentine black and white tegu, *Salvator merianae* (Reptilia: Teiidae).

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Abstract: Costal aspiration, in which rib movements generate the necessary thoracic pressures for lung ventilation, is the basal mode of breathing in amniotes. These movements are a complex combination of three-dimensional rotations that vary considerably within and between clades. Each rib can theoretically rotate about three axes: bucket-handle around a dorsoventral axis, caliper around a craniocaudal axis, and pump-handle around a mediolateral axis. The objective of this study is to understand the rib kinematics during breathing in the Argentine black and white tegu lizard, *Salvator merianae*. Tegu thoracic ribs have three mineralized segments: vertebral, intermediate, and sternal, whereas most non-serpentine squamates have only two segments, and snakes retain just the vertebral segment. We implanted radio-opaque markers into the vertebrae, sternum, vertebral, intermediate, and sternal ribs of three individuals, and the caudal-most cervical rib of one individual. With marker-based XROMM we generated 3D animations and quantified the axes of rotation. We found no measurable motion between vertebral and intermediate ribs, but there was motion between vertebral and sternal segments. This indicates that tegu ribs are functionally bipartite during breathing, despite their tripartite anatomy. Previous work in iguanas showed rib motions dominated by bucket-handle rotation, with very little caliper or pump-handle. Similar to iguanas, our data for tegus showed primarily bucket-handle rotation, but also showed substantially greater caliper and pump-handle motions, with high variability in the polarity, magnitude and relative timing of these rotations. The caudal-most cervical rib, which has no sternal attachment, showed substantial bucket-handle motion similar in magnitude and direction to the thoracic ribs. These findings have implications for understanding how ribs rotate without ventral articulations, including how snakes ventilate their lungs in the absence of a sternum.

POS2-58 4:30 pm

The effect of craniokinesis on the middle ear of domestic chickens (*Gallus gallus domesticus*).

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Abstract: The mammalian middle ear consists of an eardrum, three ossicles, two muscles and a number of ligaments, and is enclosed in a single bony structure. Ossicle movements, mediated by these muscles and ligaments, adapt sound transmission. The avian middle ear is simpler: an eardrum connected to one ossicle (columella), one muscle and one ligament. This seems to constrain adaptation capabilities. We hypothesize, however, that craniokinesis may play a role in the adaptation of sound transmission as the avian middle ear is not enclosed in one rigid structure, but also by the quadrate and by soft tissue. The eardrum is connected to the movable quadrate. Craniokinetic movements of the latter may thus effect the eardrum as well as the columella. To test this, hens and roosters (*Gallus gallus domesticus*) are used as models that differ in vocalization capacity. μ CT-scans were made of the heads of 3 hens and 3 roosters, once with the beaks closed and once fully opened. A surface model was created to measure quadrate motion, displacement of the columella and changes in eardrum shape. Bony semi-circular canals of the inner ear were used to align models. We found no significant difference in beak opening, consequently neither in forward rotation of the quadrate, between hens and roosters. However, axial rotation of the quadrate about its squamosal-mandibular axis is significantly larger in roosters. These quadrate movements do not result in significant displacements of the columella, but do effect the eardrum. The strain of the membrane changes with beak opening in both sexes, and there is a clear displacement of the membrane, hence a deformation of the columella, in roosters. Based on these results we assume that craniokinesis may play a role in the middle ear. As sound production strongly differs between hens and roosters, the subtle difference in craniokinesis and its potential influence on eardrum mechanics may provide a protective mechanism for loud sounds during vocalization.

POS2-60 4:30 pm

The role of cervical air sacs in the vocalization of songbirds.

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Abstract: Whereas the structure and function of the sound-producing organ of birds, the syrinx, have been studied extensively, the structure and function of the supra-syringeal sound-resonating organs still await basic studies. To understand the complex interactions of these organs and their roles in generating the articulated tonal vocalizations of songbirds (e.g., the Northern Cardinal, *Cardinalis cardinalis*, and House Sparrow, *Passer domesticus*), a variety of complementary functional-morphological methods were applied: Micro-dissection; 3D imaging and modeling based

on x-ray CT; and animation based on x-ray videography. Two pairs of cervical air sacs were discovered enveloping the supra-syringeal vocal apparatus and being enveloped by the cervical integument with its dermal musculature and the cervical cutaneous fasciae and musculature: The cervical diverticula of the cervico-cephalic air sac system cranially, and the parapatagial diverticula of the clavicular air sac of the pulmonary air sac system caudally. 3D animated models of singing Cardinals revealed that the tongue-larynx-trachea complex is protracted while the cervical vertebral column is retroflexed into a C-shape, thereby creating a space between the two structures when low-frequency sounds are produced. When high-frequency sounds are produced, the tongue-larynx-trachea complex is retracted, the cervical vertebral column returns to its relaxed S-shape, and the space between the two structures is reduced. We infer that the paired air sacs in the neck of songbirds are passively inflated and deflated to adjust to the fluctuating space between the trachea and cervical vertebral column and that their resonance can be regulated independently by the musculo-elastic system of the cervical cutaneous and dermal muscles to track the frequencies produced separately by the left and right parts of the syrinx. Supported by NIH grant NINDS R01 NS029467 & LSU Foundation fund "Functional Morphology of Birds"

POS2-62 4:30 pm

Virtual reconstruction of the skull of a large parrot (Aves: Psittaciformes: *Ara macao*), highlighting the anatomy of the brain endocast, inner ear, rhamphotheca, and kinetic apparatus.

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Abstract: Parrots and their allies (Psittaciformes) are a speciose and highly divergent group of non-passerines known for their complex feeding behaviors and high cognitive capacity. As an outgrowth of projects on the evolution of the avian brain and cranial kinesis, an interactive 3D model of the skull of a scarlet macaw (*Ara macao*, OUV 10633) was constructed. Voxel data were collected using micro-computed tomography (microCT). Subsequently, segmentation of anatomical structures was done in Avizo and 3D modeling in Maya. 3D PDFs were generated in Deep Exploration and Acrobat, and movies in QuickTime and Adobe Premiere. Interactive 3D models were also made available on Sketchfab. The resulting virtual skull highlights the anatomical basis for the prokinesis seen in large parrots: a well-developed craniofacial hinge, as well as the development of syndesmoses and diarthroses at the jugal and palatine articulations. The model also shows the high disparity between the extent of the rhamphotheca and the underlying bony jaws. Among the virtually reconstructed endocranial structures are the brain endocast, endosseous labyrinths of the inner ears, and neurovasculature. The endocast confirms previous descriptions of the *Ara* brain surface, including an expanded telencephalon with pronounced rostral notch and sagittal eminence, while resolving additional details, such as floccular shape and cerebellar foliation. We have assembled the resulting visualizations as an open-access online resource called the Visible Interactive Parrot (VIP) to serve as an educational tool for K–12 STEM educators, undergraduate and graduate students, and the public. Scarlet macaws are well-known members of this charismatic group, making them an ideal species for fostering public engagement. The VIP joins the existing library of Visible Interactive Animals on the WitmerLab website.

POS2-64 4:30 pm

Turbinal variation in high and low altitude populations of *Peromyscus maniculatus*.

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Abstract: At high altitudes, hypoxic and low-humidity conditions are common, contributing to a highly stressful environment and necessitating behavioral and physiological means of heat and water conservation. In many mammals, the challenge of water retention is handled by countercurrent airflow through a nasal turbinal complex, which reduces evaporative water loss and also helps retain heat. North American deer mice have one of the largest altitudinal ranges of any mammal, and display physiological and behavioral adaptations to stressful high-altitude conditions. Previous work has shown that mice living at high and low altitudes are genetically divergent, and that the hemoglobin of high-altitude mice has an increased affinity for oxygen. In addition, deer mice at higher elevations have increased ventilation rates. However, with increased ventilation also comes the potential for increased heat and water loss. Given these physiological stressors, we might expect to see compensatory modifications in the morphology of the turbinal system or nasal cavity. We tested this hypothesis by quantifying and comparing the surface area of the nasal turbinal surface areas of 28 deer mice specimens from high and low altitudes, using high-resolution CT scans, as well as performing a morphometric analysis of the skulls to assess if physiological stress affected skull morphology. Preliminary results suggest that there are small but significant differences between high and low altitude mice in turbinal surface area, but not nasal cavity dimensions. If preliminary results hold, this would be the first example of intraspecific variation in turbinal morphology in response to differences in habitat.

POS2-66 4:30 pm

Functional anatomy of the hind limb in Japanese cormorants (Aves: Phalacrocoracidae).

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Abstract: Cormorants are excellent foot-propelled aquatic diving birds. They use two stroke phases during foot-propelled diving, the power stroke and the recovery stroke. In the recovery stroke, the foot is brought forward with flexing the digits, which closes the foot web and reduces water resistance. However, few functional anatomical

studies have reported on digit movements during the recovery stroke in cormorants. The present study evaluates the muscles of the hind limbs associated with digit movement during the recovery stroke in the Japanese cormorant *Phalacrocorax capillatus*. Three muscles play an important role in the recovery stroke: Musculus flexor perforatus digiti III (FPDIII), M. flexor perforans et perforatus digiti III (FPPDIII), and M. flexor perforatus digiti IV (FPDIV). The tendons of the FPDIII and the FPDIV perforate the lateral surface of the tendon of the FPDIII on the distal end of the tibiotarsus. As FPPDIII engages, digits III and IV are initially flexed together, as the three tendons cohere with one another. However, the tight contact of the tendons gets lost as the flexion progresses, as the tendons of FPDIII and FPDIV taper off distally. Accordingly, digit III is more strongly flexed than digit IV, so that the two digits get in line anteroposteriorly. Thus, Japanese cormorants can decrease the water resistance occurring around the foot web during the recovery stroke.

POS2-68 4:30 pm

Morphological disparity, growth and life history variation in domesticated horses.

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Abstract: Domesticated mammals offer a rich subject of investigation into the origins of morphological variation (disparity) within a species; experiments in evolution in which the developmental bases of such variation can be studied. We aimed to investigate in horses the influence of domestication on disparity and how it is generated in development by including the whole breadth in size (from the Falabella to the Shire). To quantify disparity of juvenile and adult skull shape we used three-dimensional geometric morphometrics in 30 domesticated horse breeds and 5 wild equid species. Statistical analyses showed that the morphological disparity in adult domesticated horse skulls exceeds that of the wild species and that domesticated breeds occupy regions of the morphospace that are not occupied by wild equids. Furthermore, results showed that paedomorphism serves to describe some of the shape changes in the skull of the Falabella when compared with normal-sized breeds. We also investigated the influence of domestication on life history variables by comparing gestation length, skeletal maturity, and growth rate among different horse breeds. For the gestation length our dataset included 27 breeds and results of multivariate statistics did not show significant differences among breeds. We further examined growth rates using histological markers in the femur of 7 breeds to investigate growth rate differences. Additionally, we investigated the timing of skeletal maturity by determining the state of cranial and epiphyseal suture closure in 30 breeds, and found that most markers of growth are conserved. Specific aspects of the anatomy are shown to exhibit differences (e.g., inner ear anatomy) between domesticates and wild forms, but separating adaptive from genetic drift effects, or other mechanisms, is difficult in these morphological studies.

POS2-70 4:30 pm

Morphology and mechanics of remora adhesion.

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Abstract: Adhesion, and in particular long-term reversible adhesion, to a wet or submerged surface is challenging. In the natural world, few organisms can adhere to underwater substrates and those that do generally use glue-like mechanisms or attach only to stationary objects. Remora fishes have evolved a unique adaptive ability - an adhesive disc formed from dorsal fin elements - that allows them to attach reversibly to actively deforming bodies of varying roughness and compliance that move at high speed. The adhesive disc is a hierarchical structure, in which the lamellae, spinules, fleshy outer lip, and cranial vessels all contribute to the generation of suction and friction for initial attachment and long-term hold. We found that remora body shape adds hydrodynamic advantages to adhesion and resistance to drag as well. The wall effect created by the flat disc approaching a host organism generates a suction pressure that helps to pull the remora to its host. Upon contact, the fleshy outer lip generates a viscoelastic seal as the lamellae rotate to produce a subambient pressure beneath the disc. Individual lamellar chamber pressures are equalized by the anterior cardinal sinus. Lamellar contact with the host engages spinule interaction with the host surface, thereby generating frictional forces that oppose shear. Our continued assessment of these mechanisms and the material properties of these structures is leading towards a bioinspired adhesive device that will be useful in ecology, medicine, and defense.

POS2-72 4:30 pm

Structure and motion over the fin-to-limb transition.

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Abstract: The fin-to-limb transition was a major evolutionary event in the history of life that influenced the subsequent morphology, lifestyle, and biodiversity of land vertebrates. Two questions remain relatively poorly understood: (1) how the various anatomical parts of limbs evolved semi-autonomously (modularity) while still growing and adapting in coordination (integration) and (2) the functional implications of these fundamental transformations in appendage morphology. This poster outlines our combined efforts to explore the structural and functional changes brought about by the fin-limb transition. We seek to unravel the evolutionary changes in modularity of the musculoskeletal system that occurred during the evolution of early tetrapods, how these newly acquired modular organizations facilitated the

evolution of different morphologies for the forelimb and hindlimb, and how morphological changes in the limb bones and muscles of early tetrapods influenced their abilities to generate forces against the substrate and thereby achieve the water-land transition. The combined results of these two complementary projects are illuminating new aspects of limb evolution across the fin-limb and water-land transitions.

POS2-74 4:30 pm

Ontogeny of the West African caecilian *Idiocranium russeli* (Lissamphibia: Gymnophiona: Indotyphlidae).

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Abstract: Very few detailed descriptions of the skeletal and muscular development of caecilian amphibians are currently available. The recent studies show that there are disagreements concerning the homology of different skull bones and the number of different ossification centres. We investigated the embryonic and juvenile development of the skeleton and musculature of *Idiocranium russeli*, a miniaturised caecilian endemic to southwestern Cameroon. *Idiocranium* was suggested to be a direct developing genus like other members of the Indotyphlidae (e.g. *Hypogeophis rostratus* or *Gegeneophis ramaswamii*). Our results strongly support this hypothesis. The external morphology of different embryonic stages, the ossification sequence and the muscle configuration of *I. russeli* indicate heterochronic shifts of adult characteristics into embryonic development, as well as the loss or absence of various larval and metamorphic traits. For example, the maxilla and the palatine fuse to form the maxillopalatine well before hatching. This compound bone is typical for adult caecilians and forms during metamorphosis in most biphasic species. The tentacle, which normally also develops during metamorphosis, is already fully developed in late embryos. Furthermore, exclusive larval muscles like the M. interhyoideus or M. hyomandibularis are completely absent during ontogeny. The M. genioglossus and M. cephalodorsosubpharyngeus are present in embryonic development – a typical feature of direct developing caecilians. A larval ceratobranchial IV is also present, but fuses to the ceratobranchial III very early in ontogeny. The ossification sequence of *Idiocranium* is highly similar to those of *G. ramaswamii* and *H. rostratus*, but there are small differences like the coronoid starting to ossify earlier than in other indotyphlid species and the dermal pterygoid appearing comparatively late in ontogeny.

POS2-76 4:30 pm

Modeling the skeletomuscular system in Sea Lampreys (*Petromyzon marinus*): An integrative approach from microdissection, 3D imaging, and field observations.

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Abstract: Lampreys play a key role in the reconstruction of the evolutionary history of vertebrates, but little is known about their functional morphology or their interactions with their environment. Our study integrates field observations and functional morphological studies of adult Sea Lampreys. We observed and video-recorded the body movements of spawning lampreys transporting stones to build nests and defending their territories in the high-velocity tributaries of the Connecticut River. Lampreys are capable of a much wider range of motion than gnathostomes: Dorsal and ventral flexions in excess of 90 degrees, lateral flexions up to 180 degrees, and twisting motions over 300 degrees. We hypothesize that the lamprey's greater mobility may be at least partly due to the absence of a pectoral girdle, stiff vertebral column, and horizontal septum, which are characteristic of gnathostome fishes. To test this, we analyzed the fiber arrangement and orientation of the connective tissue and musculature of the trunk by microdissection and 3D modeling based on x-ray CT and MRI. The connective tissue skeleton comprises the dermis, a sub-dermal dorsal longitudinal ligament, and myosepta. The ligament sends and receives fibers from the dermis and medio-dorsal fascia, thereby acting as a node linking the dermis to the connective tissue skeleton anchored to the notochord and surrounding the coelom. The myosepta are actually formed by tendons extending from myomeric muscle fibers. Superficial tendons between muscles fibers of adjacent myomeres are aligned and, therefore, look like a "myoseptum." Tendon fibers that dive medially join the deeper connective tissue skeleton. Hence, forces of contracting myomeres are transmitted across the myosepta as well as to the connective tissue anchored to the notochord and coelom enabling great flexibility of the body.

POS2-78 4:30 pm

Ultrastructural study of the skin of three caecilians (*Ichthyophis tricolor*, *Uraeotyphlus oxyurus*, and *Gegeneophis ramaswamii*) from Western Ghats, India.

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Abstract: The aim of the present study is to investigate the skin structure of three adult caecilians belonging to Ichthyophiidae such as *Ichthyophis tricolor*, *Uraeotyphlus oxyurus*, and Indotyphlidae as *Gegeneophis ramaswamii*. The SEM and TEM observations of their skin shows that skin is segmented with numerous glandular outlets in the dorsal, ventral and lateral regions. Round, oval, and polymorphic shaped glandular outlets were distributed in the skin. *Ichthyophis tricolor* skin has both collar type and funnel type glandular outlets but *Uraeotyphlus oxyurus* and *Gegeneophis ramaswamii* has only collar type glandular outlet. Pore size and pore distribution in the

skin are different in three species. The glandular outlets are situated on borders between adjacent cells and near one of the angles of the multifaceted epithelial cells in all the three species. Skin of *Gegeneophis ramaswamii* has many grooves distributed in the dorsal, lateral, and ventral skin surfaces along with the glandular outlets. These grooves were not present in skin of *Ichthyophis tricolor* and *Uraeotyphlus oxyurus*. Skin has irregular shaped epidermal cells having microridges in them. Dorsal skin observed under TEM shows three layers of epidermis, stratum corneum, stratum spinosum, and stratum germinativum followed by the dermal layer. Flask shaped cells and merkel cells are also found in the epidermis. Two types of glands, mucus and granular glands, are present in *Ichthyophis tricolor* and *Uraeotyphlus oxyurus* but *Gegeneophis ramaswamii* has only mucus gland. They were distributed in the dermis layer. Secretary granules are present in the granular glands. Mucus secreting granules are present in mucus glands. Both glands are layered by myoepithelial cells. This is the first report on the skin, skin glands, and glandular outlets of these three caecilian species. We hope that this study will penetrate deeper in to the knowledge about the skin morphology and poison biochemistry and pharmacology of these three species.

POS2-80 4:30 pm

Flow sensing in the deep sea: Novel observations on the mechanosensory lateral line system in stomiiform fishes.

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Abstract: The mechanosensory lateral line system (LL) in deep-sea fishes is relatively unknown, especially with regard to the Stomiiformes. Unlike melamphoids and gadiforms, which have obvious widened cranial LL canals with large neuromasts, hatchetfishes are reported to have less prominent LL canals and few superficial neuromasts (Handrick, 1901). We examined two important, commonly caught and widely distributed stomiiform taxa: hatchetfishes (*Argyropelecus*: Sternoptychidae) and bristlemouths (*Cyclothone*: Gonostomatidae) using modern methods to re-assess their LL morphology. High quality specimens were collected at sea (Tucker trawl) or obtained from museum collections and were examined using clearing and staining, whole mount hematoxylin staining, histology, μ CT imaging, and SEM. Contrary to Handrick, who reported the presence of an unusually small number of neuromasts in *Argyropelecus*, we found lines and clusters of densely placed superficial neuromasts above and below the eye, on the cheek, along the mandible, and in discrete vertical lines on the trunk. In addition, canal neuromasts were identified in the predominantly unossified supraorbital canal and in unossified mandibular and preopercular canals. In contrast, *Cyclothone* lacks cranial canals and has small superficial neuromasts distributed in similar locations on the head and trunk, but they are not as proliferated as those in *Argyropelecus*. MicroCT imaging of representatives of several other stomiid genera reveals the presence of completely and incompletely ossified cranial canals in contrast to the reduction or absence of canals in *Argyropelecus* and *Cyclothone*. These findings suggest that the LL of stomiiforms is likely more important for mediating behaviors in the hydrodynamically quiet, and light limited deep sea than previously thought. Funded by NSF Graduate Research Fellowship and ANMH Lerner Grey Fund Award to ANM.

POS2-84 4:30 pm

Comparative anatomy of the facial muscles in *Myocastor coypus* (Mammalia: Myocastoridae).

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Abstract: The Musculus platysma and M. sphincter colli are specific facial muscles in rodents that facilitate their classification. The form of these facial muscles have been described in some species of Myomorpha and Sciuromorpha, but there have been few anatomical studies of the facial muscles in the Hystricomorpha. Here I report on the morphological characteristics and innervation of the facial muscles of three specimens of *Myocastor coypus* of the suborder Hystricomorpha. The origins of the M. platysma myoides and M. platysma cervicale are fascia on the M. masseter. The M. platysma myoides and M. platysma cervicale are inserted on the M. cutaneous maximus pars ventralis and M. cutaneous maximus pars dorsalis, respectively. These muscles are fused to each other at their origin. The cervical nerve inserts on the insertional part of the M. platysma myoides. Thus, the M. platysma myoides is not homologous to the M. platysma in terms of nerves supply from the facial nerve. The M. sphincter colli profundus originates from the cranial one-third of the sternum and inserts on the zygomatic arch. This M. sphincter colli profundus is described as covering almost all of the ventral neck region and is innervated by extra cranial branches of the facial nerve which supply the facial muscles. The M. sphincter colli profundus changes to a muscle when connecting bone to bone, although it is one of the facial muscles that are generally described as cutaneous muscles. These muscle features of M. platysma myoides and M. sphincter colli profundus have not yet been describe in other mammals.

POS2-86 4:30 pm

Preliminary investigations of cranial morphology in the Paradoxurinae (Mammalia, Carnivora, Vivveridae).

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Abstract: Paradoxurinae (e.g. palm civets, binturongs) are a subfamily of viverrids, which are primarily found in India, southeast Asia, and across some of the Philippine islands. The members of this group are arboreal, living high in dense forest canopy, and most individuals are solitary but not strictly territorial, and mainly nocturnal. Many aspects of this group are still relatively unknown, such as specifics related behavior and activities, as well morphological

characters that would influence an understanding of those behaviors. For example, relationships among the group and other viverrids have been based on genetic characters with only a cursory examination of skeletal characters. Some molecular studies have placed *Arctictis* as the sister taxon to *Paguma*, while others have resulted in a closer association of the binturongs with the Viverrinae. Crania of *Arctictis* were compared to those of *Arctogalidia*, *Paguma*, and *Paradoxurus* in an attempt to resolve the molecular relationships with morphological data and characters. *Arctictis* easily separates based on its larger size and also differs significantly when viewed dorsally in the constriction of the braincase. This postorbital constriction occurs just behind the postorbital processes in the other paradoxurines and viverrinae but in *Arctictis* it is far posteriorly positioned. *Arctictis* does align with the others in the ventral extension of the paraoccipital bone below the ectotympanic bullae, except for *Arctogalidia* in which there is no ventral extension and the bullae are not enlarged. *Arctictis* also lacks a distinct sagittal crest and has very short postorbital processes. At present, there are many shared viverrid characters exhibited by *Arctictis* but the other characters examined do not strongly support its association with any of the other members of paradoxurinae nor those of Viverrinae.

POS2-88 4:30 pm

Comparative anatomy of the subscapularis, teres major, and latissimus dorsi muscles from salamanders to humans.

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Abstract: The shoulder girdle muscles in tetrapods, adapting to the terrestrial locomotion, have shown notable morphological changes in evolution. In this study, the phylogenetic differentiation of the subscapularis, teres major and latissimus dorsi muscles is studied. The observations were performed by dissecting the muscles together with the supplying nerves in amphibians (salamanders), reptiles (monitor lizards and iguanas), monotremes (platypuses and echidnas), marsupials (koalas and possums) and placental mammals (pigs, rats, dolphin, cats). The subscapularis in therians is innervated by the several subscapular nerves from the posterior cord of the brachial plexus. The proximal branches are originated from the ventral layer of the posterior cord and distal ones are from the dorsal layer near to the branches to the teres major. The thoracodorsal nerve to the latissimus dorsi arises independently from the posterior cord distal to the subscapular branches. In reptiles, the subscapularis and the scapulohumeralis posterior, which seems to correspond to the procoracohumeralis muscle in salamanders, are blended at insertion and receive common nerve branches. This fact suggests that the subscapularis in reptiles has a close relationship to the scapulohumeralis posterior, and probably to the procoracohumeralis in salamanders. The origin of the subscapularis in monotremes develops over the external surface of the scapula and this external part is innervated by the independent branch arising near to the branch to the teres major, which appears in mammals. Furthermore, this subscapular branch in monotremes, judging from its origin from the plexus, is thought to be homologous with the branch to the scapulohumeralis posterior in reptiles. These results suggest that the caudal part of subscapularis and the teres major in therians can be differentiated from the scapulohumeralis posterior in reptiles and may have a close relationship to the procoracohumeralis in salamanders.

POS2-90 4:30 pm

The Myosin Heavy Chain specific A4.1025 antibody discriminates different cardiac segments in ancient groups of gnathostomes: Morphological and evolutionary implications.

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Abstract: The pan-Myosin Heavy Chain (pan-MyHC) marker MF20 have been reported to show similar, homogeneous signal in the myocardial segments of the heart of teleosts and tetrapods. However, in an ongoing study of the myocardial structure of the dogfish (*Scyliorhinus canicula*; Chondrichthyes), we observed differential immunostaining of the cardiac segments using another pan-MyHC, the A4.1025 antibody. In order to investigate the relevance of this finding for better understanding of the morphology and evolution of the vertebrate heart, we performed immunohistochemistry, slot blot and western blot in several species of chondrichthyans, actinopterygians and mammals using the above mentioned antibodies. In the dogfish heart, A4.1025 and MF20 specifically recognized MyHC isoforms, although with different degree of affinity. MF20 reactivity was homogeneous and high in all the myocardial segments. However, A4.1025 reactivity was heterogeneous. It was high in the sinus venosus (external layer), atrium and atrioventricular region, low in the ventricle and conus arteriosus, and null in the internal layer of the sinus venosus. A heterogeneous pattern of A4.1025 immunoreactivity was also detected in two other elasmobranchs, a holocephalan, a polypteryform and an acipenseriform. In all of these species, MF20 immunoreactivity was homogeneous. In addition, both markers showed a homogeneous immunoreactivity pattern in teleosts and mammals. Our results indicate that in the hearts of ancient gnathostomes, in all of which a conspicuous conus arteriosus exists, one or more MyHC isoforms with low affinity for A4.1025 show segment-specific distributions. Thus, A4.1025 appears to be an appropriated marker to identify the cardiac segments and their boundaries. We propose that the segment-specific distribution of MyHC isoforms may generate a particular type of myocardial contractility associated with the presence of a conus arteriosus. This work was supported by CGL2014-52356-P, CEIMAR, BIO 203 and FEDER.

POS2-92 4:30 pm

Comparative morphology of *Horadandia* Deraniyagala and *Rasboroides* Brittan (Teleostei: Cyprinidae).

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Abstract: Comparison of all congeners of *Horadandia* and *Rasboroides* disclosed two distinct genera by means of morphological differences except certain reliable characters; *Horadandia* (i.e., *brittani+atukorali*) differs from *Rasboroides* (i.e., *vaterifloris + nigromarginatus + pallidus + rohani*) by a consistent set of synapomorphies: (1) absence or presence of a bowl-shaped depression on the supraethmoid; (2) attachment of Baudelot's ligament on the dorsal part of the cleithrum, to distal end or not at the distal end, apart from the tip; (3) number of rows of pharyngeal teeth either 2 or 3; (4) presence of cusps or grooves at apex of pharyngeal teeth and (5) lateral line absent or present (when present, incomplete). *Horadandia* and *Rasboroides* have long been in an uncertain taxonomic position. Hence, this study confirms the identity of both genera by giving modest (about 15) characters, of which three character states were revealed by a previous study. The intraspecific variations of *Horadandia* and *Rasboroides* disclosed two distinct species represented by the former genus, whereas latter consisted of four. South East Asian cyprinid genus *Trigonostigma* Kottelat & Witte appears to be the sister genus of both *Horadandia* and *Rasboroides*. Congeners of *Trigonostigma* superficially resemble *Rasboroides*. Currently, these three genera show a disjunctive distribution pattern in South East Asia and in South Asia. However, according to a recent study, two regions were confluent during the early Eocene (about 35 Ma) as a single land mass (Eurasia+India). Hence, the common ancestor of *Horadandia*, *Rasboroides* and *Trigonostigma* may have lived around 35 Ma in the land mass of Eurasia+India.

POS2-94 4:30 pm

Anatomical, histochemical and immunohistochemical characterization of the outflow tract of ray hearts (Rajiformes; Chondrichthyes).

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Abstract: Recent work has shown that the cardiac outflow tract of sharks and chimaeras does not consist of a single myocardial component, the conus arteriosus, as classically accepted, but two, namely, the myocardial conus arteriosus and the non-myocardial bulbus arteriosus. However, the anatomical composition of the outflow tract of the batoid hearts remains unknown. The present study was designed to fill this gap. The material examined consisted of hearts of two species of rays, namely, the Mediterranean starry ray (*Raja asterias*) and sandy ray (*Leucoraja circularis*). They were studied using scanning electron microscopy, and histochemical and immunohistochemical techniques. In both species, the outflow tract consists of two components, proximal and distal with regard to the ventricle. The proximal component is the conus arteriosus; it is characterized by the presence of compact myocardium in its wall, and several transverse rows of pocket-shaped valves at its luminal side. Each valve consists of a leaflet and its supporting sinus. Histologically, the leaflet has two fibrosas, inner and outer, and a middle coat, the spongiosa. The distal component lacks myocardium. Its wall consists of smooth muscle cells, elastic fibers and collagen. Thus, it shows an arterial-like structure. However, it differs from the aorta because it is covered by the epicardium and crossed by coronary arteries. These findings indicate that the distal component is morphologically equivalent to the bulbus arteriosus of sharks and chimaeras. In contrast to foregoing descriptions, the valves of the first transverse row are distally anchored to the bulbus arteriosus and not to the ventral aorta. Our findings give added support to the notion that presence of a bulbus arteriosus at the arterial pole of the heart is common to all chondrichthyans, and not an apomorphy of actinopterygians as classically thought. This work was supported by CGL2014-52356-P, CEIMAR, BIO 203 and FEDER.

POS2-96 4:30 pm

Additional articulations on the cervical and thoracic vertebrae and fossoriality in armadillos (Mammalia, Xenarthra).

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Abstract: A previous abstract reported additional articulations on the cervical and thoracic vertebrae of *Dasypus novemcinctus*, *Cabassous tatouay*, and *Euphractus sexcinctus*. To further explore this character within extant Xenarthra the present contribution add observations on most taxa (13 out of 14 genera) and better characterizes those articulations, comparing their extension in the vertebral column to the presence and development of the xenarthrous articulations, as well as to the lifestyles. The additional facets are present only within the Cingulata clade (represented by armadillos), whereas the Pilosa (arboreal sloths and anteaters) lack them. They start on the posterior portion of the mesocervical bone and its extension is variable, usually reaching the posterior half of the thoracic series, but exceptionally spanning to the first sacral element in *Chlamyphorus*. In the cervical and anterior thoracic vertebrae, these facets are convex in the anterior surface of the vertebral body and concave in the posterior surface, placed at both sides of the intervertebral disc, which is reduced in size. In the posterior thoracic elements, the facets are flattened and displaced from the epiphysis of the body, becoming contiguous with the secondary (ventral) xenarthrous facets. The body facets described here are present in all fossorial xenarthrans, plus in the non-fossorial

Tolypeutes. As the plesiomorphic lifestyle of armadillos is presumably fossorial, this condition in the latter taxon is attributed to phylogenetic inertia. In the case of *Chlamyphorus*, the greater extension of these articulations may be related to its extreme fossoriality, since it spends most of the lifetime underground. In terms of function, along with the mesocervical bone, these articulations would stiff the cervical series in lateral and torsional movements, acting as a better fulcrum for head-lifting digging [Funding: FAPESP 2014/23815-2 to MCC and CONICET to FCG].

POS2-98 4:30 pm

Evolution of spinal process shape and vertebral immobility in hominoids.

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Abstract: The nature of the human/chimpanzee last common ancestor is fundamental for understanding the evolution of human bipedalism. A particular focus is the conformation of its spine. There are multiple mechanisms for stiffening the spine of apes, including reduction of the number of lumbar vertebrae, the level of the transitional vertebra where the articular facets change from coronal to sagittal orientation, and the shape and angulation of the spinous processes. There is debate regarding whether these features are homologous or homoplastic, and thus whether bipedalism evolved from a short stiff back like great apes or a longer lumbar column more similar to monkeys and Miocene hominoids. Genetic modification of *Hox9* in mice results in the correlated modification of spinous process shape and placement of the transitional vertebra independent of alternation in lumbar number, mimicking evolutionary changes observed in hominoids. This indicates that the articular facets and spinous processes may be associated developmental modules. To test this hypothesis, we examined this change in spinous process across the thoracolumbar transition in hominoids. We used a NextEngine3D scanner to create surface scans of the lower thoracic and lumbar vertebrae of humans, gorillas, chimpanzees, orangutans, and gibbons in order to assess the angulation, orientation, and shape change of the spinous process relative to the position of the transitional vertebra and lumbar number. Humans and gibbons have a similar change in spinous process orientation and shape at the level of the transitional vertebra. Chimpanzees, gorillas, and orangutans each differ in their pattern of spinous process transition across the thoracolumbar boundary suggesting that mechanisms for lumbar stiffening in these taxa may be independently derived. This material is based upon work supported by the National Science Foundation under Grant No. DGE1255832 and by the Pennsylvania State University Hill Fellowship.

Contrast-enhanced CT (DCT)

POS2-100 4:30 pm

Physiological examination of ratite orthopedic disorders and soft-tissue visualization via micro-CT.

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Abstract: Many hard-tissue (e.g., bone, dentine, enamel) pathologies directly impact the development and function of soft-tissue structures. Such pathologies can be unique to captive individuals and tend to be more common among large-bodied captives such as crocodilians, elephants, and flightless birds. Emus (*Dromaius novaehollandiae*) are large-bodied flightless birds that are uniquely efficient at both anaerobic sprinting and aerobic, sustained running. Native to Australia, they are commonly farmed in North America for oil and meat, but growth of the emu industry has been hampered by poorly understood orthopedic disease states (i.e., splayed-leg disorder). Few studies have examined captive emu skeletal muscle, and none have documented the enzymatic profile of ratite cardiac tissue. We sought to bridge this gap by providing a quantified understanding of physical degradation in this large farm-raised species. Surprisingly, we found the metabolic profile of captive emu cardiac tissue to be most similar to that of active, flying birds. Additionally, metabolic baselines for primary locomotor muscles between splayed and non-splayed limbs indicate enhanced metabolic enzyme activities and myoglobin levels, resulting in a distinctly more "athletic" phenotype than control limbs. This compensatory increase in aerobic capacity demonstrates how soft tissues can mitigate functional issues caused by pathologies and suggests that muscle atrophy does not contribute to splayed-leg disorder. Likely, other factors are to blame (e.g., nutrition). With the advent of more detailed imaging techniques, such as contrast-enhanced micro-CT imaging, we hope to test for signal of these factors and better understand the anatomy and physiology of health and disease states in ratite birds. Through documentation of the interplay between hard and soft structures, including their physiologies, we are now beginning to apply new tools to an ancient clade of poorly-understood birds.

POS2-102 4:30 pm

Contrast-enhanced versus phase-contrast imaging: costs and benefits of different methods.

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Abstract: Recent years have seen a boom in the use of imaging for anatomical and functional studies. Tomography - based methods provide direct access to 3D structures, yet typically allow the visualization of 'hard' tissues (i.e., bone) only. Over the past decade contrast-enhanced methods have been proposed that allow the simultaneous imaging of 'soft' (e.g. muscle, nerves, organs, etc.) and 'hard' tissues by increasing the absorption of X-rays by soft tissues. These methods make use of contrast agents that stain the tissues and increase their density through the infiltration of

radio-opaque solutions. Iodine staining is one of the most popular methods, but a host of other staining agents have been proposed. We here provide comparative results on the efficacy of different agents to stain different soft tissues (muscle, nerve, cartilage). However, for the imaging of museum specimens contrast-enhanced methods are often not allowed. Phase-contrast imaging can in this case provide an excellent and non-invasive alternative to contrast-enhanced methods. We briefly explain the method and show results in comparison with more traditional contrast-enhanced imaging.

POS2-104 4:30 pm

DiceCT and its applications for understanding the reptile musculoskeletal system.

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Abstract: Diffusible iodine-based contrast-enhanced CT visualization is now a standard approach to exploring morphology, refining phylogenies and testing hypotheses of animal function. Fewer anatomical systems lend themselves better to diceCT than the musculoskeletal system of reptiles, which arguably use more tendon and cartilage to construct their heads and limbs than do other amniotes. Here we showcase several lines of inquiry that use diceCT data collected from lizards, crocodylians, birds and mammals. First we use diceCT data to build 3D anatomical models to complement studies of trigeminal nerve evolution, sesamoid development, and jaw and limb muscle anatomy in alligators. Second, we use diceCT data to better understand morphologies of muscle architecture, aponeuroses, and other connective tissues to better inform 3D biomechanical models of skulls to test for patterns in cranial evolution. Third, we use diceCT data to investigate variation in muscle modeling methods.

Ecological Morphology (ECO)

POS2-106 4:30 pm

Substrate and limb evolution: a global ecomorphological analysis of ruminant unguals.

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Abstract: The Ruminantia (Artiodactyla, Mammalia) are prolifically found in a variety of environments. However, the suborder is considered to be best adapted to open habitats, in large part because of their simplified unguligrade morphology of two weight-bearing digits per hoof. The apparent discrepancy between the unified ecomorphology of ruminant feet and the variety of environments they inhabit calls for closer study of variation in limb morphology with respect to habitat. Previous studies have linked ungual features to environmental parameters in several dozen ruminant species. This research seeks to expand upon these studies by 1) examining ungual plantar morphology across the suborder to see if larger scale trends are ecologically, phylogenetically, or body size driven and, 2) generating an analogue that will be used for ecometric comparison to fossil unguals to allow for the reconstruction of paleoenvironments and the elucidation of ruminant response to climate change across the Cenozoic. Our study includes 720 unguals from 93 ruminant species; allowing us to examine ungual ecomorphological association with a global spectrum of habitats (i.e. prairies, deserts, tundras, forests, and swamps) and substrates (i.e. wet, ecotone, rocky and dry). We photographed skeletal ungual plantar (i.e. in contact with the ground) surfaces. Outlines with 100 semilandmarks were then Procrustes superimposed to produce shape variables for subsequent analysis. Results show, regardless of taxonomy, that species which live on fluidly unstable substrates- such as snow or sand, tend to have overall blunter shapes and flatter surfaces to the unguals, undoubtedly to aid in locomotion over the dynamic surface. Furthermore, this effect is strong in wild animals, but muted in captives suggesting that it is a plastic response to substrate. These results show that substrate is also an important factor in ruminant limb evolution-making ungual shape more than just a reflection of phylogeny.

POS2-108 4:30 pm

Ecomorphology of the hind limb long bones in Mustelidae (Mammalia: Carnivora).

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Abstract: Mustelidae display a wide range of ecologies, associated with a diversity of locomotor behaviors. The Mustelidae includes semi-arboreal, scansorial, terrestrial, semi-aquatic and semi-fossorial species with various degrees of specialization in each category. Bone anatomy reflects the interaction between functional adaptations, the phylogenetic background of an organism and the architectural and developmental constraints. Therefore the study of locomotor apparatus in a phylogenetic context is of great interest for understanding the adaptive nature of morphology. Here we investigate the anatomical trends associated with the different locomotor ecologies in Mustelidae. In contrast to the forelimb, the hind limb is almost exclusively devoted to locomotion making the hindlimb crucial in inferring locomotor ecology. Using 3D geometric morphometrics we investigated the hind limb long bone anatomy in Mustelidae. Using both anatomical and sliding semi-landmarks we quantify both the global geometry, the articular surfaces, and the diaphysis. We used these quantitative shape descriptors to test for the presence of a phylogenetic signal. Next, we test for differences in bone shape in animals with different locomotor ecologies while taking into account variation in body mass. Finally, we describe the changes in bone shape associated with each ecological group and discuss the functional consequences thereof.

POS2-110 4:30 pm

The evolution of median fin shape and its implications for swimming performance in the fish superfamily Balistoidea (Order Tetraodontiformes).

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Abstract: Reef-dwelling fishes come in all shapes and sizes, and their high degree of morphological diversity is reflected by the large number of biomechanically distinct swimming modes employed by these fishes. Triggerfishes (Balistidae) and filefishes (Monacanthidae), comprising the monophyletic superfamily Balistoidea, exhibit a unique swimming mode, balistiform swimming, in which the median dorsal and anal fins provide most of the power. Balistiform swimmers lie on a biomechanical continuum from swimming powered by broad oscillations to precise undulations of the median fins. Interestingly, balistiform swimmers also possess median fins that lie on a morphological continuum from high to low aspect ratio (AR). Hydrodynamic theory predicts that fishes using higher AR fins for propulsion should be capable of higher endurance swimming performance, but reduced maneuverability. This performance trade-off is expected to correlate with habitat choice. Using morphometric analysis of museum specimens and photos from online databases and phylogenetic ancestral state reconstructions, I found multiple, independent decreases in dorsal fin AR within Balistoidea from a common ancestor with a mid-high AR dorsal fin. Additionally, nearly all filefishes have low AR dorsal fins. These results raise the possibility of declines in endurance swimming performance among multiple balistoid lineages. Alternatively, lineages with decreased AR fins may have evolved compensatory morphological or behavioral traits to maintain endurance swimming performance. Swimming performance tests and median fin kinematic analysis of balistoid fishes will determine whether decreases in median fin AR necessarily decrease endurance swimming performance and may reveal a potential relationship between fin shape and oscillatory versus undulatory fin kinematics. These experiments may also help elucidate the evolutionary origins, biomechanics, and habitat use of early balistiform swimmers. Funded by NSF grant IOS-1425049.

POS2-112 4:30 pm

A functional role for bipedal locomotion in lizards.

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Abstract: A crucial aspect of the ecological morphology paradigm is the role of performance as the link between organismal traits and their fitness consequences in the environment. Behavior is also included in the paradigm as an additional link, especially when habitat variation is considered. Behavior serves to modulate, or potentially filter, performance variation, in direct and indirect ways. I will present data from studies examining the role of bipedal vs. quadrupedal locomotion in lizards. Bipedalism has been studied extensively, however the functional consequences and/or benefits of this behavior have remained elusive. I will show that some species of lizards modulate their use of bipedalism, and the use of the posture provides an advantage when crossing an obstacle. Furthermore, lizards employ a bipedal posture in a predictable manner as they encounter obstacles. Hence growing evidence supports a functional role for bipedal running behavior, and regardless of its origin, provides a mechanism for selection to maintain, or potentially enhance, its use in some lineages. In particular, this would be true for animals whose microhabitat might constrain performance traits such as maximal sprint speed. Instead acceleration, agility, or their combination, may be key traits correlated to fitness, and locomotor behavior may be a key selective filter.

POS2-114 4:30 pm

Do parasites have a place in ecomorphology?

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Abstract: The mechanisms underlying parasite-altered host behavior and fitness remain largely unanswered. We argue that performance capacity is an important target of parasitic manipulation and we aim to integrate the study of animal performance and ecomorphology with that of parasitic manipulations of host behavior and fitness. We performed a meta-analysis of 101 measures of the effect of parasites on host performance capacity from the published literature to address the following questions. (1) Do parasites exert an important effect on host performance capacity? (2) Is that effect routinely to decrease or enhance performance capacity? (3) Which factors explain the effect of parasites on host performance capacity? and, (4) Do parasite impacts on morphology explain the changes in host performance? Although negligible-small effect sizes were detected in 40/101 measures, host performance capacity was overall affected by parasitic infection with a negative direction and medium-large magnitude in 58/101 measures and an increase in performance capacity in 3/101 measures. Host age, type of host performance, the host tissue infected by the parasite, and whether the study was experimental or based on natural infections each explained a significant amount of the variation in effect size. Finally, we explore how changes in host morphology result in changes in host performance. Overall, this work clearly demonstrates the link between parasites and host performance and function.

Fossoriality (FOS)

POS2-116 4:30 pm Digging for clues: Methodological review of subterranean lifestyle inferences in fossil mammals.

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Abstract: Current mammals include approximately 325 subterranean species over 4768 species in total. Although they are all subjected to the same underground environment stresses, extant taxa have very diverse lifestyles with different ecologies, diets and locomotion habits. Even the way to dig takes different forms: with the teeth, claws, paws, and head. Is the past diversity of the subterranean taxa similar? And how do we infer subterranean lifestyle on fossils? The oldest occurrence of fossorial behavior has been documented through taphonomy. Indeed burrows are often found on paleontological sites since their sedimentation is different from the surrounding area. For example, fossils of the fox-sized cynodont *Thrinaxodon* are relatively common in the Lower Triassic deposits of South Africa. The fossorial skeletal specializations are also clues to determine the subterranean lifestyle for mammaliaform lineages. Hypertrophied burrowing limb features reflect scratch digging activity. Specific head morphology could translate adaptations for chisel-tooth or head-lift digging activities. The aim of this study is to set up a new subterranean lifestyle inference model based on the inner ear morphology. The sensitivity to head rotations and locomotor behaviors are related to the inner ear. The head movements play a significant role in the subterranean lifestyle: no matter how digging, the head is much sought. The inner ear had to manage this intensive and frequent head movements, thus these mechanical stresses must influence the morphology of the organ. The project aims to highlight the correlation between the anatomy of the inner ear and the burrowing lifestyle. Placed in an evolutionary and temporal context, these results will clarify the importance of this way of life in the mammal history, particularly during major biological crises.

Inner and Middle Ear (EAR)

POS2-118 4:30 pm

The bony labyrinth morphology helps to recalibrate the Cervidae tree.

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Abstract: Molecular clock analyses calibrate the origin of crown Cervidae within the Late Miocene (7-10Ma), even if stem Cervidae appeared almost 10Ma earlier. The relationships within the living deer appear to be resolved based on molecular data (mitochondrial and nuclear). However, no phylogenetic hypothesis based on morphological characters alone reflects the molecular-based topology. For example, *Megaloceros* is either part of the basal radiation of *Cervus* (molecular data), or of the *Dama* radiation (combined analyses of molecular and morphological), or closely related to the "basal Cervini" *Eucladoceros* (morphological). In addition, morphological studies indicate crown Cervidae could have arisen in the Middle Miocene. Our study on cervid evolutionary history includes 13 living species in all the tribes and 14 fossil ones. We investigated the bony labyrinth shape and perform a 3D geometric morphometrics analysis. We show that Early Miocene Cervidae have similar primitive bony labyrinth morphology that (together with their ancestral antlers) support an attribution to stem Cervidae. The Middle Miocene *Euprox* possesses a derived morphology of the inner ear corresponding to those of crown deer. Considering its antler morphology, it possibly represents Muntiacinae and accordingly the oldest known crown deer (13.5Ma). Further morphological distinctions can be done between the bony labyrinth of the different subclades (Capreolinae and Cervinae) based on the lateral canal. Moreover, closely related genera present a similar endolymphatic sac shape supporting molecular data (*Dama*/*Pseudodama*/*Megaloceros*; *Rusa*/*Cervus*; *Hydropotes*/*Capreolus*). Based on these new data, a molecular clock analysis is under process testing previous results on the divergence times of the various cervid genera. Study supported by the SNF project 200021-159854.

POS2-120 4:30 pm

Sound transmission pathway in protocetids (Mammalia: Cetacea).

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Abstract: Extant cetaceans are fully aquatic mammals which diverged from terrestrial artiodactyls around 55 million years ago. They present deep modifications of their sensory organs, notably of the sound perception pathway. Archaeocetes are a paraphyletic assemblage of early diverging cetaceans. They show a diversity of morphologies of the petrotympanic complex and ossicles documenting a variety of sound transmission mechanisms from mostly terrestrial configuration to fully aquatic layout. Protocetids are semi-aquatic archaeocetes that maintain a strong relation with land (e.g. parturition on land). The auditory region of these so called "transitional" forms is only partly known. The middle Eocene locality of Kpogamé, Togo (46–43 Ma) has yielded abundant material documenting the auditory region of protocetids cetaceans including twelve fragmentary bullae, one isolated petrosal and one

petrotympanic complex. The CT-scan investigation of the petrotympanic complex revealed for the first time in situ ossicles of a protocetid. These remains allow refining the hypothesized mechanism of the sound transmission pathway from the surrounding environment (air or water) to the fluid filled cochlea in protocetids. The morphofunctional study of the auditory region remains from Kpogamé indicates that optimal audition abilities in both air and water were most probably possible in protocetids. The latter indeed retained i) a wide tympanic ring indicating the presence of a functional tympanic membrane, ii) non-fully modified ossicles and cochlea, and iii) a petrosal-bulla contact suggesting a possible bimodal functioning of the petrotympanic complex with a "switch system" that could "open" or "close" the middle ear. Finally, the morphology of the cochlea supports the hypothesis of ancestral low frequency sensitivity in cetaceans and sets this state of character back to middle Eocene times.

POS2-122 4:30 pm

Inner ear orientation shows head posture in extant rhinos (Perissodactyla: Rhinocerotidae).

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Abstract: Among extant perissodactyls five rhinoceros species exist. Two of them are African species and three are Asian with different feeding strategies. The African black rhino (*Diceros bicornis*), and the Asian Indian (*Rhinoceros unicornis*) and Sumatran rhinos (*Dicerorhinus sumatrensis*) are all mixed feeders. In comparison, the Asian Javan rhino (*Rhinoceros sondaicus*) is a pure browser, while the African white rhino (*Ceratotherium simum*) is a pure grazer. The latter two species display different habitual head postures: "horizontal" in the Javan rhino and "hanging" in the white rhino. Behavioral studies show that mixed feeding species are carrying their heads between "horizontal" and "hanging". The different head postures are expressed by the inclination of the occiput, which is backward inclined in grazers and forward inclined in browsers. Re-organization of the occipital region during phylogeny also involves the ear region. Therefore, nine skulls of extant rhinos have been scanned with CT to virtually reconstruct the bony labyrinth. The orientation of the inner ear's lateral semicircular canal, normally aligned parallel to the ground, was used to show the resulting habitual head posture. In accordance with occiput inclination the browsers show a horizontal and the grazers a downward oriented skull. During rhinoceros evolution two trends became obvious, some rhinos developed large horns, while others evolved lower tusk-like second incisors. Both characters were used for fighting. The results of the study furthermore suggest, that the adaptation to feeding preferences developed first while protectable weapons (large horns in downgrade headed grazers, lower tusks in horizontal headed browsers) developed later via natural selection. This research received support (FR-TAF-3483) from the SYNTHESYS Project <http://www.synthesys.info/> which is financed by European Community Research Infrastructure Action under the FP7 "Capacities" Program.

POS2-124 4:30 pm

Digging into mammal inner ear morphology: new insights into subterranean lifestyle determination using 3D landmarks inference model.

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Abstract: The sensory systems of balance and hearing is located in the bony labyrinth in the periotic bone. Across mammals, the general morphology of this bony labyrinth is similar, but the detailed morphology varies even among closely related groups showing that the shape of the labyrinth carries valuable functional and phylogenetic information. The sensitivity to head rotations and locomotor behaviors are related to the sizes, shapes and orientations of the bony labyrinth and particularly the semicircular canals. The head movements play a significant role in the subterranean lifestyle: depend the way of digging, the head is much sought. The bony inner ear had to manage this intensive and frequent head movements, thus these mechanical stresses must influence the morphology of the organ. In this study, to characterize the particular morphology of the bony inner ear of subterranean mammals, we constituted a comprehensive sampling including at least one species within every strictly subterranean clades. Adding to this 45 species, we completed our sampling with two phylogenetic closest species one belonging to a fossorial lifestyle and one to a terrestrial lifestyle (total of 130 specimens). This was done for control purposes, to discriminate phylogenetic and functional signals. Thanks to semilandmarks-based three-dimensional geometric morphometric approach, we characterize the shape of the labyrinth. Preliminary results suggest that subterranean mammals have an osseous labyrinth thicker than terrestrial generalist. Using multivariate statistics, we set up a subterranean lifestyle inference model. The established correlations will allow inferring a lifestyle to fossil taxa. Placed in an evolutionary and temporal context, these results will clarify the importance of this way of life in the mammal history, particularly during major biological crises.

Muscle Functional Morphology (MFM)

POS2-126 4:30 pm

Comparative myology and adductor leverage in phalangeriform possum jaws.

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Abstract: Phalangeriform possums are a radiation of omnivorous arboreal marsupials native to the Australian Biogeographic Region. These species utilize highly variable ecological strategies, with a concomitantly diverse range of dental morphologies and cranial geometries. For instance, there is considerable variation in the degree of development of the plagiaulacoid lower third premolars, reduction in size and number of cheek teeth, and conical to chisel-shaped lower procumbent incisors with variably present post-incisor diastemata. This morphological diversity is interesting in its own right, but also presents a unique opportunity to investigate a largely unrecognized case of marsupial-placental convergence, as the earliest ("plesiadapiform") primates show many general and detailed morphological similarities with these possums. To characterize the myology and occlusal forces correlated with the above-mentioned hard anatomy, the dissections of four possum taxa are reported here. The sampled genera include *Acrobates*, *Petaurus*, *Trichosurus*, and *Phalanger*, representing the range of body sizes and foraging modes found in this suborder. The muscles of mastication were resected and then chemically dissected to analyze the distribution of skeletal muscle fiber lengths in each discrete muscle belly. This information was used to estimate Physiological Cross Sectional Area (PCSA) and to test for adaptation for wide gape. The attachments, orientations, and lever arms corresponding to the major jaw adductor groups were defined using photographs of dried specimens, and estimates of bite force and joint reaction force were calculated using simple lever mechanics. Results of this project include the finding of a stark divergence in the relative size of the temporalis group between *Acrobates* and *Petaurus*, two otherwise similar small, gliding possums; and the lack of adaptation for wide, muscularly-limited gape in these same taxa.

Secondary adaptation to aquatic life (AQU)

POS2-128 4:30 pm

Ontogenetic development and intraspecific variability of bone microstructure in the king penguin *Aptenodytes patagonicus*: considerations for paleoecological inferences in Sphenisciformes.

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Abstract: Birds have colonized various ecological niches during their evolutionary history and several lineages adapted to the aquatic environment. Numerous papers focused on the long bone microstructure in aquatic birds. Some studies attempted to reconstruct the evolution of aquatic adaptations in a given lineage, based on the bone microstructure of fossil taxa, without referring to a comparative set of modern taxa. These works often drew ecological deductions from one or two bones of a single specimen. However, the ecological signal contained in bone microstructure is known to vary between skeletal elements. Bone microstructure can also be affected by other factors (besides lifestyle), which have been overlooked in lifestyle inferences. Studies on intraspecific variability and bone microstructural development during ontogenesis are rare in the field of comparative bone histology, although such works are essential for the choice of standard parameters for bone description and for drawing rigorous paleobiological inferences. We sampled all major limb bones of hatching, juvenile and adult specimens of the king penguin *Aptenodytes patagonicus*, in order to assess the extent and the causes of limb bone microstructural variability during ontogenesis. This species is ideal for such study because factors that could affect its bone microstructure (a unique growth cycle and distinct locomotor behaviors between juveniles and adults) are well documented. Histomorphometric observations reveal that bone microstructure vary greatly during ontogenesis. Limb bones undergo an intense remodeling episode during the juvenile molt. Moreover, these bones show different developmental patterns during the individual's life. Finally, for a given long bone, even adult specimens exhibit variability in compactness. This work is intended to constitute a comparative basis for the histological study of extinct Sphenisciformes, and thus provide a better framework for paleobiological reconstructions.

POS2-130 4:30 pm

Biomechanical and physiological signals in the vascular system of Squamata in the context of secondary adaptation to an aquatic life.

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Abstract: Bone vascularization has been shown to be an important marker for bone mechanical properties and animal growth. Consequently, different inner vascular structures should be observed in animals with distinct physiologies and ecologies. Major changes in vascularization are thus supposed to occur in the context of secondary adaptation to an aquatic life, where various habitat, swimming modes, gravity control strategies and physiologies occur. For such a study, it was of great interest to focus on ectotherms. We decided to analyze squamates. Indeed, this group displays several forms that are adapted to a marine habitat (e.g., marine snakes, "dolichosaurs", mosasauroids) and also illustrates various steps in a progressive transition from terrestrial to aquatic lifestyles. As this lineage includes snakes, we focused our research on vertebrae. We used synchrotron microtomography in order to qualify and quantify precisely their vascular network in three dimensions. Clear variations in the vascular organization (e.g., vascular canal diameter, volume, orientation, connectivity) show that distinct locomotion mechanisms affect the vascularity of vertebral centra. Differences in vascular orientation are clearly observed: terrestrial forms have no or a

few radial vascular canals, aquatic forms present a dense radial organization with anastomoses, and aquatic mosasauroids forms have a more longitudinal organization. These results confirm previous (2D) histological observations, but deliver a more precise quantification of the canal structure in 3D. This study establishes for the first time the link between vascularization and locomotion and physiology in the context of secondary adaptation to an aquatic life.

POS2-132 4:30 pm

Dietary transitions and the evolutionary origin of whales: 3D texture analysis of tooth microwear in archaeocetes and extant analogues.

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Abstract: The origin of whales is associated with a significant dietary transition: from terrestrial omnivory/herbivory to aquatic piscivory/carnivory. This occurred between the evolution of the earliest Pakicetidae (early Eocene ca. 52.5 Ma) and the emergence of crown group whales near the Eocene/Oligocene boundary (ca. 33.7 Ma). Morphological and isotope analyses suggest an extensive mid-late Eocene semi-aquatic stem lineage, preceding obligate aquatic lifestyles in later stem clades, and transition to the marine realm within protocetids. However, neither morphological nor isotope data reveal direct evidence of trophic ecology. We have employed a novel approach - quantitative 3D-microtextural analysis - to provide new tests of hypotheses of ecological transitions in whale evolution. This technique, developed from engineering approaches to surface metrology, uses quantification of tooth surface textures to provide direct evidence of tooth-food interactions and diet. It is a well-established technique for dietary analysis in terrestrial mammals, but has not previously been applied to aquatic mammals. Our statistical comparison and multivariate analysis of microtextures in extant pinnipeds and odontocetes provides the first evidence that tooth microtextures vary with diet in modern aquatic mammals. Applying this relationship to archaeocetes, we find evidence of clear differences in diet which are not correlated with phylogenetic position. These results paint a more complex picture of dietary evolution in archaeocete whales than previously hypothesised.

POS2-134 4:30 pm

Water as a driver of evolution: the example of aquatic snakes.

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Abstract: Evolutionary trajectories are often biased by development and historical factors. However, the environment can also impose constraints on the evolutionary trajectories of organisms leading to convergence of morphology in similar ecological contexts. For example, the physical properties of the medium an animal moves through can impose strong constraints. Aquatic animals are principally faced with drag-related forces impeding movement. These hydrodynamic constraints are strong and have resulted in the independent evolution of suction feeding in nearly all groups of secondarily aquatic tetrapods. Despite the fact that snakes cannot use suction, they have invaded the aquatic milieu many times independently. Here we test whether the aquatic environment has constrained head shape evolution in snakes and converge on shapes predicted by biomechanical models. Our results show that aquatic snakes partially conform to our predictions and have a narrower anterior part of the head and dorsally positioned eyes and nostrils. This morphology is observed irrespective of the phylogenetic relationships among species suggesting that the aquatic environment does indeed drive the evolution of head shape in snakes.

Xenarthra (XEN)

POS2-136 4:30 pm

Advantages and limitations in the use of extant xenarthrans (Mammalia) as morphological analogues for paleobiological reconstruction.

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Abstract: A characteristic feature of the clade Xenarthra is the enormous disparity between extant and extinct diversity, with living species representing a severely restricted sample of the total diversity achieved by the group. The morphology of an organism is restricted or moderated by its evolutionary history and thus is not solely a product of a particular habitat. Given the constraints imposed by shared history, the extant representatives of the three major groups of xenarthrans provide a valuable basis for paleobiological inference. However, when structures and functions are unique to or autapomorphies of a fossil organism, patterns extracted from a phylogenetic framework do not necessarily lead to paleobiologically useful information. Many extinct xenarthrans are morphologically different from their living relatives to such a degree as to suggest they had very different modes of life; compare, for example, fossil sloths to living tree sloths and glyptodonts to armadillos. For such cases, the extinct forms have no modern analogues and the application of an overly straightforward actualistic approach may produce nonsensical reconstructions. For instance, due to the unusual lateral expansion of the femur, the use of a single allometric equation based on the transverse diameter of the femur -a measurement used extensively in estimating body mass in mammals- produces an estimate of 98 tons for the elephant-sized ground sloth *Megatherium*. This, however, does not invalidate actualism and the use of analogues. Rather, it requires their extension into the application of other, such as mechanical, approaches that address form-function relationships but are not necessarily based on already-known biological comparators.

POS2-138 4:30 pm

An isolated petrosal of the pampathere *Holmesina floridans* (Mammalia, Xenarthra, Cingulata) from the Blancan NALMA of Florida.

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Abstract: Work on the cranial anatomy of the pampathere *Holmesina floridans*, known primarily from abundant remains recovered from the Haile 7G quarry of north central Florida (late Blanca NALMA, Pliocene), has revealed an extremely well-preserved isolated left petrosal from a subadult individual (UF 248500). This specimen is the first isolated pampathere petrosal to be formally described. Comparisons to the extant armadillos *Dasypus* and *Euphractus* and the Miocene armadillo *Proeutatus*, the latter considered the sister taxon of pampatheres and glyptodonts, reveals a number of distinctive features. The fenestra cochleae is extremely compressed dorsoventrally, its width nearly three and a half times greater than its depth, whereas in other cingulates it is more ovate, its width no more than twice its depth. The crista interfenestralis bears a bony bridge connecting it laterally to the medial side of the tympanohyal, forming a partial floor to the facial sulcus. The promontorium bears both a narrow, spine-like anteromedial process, plus a rounded boss on its lateral surface that likely marks the origination of the m. tensor tympani. The internal acoustic meatus is deeply recessed, situated very near the ventral margins of the intracranial exposure, and its two primary divisions, the foramen acusticum superius and inferius, are separated by a very narrow, sharp ridge. There are several features linking *Proeutatus* to *Holmesina* exclusive of the living taxa, including a mediolaterally broadened crista interfenestralis and an elongated anteromedial process of the promontorium, that suggest the petrosal may prove an informative source of systematic characters among cingulates, and perhaps within pampatheres themselves.

POS2-140 4:30 pm

Pedolateralization, foot anatomy, and weight support in extinct sloths (Xenarthra, Folivora).

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Abstract: Both extant and extinct sloths show a peculiar pes configuration defined as pedolateral or invertigrade, which is present in different degrees throughout the clade. Pedolaterality was primarily described for sloths by Owen in the XIX century and later revised and discussed by Hirschfeld in 1985. Some of their features (medial rotation of the foot arch and caudal extension of calcanei tuber, for instance) can be recognized also in the non-pedolateral anteaters (Xenarthra, Vermilingua), resulting in a conflictive anatomical distinction. Morphological criteria for pedolaterality definition are discussed herein, as well as the trajectory of body weight force distributed to the pes through the talo-crural joint and its relation with weight-bearing, and the degree of pedolaterality. Miocene Santacrucian (~ 17-19 Ma) sloths showed a pentadactyl, conservative pes with slightly pronounced pedolaterality traits, where the trajectory of the weight fall within the weight-bearing surface conformed by the calcaneal tuber, the metapodials IV and V, and the ungual phalanxes. Such a configuration is kept until the Pleistocene by the Megalonychidae. On the other hand, among Pleistocene sloths (Megatheriidae and Mylodontidae) the pedes showed an extreme reduction of inner digits. In these more pedolateral morphs, the body rested exclusively on weight-bearing surfaces conformed by the calcaneum and metatarsals IV and V, almost without the participation of digits II and III (the only ones carrying functional ungual phalanxes). The weight trajectory would be inner to these foot rest surfaces, resulting in a mechanically unstable configuration, especially critical for these giant-sized sloths. As a result it is proposed the presence of a medial plantar pad that could expand the weight-bearing surface allowing a more direct and efficient weight distribution and support, analogue to the condition observed in modern proboscideans.

POS2-142 4:30 pm

Species delimitation and morphological variation in the skull of long-nosed armadillos (*Dasypus*).

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Abstract: With their Pan-American distribution, long-nosed armadillos (genus *Dasypus*) constitute an understudied model for Neotropical biogeography and the Great American Biotic Interchange. This genus comprises seven described species with distributions covering much of South America, Central America, and parts of North America. The nine-banded armadillo (*D. novemcinctus*) has the widest distribution ranging from Northern Argentina to the South-Eastern US where it became invasive less than 200 years ago. This ubiquitous species occurs in a broad diversity of habitats such as savannahs, dry forests, and rain forests. Nine-banded armadillos therefore provide an ideal model to explore the effects of climatic and biogeographic events on morphological diversity at a continental scale. For that matter, we used an integrative taxonomy approach coupling classical comparative anatomy methods with cutting-edge 3D-geometric morphometric techniques. Alongside treatment of traditional diagnostic characters,

some internal characters that could be reliably and repeatedly assessed were chosen, as they seemed to vary significantly in the specimens sampled, and 3D reconstructions were performed. Our preliminary analysis of internal structures successfully retrieved a taxonomic differentiation between *Dasypus* species and a geographical differentiation within *D. novemcinctus*. Geometric morphometric data were collected for a sample of 150 specimens using μ CT-scans, and results were contrasted with new molecular-based species delimitations. Our study first revealed strong phylogenetic and geographical imprints on the cranial and mandibular morphological traits. We also made use of the morphological data to evaluate variation in skull morphology as a result of ecological factors. These data constitute a necessary step towards understanding the exceptional adaptive potential of this species distributed across a wide diversity of habitats and environments across the continent.

POS2-144 4:30 pm

Feeding ecology in Oligocene mylodontoid sloths (Mammalia, Xenarthra) as revealed by orthodontine microwear analysis.

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Abstract: Recently, dental microwear analysis has been successfully employed to xenarthran teeth. Here we present new data on use wear features on 17 molariforms of *Orophodon hapaloides* and *Octodontotherium grande*. These taxa count among the earliest sloths and are known from the Patagonian locality La Flecha (Deseadan SALMA, late Oligocene). Modern phylogenetic analyses classify *Octodontotherium* and *Orophodon* within Mylodontoidea with whom they share lobate cheek teeth with an outer layer of cementum and a thick layer of orthodontine but are different in showing an only narrow vasodontine center. Four representative target areas of 0.01 mm^2 were analyzed on the orthodontine surface of each tooth under incident light on a stereomicroscope at a magnification of 70x. Four quantitative (number of small pits, number of large pits, number of fine scratches, number of coarse scratches) and two qualitative parameters (presence/absence of gouges and puncture pits) were examined by only one observer (DCK). Results were compared to extant sloths (*Bradypus*, *Choloepus*) and published data from fossil sloths (*Acratocnus*, *Megalonyx*, *Megatherium*, *Thinobadistes*). Numbers of small and large pits, of fine scratches as well as presence of puncture pits are very similar in *Octodontotherium* and *Orophodon*, but the latter shows more coarse scratches (not significantly different). Microwear features suggest that both taxa fed on plant material with low to moderate intrinsic toughness with both taxa also including tougher food items (e.g. fruit) in their diet. Frequent gouging of the tooth surfaces also suggests that extrinsic factors, such as possible heavy intake of abrasive grit, may be influencing tooth wear. These interpretations support the reconstruction of (1) Deseadan environments as open habitats with spreading savannas/grasslands and (b) both taxa as wide-muzzled bulk feeders at ground level.

POS2-146 4:30 pm

Tarsal morphology and weight support in the evolution of glyptodonts (Mammalia, Xenarthra, Cingulata).

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Abstract: Glyptodonts (middle Eocene-early Holocene) are a group of herbivorous placental mammals that evolved in America, characterized by a rigid dorsal carapace and elephantine hind-feet, among other features. Several authors considered that the relationships between the tarsal elements in the small Miocene taxa and in the larger Pleistocene glyptodonts were different. A reexamination of the tarsal joint pattern of glyptodonts, their sister-group pampatheres, and armadillos is presented here. Among glyptodonts, the tarsal bones of the Miocene *Propalaeohoplophorus* (~80 kg), and the Pleistocene *Glyptodon* (~800-2000 kg), *Neosclerocalyptus* (~600 kg), *Doedicurus* (~1500 kg) and *Panochthus* (~1000 kg) share a unique articulation pattern, in which the distal facet of the lateral cuneiform articulates with both metatarsals III and IV. This pattern allowed an interlocking of the mid-tarsal segment of the foot, and would enable a more widespread distribution of the weight loads from astragalus to I-IV digits. In the Pleistocene pampatheres *Holmesina* (~180 kg), extinct armadillos *Proeutatus* (Miocene; ~15 kg) and *Eutatus* (Pleistocene; ~50 kg), and extant *Chaetophractus* (~4 kg), *Priodontes* (~45 kg) and *Dasypus* (~2.5 kg), the distal facet of the lateral cuneiform articulates only with metatarsal III, allowing distribution of the weight load from talus to digits I-III. The glyptodont pattern showed variation throughout the clade, concurrent with the increase in body size of this group from Miocene to Pleistocene. The articular contact between the ectocuneiform and the metatarsal IV increases from 1/5 of the distal facet of the cuneiform in the smallest Miocene taxon, to 1/2 of the facet in larger Pleistocene genera. Although it seems clear that the role of this articulation pattern was not to support a large body size in Miocene glyptodonts, it enabled reaching giant body sizes throughout the evolution of the group.

POS2-148 4:30 pm

3D finite element analysis of lower jaws in glyptodonts.

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Abstract: Finite element analysis (FEA) has proved to be a powerful tool for biomechanical studies in comparative frameworks. In the case of xenarthrans, the analysis of the mandible of extant and extinct armadillos showed a correlation of the stress patterns with diet preferences and variability. In this work we analyze the mandible of 3 glyptodonts, two Pleistocene giants *Glyptodon* and *Panochthus*, and the smaller Miocene *Pseudoplohophorus*, to evaluate the diet preferences inferred by ecomorphological studies. Their peculiar jaw anatomy, with the toothrow located medially to the ascending ramus, renders most morphometric analyses nearly inviable. In order to comprehend their complete anatomy, the mandibles and skulls were 3D digitized. The musculature modeled to determine the vector forces in the FEA models includes temporalis, masseter and pterygoid. A transformation was applied to the FEA models to render the forces applied comparable. Four cases were evaluated: A, vertical constrain in the anteriormost tooth; B, vertical constrain in the posteriormost tooth; C, horizontal constrain in the posteriormost tooth and D, vertical and a horizontal constrain in the posteriormost tooth. In all glyptodonts, case B generated the highest amount of stress in the occlusal surface. This is congruent with the proposed propalinal mastication at the posteriormost tooth due to the telescopic migration of the mandible. Regarding cases A, C and D, highest amount of stresses are located in the ascending ramus and the posteriormost part of the symphysis. According to the mechanical advantage value, *Panochthus* has the highest bite force values, followed by *Glyptodon* and *Pseudoplohophorus*. This could be congruent with the proposed bulk-feeding diet for *Panochthus* and selective-feeding diet for *Pseudoplohophorus*, while *Glyptodon* could be intermediate between these.

POS2-150 4:30 pm

Inner and middle ear 3D reconstruction of the extinct giant sloth *Lestodon armatus*.

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Abstract: Here we describe the bony labyrinth and middle ear ossicles of the giant ground sloth *Lestodon armatus* from the Arroyo del Vizcaíno site (AdV), through CT scans and structured light scanning, and compare it with those of extant and extinct sloths. Recent descriptions of the inner ear of *Megatherium americanum* and extant sloths have shown that semicircular canals (SCs) morphology of the giant ground sloth departs from the morphology of extant sloths. The SCs of *Lestodon* are thin and larger than in extant sloths, similar to *Megatherium*; the lateral and posterior canals do not form a secondary crus commune. With an average radius of curvature of 3.8 mm and a body mass estimation of 4500 kg, *Lestodon* shows levels of agility similar to *Megatherium*, that is, higher than extant sloths. A preliminary analysis of the inner ear of the extinct ground sloth *Catonyx cuvieri* shows that the morphology of the SC is very similar to that of *Lestodon* and *Megatherium*. In a phylogenetical context, this corroborates the convergent size reduction of the SCs in both extant sloth taxa due to the parallel acquisition of slow and suspensory locomotion. Several middle ear bones of *Lestodon* has been recovered from the AdV site. A complete chain of middle ear ossicles, malleus, incus and stapes, has been recovered from the right side of one skull. They have an excellent preservation, keeping even the most delicate structures as the manubrium mallei throughout its length and the lenticular process of the incus, a very small and delicate structure that articulates with the stapes. The ossicles were digitized using a structured light scanner. The digital models were used to reconstruct the life position in the middle ear and subsequently to perform finite element analysis and physical models to assess the hearing capabilities.