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EDITORIAL

This supplement of the Journal of Morphology presents over 750 abstracts of contributions to the 12th International Congress of Vertebrate Morphology, held July 21 – 25, 2019 in Prague, Czech Republic. The Journal of Morphology and the International Congress of Vertebrate Morphology have a long and fruitful relationship, supporting and promoting animal morphology – the roots of that relationship date back to 1983, when Carl Gans, at that time editor of the Journal of Morphology, promoted establishing the first Congress of Vertebrate Morphology in Giessen, Germany. We are proud and delighted to continue this relationship now using modern online publishing tools, allowing free access to all those enthusiastic about morphology.

Morphology as science is as diverse as life is and the topics of the conference range from macroscopic studies to ultrastructure, and from experimental research in functional morphology to comparative studies exploring the historical perspectives conserved in fossils. Morphology indeed provides two kinds of explanations in biology, functional explanations based on experiments, and historical / evolutionary explanations based on comparative studies. The diversity of topics and explanations provided are integrated by the simple fact that morphology is central to all biological science because it analyzes the structures that ultimately carry the functions of life. The diversity of topics is orchestrated by a breathtaking array of methods. This year's conference, in particular, witnesses a surge of microCT-scanning, 3D-reconstruction and 3D-morphometrics as a means for understanding complex morphologies. Technological advances in non-destructive imaging methods, such as microCT, have been and are undoubtedly beneficial for the field of morphology. The challenge is not to ignore the limited resolution that microCT offers for small vertebrates, hence potential data loss, nor to neglect the time-consuming, yet rewarding contemplative observations associated to low throughput systems.

From the first conference in 1983 on, the aim of the congress has been to provide a platform for presentation, discussion and exchange of research on vertebrate morphology for the community of morphologists. Over the 36 years of its existence, the congress has continuously grown, from about 300 participants to now over 800 forecasted for the meeting in Prague. The topics cover all aspects of vertebrate morphology, presented in no less than 20 symposia, around 350 contributed talks and close to 200 posters. For delegates from more than 35 countries, ICVM-12 offers the appropriate setting to share knowledge, interpretations and 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.

Matthias Starck
Editor in Chief
Journal of Morphology
Munich, May 2019

Ann Huysseune
Chair Scientific Program Committee
International Congress of Vertebrate Morphology
Ghent, May 2019

NOTE FROM THE PRESIDENT

On behalf of the International Society of Vertebrate Morphologists, I'm delighted to offer some opening words for this abstract volume for the 12th International Congress of Vertebrate Morphology to be held in Prague from 21-25 July 2019. This is an exciting time for the field of vertebrate morphology, as shown by the more than 750 abstracts submitted for ICVM12. This is the largest number of abstracts for any ICVM, breaking our prior records from ICVM6 in Jena and ICVM11 in Washington DC, and demonstrates that vertebrate morphology is a vibrant and growing field worldwide! New methods, technologies and the open data movement are enhancing all the subdisciplines within vertebrate morphology, increasing the scope and influence of our research. For example, the now widespread availability of microCT scanning and open microCT data are enriching nearly all subfields, including vertebrate paleontology, evolutionary developmental biology, functional morphology/biomechanics, and evolutionary morphology most broadly. The grassroots #scanAllFishes and US National Science Foundation funded oVert projects aim to CT scan all of vertebrate diversity and make the data freely available to researchers and the general public. These kinds of projects, and there are many other open data projects in our field, are making vertebrate morphology part of the 'Age of Big Data.' Hand in hand have come new statistical and other comparative methods for handling big data in morphology, enhancing the power of open data to transform our field.

Ever since the first ICVM was held in Giessen in 1983 with about 300 participants, through the formal founding of the International Society of Vertebrate Morphologists during ICVM4 in Chicago in 1994, and now to ICVM12 with more than 750 scientific presentations, the ICVMs have been important catalysts for innovation and collaboration, and a great time to get together to celebrate all the branches of vertebrate morphology with our colleagues from all over the world. The partnership between the ISVM/ICVM and the *Journal of Morphology* has always been strong, and we thank Editor Matthias Starck for inviting and editing this volume. We are delighted to have this collaboration continue with the publication of the abstracts for ICVM12 here in our esteemed *Journal of Morphology!*

I would like to acknowledge our many colleagues who volunteer their precious time to ISVM and ICVM. The ICVM12 Scientific Program Committee is chaired by Ann Huysseune (Belgium) with generous assistance from SPC members: Colleen Farmer (USA), Daisuke Koyabu (Japan), Kinya Ota (Taiwan), Olga Panagiotopoulou (Australia), Robert Cerny (Czech Republic), Matt Vickaryous (Canada), Tiana Kohlsdorf (Brazil), Anusuya Chinsamy-Turan (South Africa), Casey Holliday (United States), John Nyakatura (Germany) and Emily Rayfield (UK). My fellow ISVM officers are President-Elect Nadia Fröbisch (Germany), Past President Ann Huysseune (Belgium), Secretary Adam Summers (USA), and Treasurer Dominique Adriaens (Belgium). The Elected Members of the ISVM Executive Committee are: Karen Sears (USA), Kinya Ota (Taiwan), Colleen Farmer (USA), Anusuya Chinsamy-Turan (South Africa), Olga Panagiotopoulou (Australia), Ellen Schulz-Kornas (Germany), Daisuke Koyabu (Japan), Emily Rayfield (England), Sharlene Santana (USA), Vera Weisbecker (Australia). Thank-you!

In closing, I'd like to send special thanks to our sponsors and exhibitors for ICVM12: American Association for Anatomy, Company of Biologists, Developmental Dynamics, Gans Fund, Journal of Morphology, Oklahoma State University Center for Health Sciences, Peer Community in Paleontology, PosterSmith, Royal Society Publishing, Zoological Society of Japan, Transmitting Science, and YXLON International.

Elizabeth L. Brainerd
President, ISVM
Rhode Island, May 2019

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Previous editions of the International Congress of Vertebrate Morphology (ICVM)

1. Giessen 1983 (ca. 300 Participants)
2. Wien 1986 (ca. 350 Participants)
3. Antwerp 1989 (ca. 430 Participants)
4. Chicago 1994 (ca. 450 Participants)
5. Bristol 1997 (ca. 450 Participants)
6. Jena 2001 (ca. 700 Participants)
7. Boca Raton 2004 (ca. 470 Participants)
8. Paris 2007 (ca. 600 Participants)
9. Punta del Este 2010 (315 participants)
10. Barcelona 2013 (450 participants)
11. Washington DC 2016 (650 participants)

ABSTRACTS

Plenary lectures

What, if anything, is a Placoderm? New Light on the Origin and Early Evolution of Jawed Vertebrates

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The extant gnathostome clades, Chondrichthyes (cartilaginous fishes) and Osteichthyes (bony fishes and tetrapods), have substantially contrasting morphological and histological character sets. It is impossible to polarize most of these character differences by outgroup comparison with cyclostomes (hagfishes and lampreys), so evidence from fossils becomes central to understanding the origin of jawed vertebrates and the chondrichthyan-osteichthyan divergence. Here, I review how new fossil discoveries, and the application of phase contrast synchrotron microtomography (PPC-SRμCT) to fossil imaging at morphological and histological scales, are overturning established perceptions of the early fossil record of vertebrates. I will focus on the significance of the 'placoderms', jawed armored fishes of the Silurian and Devonian periods. Traditionally these have been regarded as a clade, the sister group to osteichthyans + chondrichthyans. Like the osteichthyans they have a dermal skeleton consisting of large bony plates, but this similarity has been dismissed as the product of convergent evolution. Placoderms have also been held to lack true teeth. Consonant with these interpretations, the distinctive features of osteichthyans (including tooth-bearing marginal dermal jawbones) have been regarded as specialized relative to conditions in chondrichthyans. All of these positions are now being overturned: placoderms appear to be a 'grade taxon' paraphyletic to osteichthyans + chondrichthyans, their osteichthyan-like features are homologues not parallellisms, and the phylogenetically most basal forms have marginal tooth-bearing jawbones. Osteichthyans retain more of the primitive gnathostome character complement than chondrichthyans. The early evolution of jawed vertebrates is best understood as a "placoderm-osteichthyan continuum" of gradual change, with chondrichthyans representing a highly divergent offshoot.

Unravelling the Biology of Extinct Animals Using Bone Histology

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The histology of fossil bone permits a direct assessment of various aspects of the biology of extinct vertebrates. Experimental studies on the bones of modern vertebrates show that bone is a plastic tissue that is highly responsive to its environment, and that its histology (or osteohistology) is affected by the rate at which it forms, by biomechanical functioning of the skeletal element within the skeleton, by ontogenetic age of the individual, disease, mineral homeostasis, etc. Thus, comparisons of fossil bone histology with that of modern animals have permitted valuable insight into various aspects of the life history and biology of extinct animals. In this talk, I will provide an overview of the highlights of my research in the field of osteohistology, as well as in science communication. Through case studies I will show how osteohistology has provided insights into the biology of a variety of extinct vertebrates such as the nonmammalian synapsids, dinosaurs (including birds), as well as pterosaurs. More specifically, I will detail how studies of fossil bone histology have allowed us to unravel how extinct animals grew and how their skeletons responded to disease and biomechanical function, as well as how growth patterns of birds evolved. I will also give you a glimpse into the ongoing osteohistology studies being undertaken with my postgraduate students and other collaborators on a wide spectrum of extinct and extant vertebrates to better understand skeletal responses to ecological adaptations, ontogenetic growth, and pathology. Going forward, it is imperative that interdisciplinary research and closely constrained studies of the factors that affect bone growth and biology of modern animals are needed to better understand and interpret fossil vertebrate bone tissues. Furthermore, we also need to be more proactive in communicating our research with the wider public.

Origin and Early Evolution of the Vertebrate Body Plan: Defining the Head in the Embryo

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Vertebrates are characterized by the possession of a well-differentiated cranium, whose evolutionary origin still remains enigmatic. In gnathostome embryos, two sources of mesenchyme contribute to the formation of the cranium: the mesomesenchyme that forms the posterior half of the brain case, or the neurocranium, and the neural crest-derived ectomesenchyme differentiating into the viscerocranium, which supports the pharynx as well as the rostral neurocranium. The ectomesenchyme is formed of cranial neural crest cells that occupy the ventrolateral part of the embryonic head, mirroring the distribution of unsegmented head mesoderm and pharyngeal arches, in contrast to trunk crest cells that are segmentally distributed and defined by somitic segmentation. To reconstruct the evolutionary scenario behind the origin of the cranium, it is necessary to observe the embryos of cyclostomes, the sister group of gnathostomes, to assess the plesiomorphic pattern. Cyclostomes consist of two lineages, lampreys and hagfish, whose anatomical patterns conspicuously differ from each other. By obtaining a series of embryos of a hagfish species, *Eptatretus burgeri*, mid-embryonic stages of cyclostomes were found to show mutually comparable patterns, making it possible to homologize cranial elements in older embryos or adults. With a single nostril and absence of the maxillary process, this cyclostome pattern is not shared by gnathostomes, even if earlier pharyngula embryos show similar patterns of distribution of neural crest cells among the entire vertebrate group. On the other hand, previous embryonic and paleontological studies have suggested that cyclostomes do not possess true trabeculae in the neurocranium. Since the cyclostome cranium likely represents the plesiomorphic state, mesoderm/neural crest distinction in

the cranium is suggested to have originally corresponded to the neuro-/viscerocranium of ancestral vertebrates.

Walking and Chewing Gum at the Same Time: What Comparisons of Feeding and Locomotor Systems Teach us about Musculoskeletal Design

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Traditionally, evolutionary biomechanical studies address diversity between lineages and within functional systems, but recent comparisons of tetrapod feeding and locomotor systems reveal similarities and differences in kinematics and kinetics related to inter-lineage variation in metabolism and motor control, and to inter-system variation in performance criteria. In tetrapod jaws and limb bones, strain magnitude is modulated by varying loading rate, reflecting common mechanisms for modulating skeletal muscle force. Tetrapod feeding and locomotion systems also share patterns of inter-clade differences in kinematic rhythmicity—tachymetabolic tetrapods chew and locomote with less variable cycle durations than bradymetabolic tetrapods—suggesting common underlying sensorimotor mechanisms. In the mammalian feeding system, greater kinematic predictability during chewing protects teeth against wear and breakage. In the locomotor system, greater kinematic predictability in tachymetabolic species is associated with less variable ground reaction forces and lower safety factors in limb bones. Limb joint angular excursions during cyclic locomotion are also larger than jaw joint excursions during chewing. These findings suggest differences in performance criteria between feeding and locomotor systems. Chewing systems are optimized for precise application of force over narrow, controlled, predictable ranges of displacement in order to fracture the substrate, the size and mechanical properties of which are controlled at ingestion and reduced and homogenized by chewing. In contrast, tetrapod limbed locomotor systems are optimized for powerful, energetically efficient application of force over a wider and less predictable range of displacements, the aim being to move the organism at varying speeds relative to a substrate whose geometry and mechanical properties need not become more homogeneous.

Bones, Brains and Babies – Mammalian Evolution through the Lens of Morphological Evo-Devo

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Research on marsupial mammals (kangaroos, koalas, possums, opossums and kin) has traditionally been in the shadow of placental mammals, due to their lower speciosity and limited ecological diversity. However, it is also widely recognized that the unique marsupial trait of altricial birth and extended time in the pouch makes them an ideal model for understanding the drivers and constraints of mammalian evolution, particularly with respect to understanding the influence of developmental traits on mammalian morphological diversity. Exploring the unique marsupial diversity and development has been facilitated by the availability of increasingly sophisticated and cost-effective computation; this particularly includes advanced data acquisition techniques such as microCT and DiceCT soft-tissue imaging as well as (3D) geometric morphometric approaches. My lab uses these methods to trace the evolution of some of the most iconic mammalian traits, based on marsupial evolution. Focus is on three questions: 1) How does mammalian brain macromorphology develop and evolve, and how much may neuroanatomy relate to brain function? 2) How much of the origins of the mammalian middle ear (and possibly other traits) can be recapitulated in marsupial middle ear development? 3) What kind of evo-devo information can be obtained from marsupial (and, for a contrast, rodent) skeletal microevolution? Finally, a case study of 3D-geometric morphometrics of wombat skulls suggests a future direction towards using the traditionally evolution-focused methods of geometric morphometrics in phenome-level conservation management efforts. This research is funded by The Wombat Foundation, Hermon Slade Foundation grant HSF12/8 and Australian Research Council grants DE120102034, DP170103227 and DP140102656.

Symposia

Variation under Domestication: An Organismal and Morphological Perspective – Organizers: Marcelo Sánchez-Villagra, Madeleine Geiger

Variation in the Structure, Expression, and Function of the Runx2 Gene as a Developmental Mechanism for Generating Species-Specific Changes in Jaw Length during Evolution

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A goal of evolutionary developmental biology is to identify genetic, molecular, and cellular mechanisms that underlie morphological diversification. In this context, domestication is especially intriguing since rapid changes in form can arise over a brief timescale. An obvious illustration of this phenomenon involves domestic dogs, which show remarkable variation in skull size and shape. Hypotheses to explain how dog skulls become so diverse include a critical role for the neural crest, which is an embryonic precursor population that generates all bone and cartilage in the face and jaws. Experiments in birds reveal that neural crest cells serve as a potent source of species-specific patterning information via the abilities of certain transcription factors to control the temporal and spatial activation of osteogenic programs. One such transcription factor is Runx2, a master regulator of osteoblast differentiation. RUNX2 contains two translational start sites, a conserved DNA-binding domain, tandem repeats of variable length, as well as C-termini and other exons that are alternatively spliced into multiple isoforms. Modulation of Runx2 gene structure and the assortment of RUNX2 protein isoforms may lead to a range of functions and effects. For example, within the tandem repeat region, the ratio of glutamines to alanines influences RUNX2 transcriptional activity and correlates with facial length in dogs and other mammals. But to what extent and through what mechanisms could the architecture of Runx2 itself govern facial length? We use white Pekin duck (*Anas platyrhynchos*), Japanese quail (*Coturnix japonica*), and chicken (*Gallus gallus*) to test if changes in Runx2 structure and expression underlie the evolution of beak morphology. We find that while Runx2 coding sequence is mostly conserved among these birds, some domains show notable exceptions, which affect transcriptional and cellular activity, differentially regulate target genes, and may contribute to beak length.

Unravelling Phenotypic Evolution during Domestication Using Modern and Archaeological Remains

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Domestication induces profound changes in the morphology of domesticated animals. These human-induced changes can be explored in modern populations but also tracked through time and space by analyzing the numerous and often well preserved archaeological remains of domesticated species. In order to better understand the phenotypic evolution of domestic dogs and pigs we use landmark and sliding-semi landmark based 2D- and 3D-geometric morphometric approaches to quantify the size and shape of teeth, mandible and crania of both recent and ancient specimens. These approaches have allowed us to reassess several key concepts in both evolutionary biology and bio-archaeology, including the extent to which domestic phenotypes are paedomorphic and the exclusive use of size to identify the wild or domestic status of ancient specimens. When phenotypic results are combined with other approaches such as ancient DNA or isotopic analyses, our understanding of the long process of domestication go one step further by revealing, in an unprecedented way, the intimate relationship between humans and these domesticated populations.

Dogs in Motion

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No other species has experienced a higher selection of body mass, body shape, size or skull shape than dogs. Studying effects of domestication is a key to the understanding of character variation and character combination ever since Darwin. In the last 15 years we (many students and coworkers) have studied locomotion and postcranial morphology of more than 400 dogs of 35 different breeds. The presentation will give a summary of these studies. While sagittal plane locomotion is not affected by any of the foregoing mentioned parameters and simply rules by the principle of limbs as inverted, zigzag-shaped pendulum with matched motion of the first and third limb element moving in the highest possible pivot, body shape has a crucial influence on 3D-kinematics. This cannot be analyzed using skin markers but solely with high-speed, biplanar fluoroscopy followed by scientific rotoscoping (see Gatesy et al. 2010, JEZ 313A: 244–261). For example, French bulldogs translate extensive femoral long axis rotation (>30°) into a strong lateral displacement and rotations about the craniocaudal (roll) and the distal- proximal (yaw) axes of the pelvis in order to compensate for a highly abducted hindlimb position from the beginning of stance. 3D-kinematics absolutely reflect the differences in body shape and limb position. Speed types and strength types (according to Chase et al. 2002, PNAS 99: 9930-9935) differ in skull and pelvis shape and in the transverse profile of their long bones (elliptical vs. round), and a difference in ribcage shape (either slim or round in cross-section). Recent breeding strategies show how easy changes can be produced.

Traditional Morphometric Evidence for the Beginning of the Dog Domestication Process during the Early Upper Palaeolithic

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The dog is the only domesticated species that dates from before the origin of agriculture when human populations were living as hunter-gatherers. Traditional morphometric studies and genetic analyses have recently pushed back the antiquity of the dog domestication from the Late Upper Palaeolithic (~15,000 years ago) to the Early Upper Palaeolithic (~36,000 years ago). Some authors question this early dog domestication claiming that the (pre-Last Glacial Maximum) Palaeolithic dogs fall within the morphological range of wild wolves. We evaluate morphological differences between the specimens of four reference groups (Palaeolithic dogs, recent northern dogs, Pleistocene wolves and recent northern wolves). Therefore, we re-analyzed a dataset of canid skulls using between-group principal component analysis and randomized discriminant analyses to assess whether the putative Palaeolithic dogs represent a distinct morphotype or are only a random subsample of wolves by using cross-validated discriminant analyses (DA) based on raw and allometrically size-adjusted measurements. The results of the randomization approach showed that the Palaeolithic dogs substantially differ from 95% of same-sized samples randomly drawn from recent and Pleistocene wolf groups, which indicates that Upper Palaeolithic dogs represent a meaningful canid group with a unique morphology well distinguishable from wolves. In addition, we compare the individual measurements, the size (i.e., geometric mean) and the size-adjusted measurements of each fossil specimen with the mean values of the recent northern wolf and recent northern dog reference groups by calculating the z-score. Our results support the view that the dog domestication process begun as early as the Early Upper Palaeolithic.

Masticatory Muscles and their Internal Architecture Under Domestication: How Do Wolves and Dogs Compare?

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The cranial morphology of domestic dogs (Carnivora: *Canis lupus* forma familiaris) is much more diverse than that of gray wolves. It remains unclear, whether the artificial selection of the dog into more than 300 recognized breeds also had a bearing on the masticatory musculature and its muscle internal architecture. Here, we present an anatomical and histological study on the fiber type composition and muscle spindle density in the masseter and temporalis muscles of wolves and long-snouted dogs of different adult age stages. We hypothesized that wolves compared to dogs had (1) a higher proportion of the slow contracting and enduring type I fibers compared to the fast contracting and fast fatiguing IIM fibers, and (2) a higher amount of muscle spindles which are proprioceptive receptors to detect the contraction state of the muscle. Using immunofluorescence and hematoxylin eosin staining on muscle thin sections we found no significant difference in the muscle fiber type composition and the muscle spindle density neither in wolves and dogs nor between young and old individuals. Yet, both groups showed significant differences between muscle regions; deeper muscle portions contain a higher frequency of slow fibers and muscle spindles, compared to superficial ones. These findings suggest that despite the skull shape diversity even within long snouted dog breeds the masticatory muscle internal architecture is more conserved maintaining a structure in which the superficial muscle portions serve as mobilizers and stabilizers, while the deep muscle portions serve as stabilizers during jaw adduction.

Beyond Pedigree Stereotypes: Defining the Genetic Underpinnings of Contemporary Canine Skull Shapes

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Among pedigree dogs, skeletal form is breed-defining. Size and face shape have evolved rapidly within the last two centuries due to intensive selection and breeding practices of dog fanciers. With advances in genotyping, sequencing, and an annotated genome assembly, researchers have made headway in explaining the genetic underpinnings of the dogs' diversity, however our understanding of complex traits like skeletal size and skull shape remains modest due to the lack of individualized data from contemporary dogs. In an effort to identify the genetic variants that are responsible for the dogs' skeletal diversity, we used geometric morphometrics (GMM) to analyze the computed tomography scans of >560 pedigree and mixed breed canine veterinary patients. Patients enrolled in our ongoing study are genotyped by array or resequencing, providing paired data from which we conduct genome-wide association and fine mapping studies to determine genetic causality. Our approach identified a retrotransposon (LINE) insertion into the SMOC2 gene as the putatively causal variant responsible for canine brachycephaly. The retrotransposon disrupts SMOC2 transcription and presumably its function. Through phenotypic modelling, we showed that the variant explains 38% of face length. Since this study we identified additional genetic variants that begin to explain the remaining 62% of face length variation. Through contrast enhancements that enable segmentation of soft tissue, we observe changes within the brain that may explain the surrounding shape of the cranial vault. Finally, to maximize the utility of our dataset, we explore the feasibility of "imputing" missing morphology information using partial scan information. Application of GMM to diagnostic imaging data enables quantitative trait mapping across this uniquely diverse species. With the recruitment of more dogs, we aim to define the molecular variants that fanciers unknowingly selected to achieve the aesthetics observable in modern dogs.

Artificial Selection as a Tool for Limb Evo-devo

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Evolutionary developmental biology, or evo-devo, has provided important insights into the role of development in the evolution of vertebrate morphological diversity. To date, however, vertebrate evo-devo has focused largely on macroevolutionary patterns and processes, e.g., defining the developmental basis of evolutionary novelties (e.g., feathers), major evolutionary transitions (e.g., fins to limbs), and extreme morphologies (e.g., bat vs mouse limbs). In contrast, much less is known regarding relationships between development and phenotypic variation *within* species, despite the latter's key role in morphological evolution. This knowledge gap is particularly salient above the genomic level, i.e., at later cell and tissue developmental processes. Artificial selection is a useful yet underutilized tool to probe these developmental processes, and to understand how their evolution biases morphological change. Over 20 generations of selective breeding, our lab created Longshanks, a mouse population in which tibia length increased by 15% compared to random-bred wildtype mice, but body mass remained unchanged. Here, we show how the Longshanks model can be used to address three key topics in vertebrate limb skeletal evolution: (1) the developmental timing of morphological variation, (2) the cell and molecular basis of intraspecific variation in limb bone length, and (3) the impact of tibia selection on correlated evolution of the skeletal system. Our work suggests that heritable phenotypic variation in tibia length originates early in ontogeny, likely by modulating the size of cell populations that give rise to future limb elements. Moreover, selection on tibia length caused systemic changes in bone shape and structure in Longshanks, some with potentially maladaptive consequences with respect to bone strength. These studies illustrate the power of selective breeding for understanding micro- and macroevolution of vertebrate limb diversity.

The Logic of Domesticated Mammals and Birds

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Old and new data show the contribution of a developmental perspective to morphological diversification associated with tameness, domestication and selective breeding – mirroring ideas of the 1989 paper of Pere Alberch on monsters (Alberch, 1989, Geobios, Memoir Special 12: 21–57). Experimental studies of domestication (on rats, on foxes and on mice) have provided insights into the association and the modularity of traits; the role of the neural crest as a driver of such association has been hypothesized. The latter could be relevant for the origin of many features of our own species (cranial feminization, brain size changes). However, it remains a challenge to find associations between neural crest developmental changes and adult morphology. Less fundamental but nevertheless significant advances can be achieved with geometric approaches to quantify developmental trajectories and morphological changes. Recent studies on postnatal growth and diversity of skulls of mammals and birds emphasize the relevance of different kinds of developmental repatterning (neomorphism, paedomorphism) and how some modules (neural crest-derived bones) diversify more than others. Size changes are important in domestication and this alone can explain the apparent differences in shape of some organs (e.g., inner ear of dogs). There is phylogenetic signal in the morphological changes that occur in domestication– as for example in brain size. The domestication syndrome as commonly defined applies for canids and not to all mammals equally; segregation of traits after selective breeding circumvent patterns canalized by development. Life history changes associated with domestication reflect much plasticity but one that is not random and universal, with some traits being highly conserved (e.g., gestation length). This affects also the tempo of morphological change, highly variable across species and organ systems and phases of domestication. Many of the above patterns mirror those reported for mammals in islands and in captivity.

Allometric Evolution on Short Time Scales

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Domestication has resulted in an extensive suite of behavioral and phenotypic modifications to wild animals. The ontogenetic processes underlying the striking phenotypic impacts of domestication remain poorly understood. Modifications to patterns of ontogenetic allometry have been shown to affect both the magnitude and mode of morphological change in several clades, reflecting potential pathways for increasing morphological disparity. The framework of 'allometric space', a multivariate morphospace in which the allometric trajectory of a species is represented by a single point, can serve to integrate the studies of ontogeny and disparity. Here, allometric space is used to illuminate understanding of the patterning and magnitude of trajectory modifications underlying domestication across mammals. The case study of domestication, which has occurred independently among unrelated groups, is used to assess similarities and differences in growth-related impacts on disparity and explore their potential basis. Ontogenetic allometric trajectories for 12 pairs of wild and domestic mammals were examined using skull growth data for 1070 specimens, including representatives from all lineages in which domestication has occurred. Domestication has modified postnatal ontogenetic allometric trajectories in mammals and has generated disparity, achieved through lengthening of trajectory slopes and alteration to slope angles. Allometric disparity was similar for domestic forms compared to their wild relatives, whereas the magnitude of dispersion along allometric vectors differed between precocial mammals and altricial mammals, underscoring the importance of life history and shared evolutionary history in patterns of ontogenetic variation. The results verify the importance of scaling in the morphological changes associated with domestication. The response to domestication for all measured trajectory parameters was variable across species, suggesting multiple pathways of change.

Niche Construction, Epigenetics, and the Extended Evolutionary Synthesis: Uncovering the Links between Genes, Development, Form, Function, Ecology and Evolution, and Implications for Vertebrate Morphology – Organizers: Rui Diogo, Virginia Abdala

The Extended Synthesis on Avian Evolution

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Studies on bird evolution played an important role in the building of the conceptual framework of the Modern Synthesis (MS). Avian systematics provided key data for understanding of geographical speciation and adaptive radiations, and the emergence of ethology was largely based on ornithological studies, helping the MS to expand towards ecological and behavioral sciences, respectively. In the last decade, proponents of an extended evolutionary synthesis (EES) challenged the ability of the MS to accommodate new insights, and advocated the necessity of an alternative conceptual framework to understand the evolutionary process. We argue that the current understanding of avian evolution makes a strong point in favor of the EES. Concepts such as homeotic transformation, heterochrony, developmental constraints, and extended inheritance are currently part of the mainstream view on avian evolution, demanding an expanded conceptual framework for the evolutionary theory.

Evolution Driven by Organismal Behavior - A Unifying View of Life, Development, Evolution, Function, Form, Mismatches and Trends

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It is a puzzling paradox that eco-morphological mismatches occur so frequently in an evolutionary process that often leads to macroevolutionary trends and in which organisms are said to be always 'adapted' for the habitats they inhabit. Here, I present a new framework to address this paradox: organisms themselves, in particular their behavioral choices and persistence, are the major active players of evolution. Within this framework, internal factors can both decrease and increase plasticity/hidden variation and therefore, together with epigenetic factors influenced by the external environment, can allow organisms to shift their behavior, e.g., as a response to environmental changes. Importantly, due to behavioral persistence related to behavioral/ecological inheritance, organisms as diverse as bacteria, plants and animals help to construct their own niches, being crucial to direct evolution. Darwinian natural (external) selection then comes into play as a secondary

- but still crucial - player, i.e., due to organismal behavioral persistence the random mutations/epigenetic factors that happen to be advantageous within the niches constructed by the organisms will be selected, further directing evolution and increasing the match between behavior, phenotype, and environment. This process can extend for long periods of time, leading to macroevolutionary trends and further increasing this match, potentially resulting in successful phenotypic overspecialization. However, behavioral persistence, loss of plasticity due to natural selection, genetic drift, overspecialization, and internal constraints can often make it difficult for the organisms to respond behaviorally and/or anatomically to new environmental changes, resulting in potential mismatches between behavior, ecology and form, and eventually in extinction. This new framework bridges the gap between ideas of Aristotle, internalism *vs* externalism, Cuvier's *vs* Geoffroy's form and function, Darwinism and Lamarckism, Baldwin, Waddington and Goldschmidt, and current Evo-Devo.

Evolution of Cetacean Backbone in Light of Phylogenetic and Ecological Constraints

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With approximately 90 living species, whales, dolphins and porpoises represent the most diverse clade of extant marine tetrapods. This high level of taxonomic diversity has been often related to ocean restructuring that resulted in an explosive radiation of oceanic dolphins within the past 10 Ma. However, this hypothesis does not entirely explain how organisms have faced environmental constraints, suggesting other factors could also explain this burst of diversification. In marine taxa such as sharks and ichthyosaurs, morphological variations have been linked to several life-styles, which have sustained their diversification in different adaptive zones. The aim of our study is to establish a relationship between the morphology of the axial skeleton of cetaceans, their ecology and their diversification. By combining the most extensive morphological dataset describing the axial skeleton of 73 cetacean species with cutting-edge phylogenetic comparative methods, we demonstrate that extant cetaceans have followed two distinct evolutionary pathways in relation to their ecology. Most oceanic species evolved towards an increased body size leading to gigantism in baleen whales. Interestingly, dolphins have evolved another way. While riverine and coastal species exhibit a small body size, lengthened vertebrae and a low vertebral count, small oceanic dolphins show an extremely high number of short vertebrae. We discuss how these modifications have operated as key innovations that contributed to the explosive radiation of dolphins.

Evolutionary Teratology: Developmental Anomalies in Evolution – Principles and Diagnoses from Penguins (Aves) and Non-avian Theropod Dinosaurs

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Evolutionary teratology recognizes the results of developmental anomalies, quantitative and qualitative, as an integral part of evolutionary phenotypes. Based on comparative anatomy and the evo-devo connection, the concept dissociates the production mechanisms (development) from validation and propagation processes (selection, speciation). As such, it allows an objective analysis of structures without the adaptationist bias. Case-by-case, hypotheses are established on the potential developmental mechanisms implied. The subsequent functional and use consequences are then investigated (neutral, contribution to adaptation, compensation through other variations). Established by phylogenetic and ancestral comparisons, diagnoses are detailed by a nomenclature derived from systems used in human medicine. Evolutionary teratologies addressed here as examples mainly concern 1) the cervical homeoses of penguins (Sphenisciformes) and 2) the drastic forelimb shortening (micromelia), associated or not with manual anomalies, in non-avian theropod dinosaurs – Ceratosauria, Tyrannosauridae, Allosauroidea and Alvarezsauria. There is also a secondary diagnostic level: growth teratology. It is expressed after birth, differentiating the adult and the juvenile states. This is the case with a type of cervical homeoses (some Sphenisciformes) and the anodontia of *Limusaurus* (Ceratosauria), i.e., the complete loss of teeth. Evolutionary teratology is part of the conceptual line of Etienne Geoffroy Saint-Hilaire and his son Isidore, the main founders of teratology, who suggested that anomalies can produce new species. The contemporary approach aims to encompass anomalies as a whole, beyond the exceptional status of other more specific historical contributions (Goldschmidt’s hopeful monster). In addition to the theoretical epistemological implications, evolutionary teratology can be seen as a tool against intelligent design and the creationist ideology.

Function Loss and Vestiges as Enablers of Adaptive Innovation

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The evolutionary consequences of losing function are often discussed only in terms of reduction and loss of structures. However, in some cases, a once vestigial organ has evolved into a complex new adaptation. Reduced structures (vestiges) accumulate neutral variation and may undergo radical morphological innovation, with increased chances of new functional specialization. Here, we review several examples from vertebrate evolution, including the evolution of wings and an opposable hallux in theropods; the evolution of the caecilian tentacle from extraocular structures of the reduced eye; the evolution of projectile tongues in lungless plethodontid salamanders; and the evolution of the tactile star of the star-nosed mole. In all cases, loss of function and reduction arguably preceded and enabled the origin of new functional specialization, which is an important difference from typical scenarios of exaptation. "Backup" from another functionally redundant structure (such as a serial homologue) is not a requisite: if present, loss of function still precedes new specialization (rather than switching directly to another function). In some cases, a new functional specialization did not occur in the vestige itself, but in functionally related structures that performed an additional pre-existing function. Far from producing evolutionary dead-ends, the loss of a major function can remove significant constraints between primitive and new functional specializations, providing a unique potential for evolutionary innovation and adaptive radiation. Research funded by grant Anillo ACT172099, Conicyt, Government of Chile.

Recent Advances in Chondrocranium Research – Organizer: Ingmar Werneburg

Fish Chondrocrania: a Mechanically Functional System or Just a Template for Bone?

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As in any vertebrate, the first Anlage of a fish skeleton starts with a cartilaginous template, against which bones gradually start to be formed. Cartilage provides a topographical template for dermal bones or a developmental precursor where chondrocytes get replaced by bone forming cells. As cartilage gradually disappears, the chondrocranium basically seems to be not much more than a template for the bony skull. Yet, the initiation of functions related to feeding and respiration mainly involve cartilaginous elements, onto which muscles start to attach and act. As larval fish initiate feeding through suction, this musculoskeletal activity is crucial to successfully make the transition to first feeding. Yet, the earliest bones enclose the gill cavity or bear teeth, suggesting an important functional role during respiration and the transition towards first feeding. Still, the first ossifications are only flimsy bones bordering the cartilage, suggesting a negligible role in musculoskeletal activity during early larval stages. To test the hypothesis that these bones at first feeding have a limited role in structurally reinforcing the chondrocranium during feeding, we quantified the contribution of the early dentary in mechanically supporting Meckel's cartilage in Japanese eel preleptocephalus larvae (5 and 60 dph) during biting. Additionally, we tested the mechanical performance of the peculiar larval teeth during biting, which are not supported by bone but are directly connected to the chondrocranium. A finite element modeling analysis showed that even a very tiny dentary is crucial for supporting Meckel's cartilage during biting, and that the cartilaginous connection with the protruding teeth compromises their capacities to deal with tangential load during biting. This suggests that, at least at the level of Meckel's cartilage and the teeth-supporting cartilage, the chondrocranium alone is not capable of proper mechanical functioning during feeding.

Connecting the Chondrocranium: Biomechanics of the Palatocranial Joints of Sauropsids

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The evolution of gnathostomes heralded new articulations between the chondrocranium, palatoquadrate, and skull roof that manifest as the otic and palatobasal joints in tetrapods. These joints occupy developmentally and biomechanically dynamic regions of the skull that offer a rich diversity of structural and biomechanical adaptations to feeding function. Among sauropsids, these joints ebb and flow under the auspices of cranial kinesis. But little is known about the structural and functional adaptations these joints and their muscles possess and how the suite of tissues evolved along the lines to living clades. Here, we give examples of articular tissue evolution in the otic joint of archosaurs, 3D-biomechanics of protractor muscles among sauropsids and patterns of loading at the otic and palatobasal joints as determined through imaging, histology and biomechanical modeling. We find that bichondral otic joints in birds were likely inherited from their theropod dinosaurs ancestors. We find that protractor muscles help mediate strains between the chondrocranium and palatoquadrate segments. Finally, we show how bony morphology of the joint surfaces and cross-sections reflect loading environments associated with deep forces in the skull. These new approaches offer considerable insight into the evolution and development of palatocranial articulations as well as new details on cranial performance and feeding biomechanics in archosaurs, sauropsids and vertebrates.

Variation and Conservation in Chondrocranial Development in the Domesticated Fowl (*Gallus gallus domesticus*) and Other Birds

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A tradition of the last 100 years on works on the chondrocranium is a challenge to summarize analytically given the terminological issues and the differences in approaches and stages examined. However, a critical appraisal and the examination of original materials of the red junglefowl and diverse chicken breeds results in the discovery of several patterns. The domestication of the fowl led to much morphological variation in chickens, as exemplified by the skull, a structure quite diverse in birds in general. The extent to which this diversity is reflected in the early cranial development (i.e., 'developmental penetrance') is tested. We traced the sequence of cranial chondrification (40 events) among birds (11 species representing most major radiations) in a phylogenetic framework. Independent of the method used, there is general agreement regarding the appearance of most chondrocranial elements in *Gallus gallus domesticus*. Comparisons with other species revealed similar sequence of major events. However, there are inconsistencies in the literature. These concern the origin of fenestrations, the presence of certain structures (e.g., intertrabecular, cranial ribs), the independence of specific cartilages and the number of hypoglossal foramina. Intraspecific variation, and individual asymmetry, in the count of hypoglossal foramina is common; the adult skull of 70 individuals representing the red junglefowl and 13 chicken breeds revealed that the number of hypoglossal foramina varies between two and four. Our study revealed much conservatism in chondrocranial shape and

ontogeny, suggesting then how much of the adult variation is related to dermal bones and to changes that occur later in development, before and after hatching.

On the Development of the Nasal Capsule and Turbinate Homology in Laurasiatherians, with Special Reference to Bats

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Multiple corrugated structures are formed within the nasal capsule of the chondrocranium, eventually developing into turbinals. During fetal and postnatal ontogeny in mammals, these turbinals change the structure by branching off and scrolling. Finally, ossified structures are formed inside almost all turbinals. Turbinate structure has been described in various mammals, but its structural complexity and interspecific variation have hindered its homologization among species. Tracing the ontogenetic process from the simple fetal to complex adult stage is essential to resolve the turbinate homology. Nevertheless, few studies explored the turbinate structure of fetal laurasiatherians. We studied the development of the nasal capsule in bats, combing DiceCT-imaging and histological techniques. We studied three types of bats: horseshoe bat (nasal echolocator), parti-colored bat (laryngeal echolocator) and short-nosed fruit bat (non-echolocator). Several other laurasiatherian species were also studied for comparison. We found that in echolocating bats the turbinate structure does not branch off, therefore, forming a simpler structure compared to others. In other laurasiatherians, the septum frontomaxillare is located rostrally and separates the recessus frontoturbinalis and recessus maxillaris. In contrast, the recessus frontoturbinalis was not observed in bats since the lamina semicircularis is possibly missing. The maxilloturbinale branches off and scrolls, forming a well-developed structure in fetal fruit bat, but it is considerably small or vestigial in horseshoe bat and parti-colored bat. We point out that the skeletal structure considered by previous investigators as the “maxilloturbinale” in horseshoe bats is actually the ethmoturbinale I and that other turbinals should also be re-identified. We found that, although vestigial, another undescribed structure is the actual maxilloturbinale but lacking an ossified structure.

The Biomechanical Role of the Chondrocranium in a Lizard Cranium

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The chondrocranium is the cartilage component of the braincase which is largely replaced by bone during growth in most vertebrates. However, in tetrapods this replacement occurs comparatively late and with varying degrees of completeness both within and between major clades. Differences between taxa tend to be studied to infer phylogenetic relationships, but the structure and mineralization of the chondrocranium might also reflect the strain it undergoes in life. To evaluate this possibility, we examine the biomechanics of the chondrocranium in the South American tegu lizard *Salvator merianae*. We built a three-dimensional computer model of the skull with patent cranial sutures (using microCT data) and a complex wrapped representation of the muscles (informed by dissection). We calculated muscle activity, bite force and joint reaction forces during anterior and posterior biting using multi-body dynamic analysis (MDA). The MDA results were used to define the boundary conditions of a finite element model, which allowed us to predict strain magnitude and distribution. A sensitivity analysis of the elastic modulus of the chondrocranium indicated that it had little effect on strain distribution in the cranium, and strain magnitude is not notably reduced by the presence of the chondrocranium unless it is given the same material properties as bone. Within the chondrocranium itself, von Mises strain was twice as great during anterior biting. Strain was also greatest in the anterior region, and tensile strain was greater than compressive strain regardless of biting location. Therefore, our results appear to contradict previous suggestions that the chondrocranium or nasal cartilage supports the snout, acts as a compressive brace, and/or absorbs dynamic strains. Interestingly the region of the pila metoptica, which exhibits variation in mineralization among lizards, experienced higher strain during posterior biting. Future work will focus on juvenile lizards where the dermal skull bones are less robust and less mineralized.

Genetic and Developmental Basis of Facial Individuality

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There is a remarkable variety of facial shapes in the animal kingdom that enables a broad spectrum of functions and various skills. In addition to the obvious functional aspects such as protection of the central nervous system and the sensitive sensory organs, feeding as well as providing points for muscle attachment, the facial shape is important in many more ways. For example, humans use facial individuality for mutual recognition that assists social interaction, communication and affects numerous important aspects of everyday life. Pathological conditions include a wide spectrum of deficiencies, and may involve eating, breathing and speech impairments, and in some species, emotional problems and low quality of life in general. The facial features reflect the underlying geometry of skeletal structures. Two types of stiff tissue, cartilage and bone, represent the craniofacial internal skeleton. Bone is predominantly derived from pre-shaped cartilaginous templates that are formed during the embryonic development. The first facial shapes are represented by forming mesenchymal condensations. The induction of a mesenchymal condensation in a specific location is instructed by signals coming from various sources, for instance from parts of the developing brain and olfactory epithelium. Enhancers influence the levels of these signals and this regulation may represent the genetic basis of facial individuality. Condensations turn into the cartilage that later expands tremendously while maintaining the perfect established 3D-shape. The control of the shape and size during the whole embryonic growth of the mammalian face is based on uncoupled mechanisms of transverse integration of clonal columns of chondrocytes, control of the cartilage thickness, and existence of growth zones. Supplementary shape fine-tuning is later achieved by additional waves of mesenchymal condensations.

Dermatocranium-Chondrocranium Interaction in Craniofacial Development and Evolution

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The cranial portion of the endoskeleton, the chondrocranium, functions to protect the developing brain and paired sense organs. In laboratory mice the chondrocranium appears prior to the dermatocranium around embryonic day 12.5 (E12.5) and begins to degenerate by ~E15-E16. Its function is gradually assumed by the dermatocranium. The transient nature of the chondrocranium and replacement by the dermatocranium is one reason why we know so little of the function of the chondrocranium in craniofacial development. To remedy this, we have developed an innovative system to dissect the chondrocranium in 3D *in silico* with tight temporal control and to investigate the potential of the chondrocranium/dermatocranium boundary as a signaling interface during craniofacial development. Using laboratory mice, we present data to test our central hypothesis, that the chondrocranium serves as a scaffold for the later development of dermatocranial elements, including the formation of cranial vault sutures. First, we estimate a precise developmental age for each embryo studied using a novel staging system for mouse embryos. Next, we determine the 3D-morphology of the chondrocranium and elements of the dermatocranium at various embryonic stages using procedures for phosphotungstic acid staining of mouse embryos that optimizes various conditions to visualize embryonic cartilage in 3D by micro-computed tomography imaging. We establish the integrity of the spatiotemporal and functional relationship between the chondrocranium and dermatocranium during embryonic development and provide preliminary data related to the nature of the boundary between these two craniofacial skeletons. Our work provides temporally precise, 3D-reconstructions of the developing chondrocranium in mice and crucial information about its role in dermatocranial development. Supported in part by NIH grant R01DE027677.

The Outer Nasal Cartilages of Mammals as Progressive Remnants of the Chondrocranium

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A rostrum equipped with a moist rhinarium, diverse mechanoreceptors and vibrissae is a derived character of therian mammals. Together they constitute a new and complex sensory organ that has been named 'rostral organ'. The sensory skin is supported by a well-defined system of outer nasal cartilages, which can be actively moved by facial muscles. Because the structures of the rostrum are composed of cartilage and soft tissues, fossils cannot contribute relevant information; therefore, we have to rely on comparative anatomy of extant mammals. Because the cartilages are known to grow and differentiate well into juvenile age stages, postnatal stages are most informative. Here, I provide a preliminary overview of the structural diversity of the outer nasal cartilages in a few therian taxa. The outer nasal cartilages of moles (Talpidae) and shrews (Soricidae) are relatively well-known and serve as reference. The soricids present a unique mode of retracting and telescoping the nasal cartilages; these peculiar structures are differentiated only postnatally by apoptosis. Several “basal” Afrotheria show a peculiar commissura alatransversalis, which is considered to be a new synapomorphy of the group. The peculiar trachea-like structure of the outer nasal cartilages of the macroscelidids is also postnatally realized by an apoptotic morphogenetic mode. Finally, the presented data are interpreted in a context of evolutionary biology of early mammals. It is shown, that the paired outer nares of early synapsids begin to fuse into a wide nasal aperture as realised in true mammaliaforms; *Tachyglossus* provides a noteworthy transitional state. It is only on this basis that a true rostral organ could evolve, expand and diversify. Whereas small arboreal mammals show relatively simple outer nasal cartilages, they tend to become very diverse in terrestrial and fossorial taxa.

The Role of FoxN3 in the Development of the Chondrocranium and Associated Head Muscles in the African Clawed-frog, *Xenopus laevis* (Anura: Pipidae)

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Studies of chondrocranium evolution and development have led to the discovery of major genes and mechanisms that govern its early development. However, many of the genetic interactions forming the gene regulatory network controlling cell condensation, chondrogenesis and morphogenesis of the chondrocranium are still poorly understood. FoxN3 has been reported to be crucial for the normal development of neural crest-derived elements of the chondrocranium and its associated muscles in *Xenopus laevis.* But the genetic interactions by which FoxN3 regulates chondrogenesis and muscle development in the head of *X. laevis* are still poorly known. We used Morpholino-mediated knock down in combination with qRT-PCR and whole-mount *in situ* hybridization to analyse potential target genes of FoxN3. The temporal and spatial expressions of different cartilage, muscle and joint markers as well as cell adhesion molecules are changed following FoxN3 depletion. Expression of N-CAM and N-Cadherin is decreased throughout development and expression of genes important for cartilage formation (Sox-9, Col2α1, Runx-2) is delayed. Joint markers (Gdf5/6) and genes (Dlx5/6) important for regional specification are also down-regulated. Additionally, expression levels of key myogenic genes such as MyoD and of structural muscle genes are reduced compared to control embryos. This results in smaller cartilage and muscle anlagen and incomplete development of neural crest-, but not mesodermal-, derived elements of the chondrocranium. Additionally, FoxN3 is important for the formation of the intermediate domain during joint development in the head of *X. laevis*. It seems that FoxN3 plays a key role upstream of a complex gene regulatory network maintaining normal cartilage and joint formation of the chondrocranium and proper development of the muscles connected to it.

Perinatal Ontogeny of the Ethmoidal Region in Muroidea (Rodentia, Mammalia)

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The cartilaginous nasal capsule of mammals becomes highly modified during ontogeny by resorption and ossification resulting in the ethmoid bone. However, the perinatal development of the ethmoidal region is not well studied though this is a craniogenetic crucial time frame. In order to elucidate the perinatal transformation of the nasal capsule histological serial sections of 23 muroid species were investigated, some of which are represented by more than one ontogenetic stage. In addition adult crania of selected species were analyzed by µCT and data from further rodent clades and Euarchontoglires were used for comparison. Perinatal stages of all altricial muroid species under study have a less mature ethmoidal region compared to other precocial rodents e.g., caviomorphs. However, in muroids resorption of the nasal capsule and ossification of turbinals, nasal septum and cribrose lamina already start before birth and follow a distinct pattern observed in many rodents. In around 14 days old stages of some investigated muroids the paries nasi and tectum nasi are almost completely resorbed except for the anterior nasal cartilages and those parts that become ossified (e.g., bases of turbinals). Surprisingly, the precocial *Sigmodon hispidus* and *Acomys* sp. resemble the developmental pattern of altricial muroids, though paries nasi resorption starts earlier in *Acomys*. Furthermore, the perinatal maturity of *Mesocricetus auratus* that has the shortest gestation period among placental mammals (15-17 days) corresponds to that of other altricial muroids. This observation indicates an accelerated development in the golden hamster. The muroid groundplan is already determined at birth and comprises a general pattern of six olfactory turbinals (two frontoturbinals, three ethmoturbinals, one interturbinal). Apomorphic patterns are restricted to the number of frontoturbinals: three in *Abrothrix longipilis*, one in *Apodemus* spp., *Micromys minutus*, *Mus musculus*, *Rattus norvegicus*.

Diverging Development of Akinetic Skulls in Cryptodire and Pleurodire Turtles: an Ontogenetic and Phylogenetic Study

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Extant turtles are characterized by an akinetic skull, whereas several stem Testudines plesiomorphically had a basicranial articulation. We demonstrate how the akinetic skull is formed through ontogeny, including the lateral closure of cavum epiptericum and the fusion of the palatoquadrate cartilage to the neurocranium. Both major clades of modern turtles, Pleurodira and Cryptodira, show strikingly different strategies on how to develop the akinetic construction in the orbitotemporal region. Whereas the ascending process of the palatoquadrate (later ossified as epipterygoid) contributes to the formation of the secondary braincase wall in Cryptodira, only the descending process of the parietal is forming that wall in Pleurodira. Related to that, the latter taxon does not develop an extended ascending process. Moreover, whereas the palatoquadrate directly fuses to the braincase with the help of appositional bone in pleurodires, it is bridged by the pterygoid in cryptodires. Phylogenetic evidence, including fossil data, suggests that the cryptodiran type of skull fixation is plesiomorphic for crown turtles and that the pleurodire condition evolved secondarily within the crown. Embryonic neck muscle activity may be the cause of this shift of the palatoquadrate. Different muscle forces in each taxon may result in differing positions of the palatoquadrate in relation to the braincase and eventually result in the two different attachment types. Moreover, the general construction of the jaw adductor chamber is affected by alternative fusion modes, which secondarily result in different types of the trochlear system of the external jaw musculature. Related to that, changes in feeding habit through turtle evolution may have also triggered increasing stabilization of the skull. Palatoquadrate fixation, finally, was an important prerequisite for the reduction of the exocranial bones of the temporal skull region.

Evolution of the Chondrocranial Lateral Wall in Lepidosaurs

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Sphenodon punctatus, the tuatara, is the last survivor of the formerly widely distributed group of Rhynchocephalia, which is considered as sistergroup of Squamata. The skull anatomy of tuatara and its fossil relatives is comparably well known; however, embryological data of skull development are rare, incomplete, and mostly represented by dated works. Knowing the anatomy of the chondrocranium of tuatara is crucial for understanding chondrocranial evolution in reptiles and particularly in lepidosaurs. Based on the historical histological collection of Hugo Schauinsland, we reexamined the anatomy of the fully formed chondrocranium in tuatara and describe a very early stage of its chondrocranium formation, which was not considered in any study before. The architecture of the fully formed chondrocranium of tuatara represents one of the most complex ones among sauropsids. We observed a number of characters, which are absent in other reptiles and were never described before in tuatara. These include (i) an unusual cartilage in the nose, (ii) a posterior fusion of the basipterygoid process, and (iii) a ventral connection of pila antotica and pila metoptica that we call taenia ventralis. We consider the structure of the chondrocranial wall in tuatara to represent an ancestral condition, which maintains potential for further diversification of the orbitotemporal region in squamates.

Certainly, it provided extra strength to the chondrocranial lateral wall. However, at the same time, this feature of tuatara could also be a rudimentary form of the more distant ancestor of the lepidosaurs, in which the chondrocranium played a more functional role.

Natural Selection and the Evolution of Phenotypic Integration – Organizers: Catalina I. Villamil – Patrick Arnold

The Origin of Morphological Integration and Modularity in the Mammalian Neck

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Despite its functional diversity, the neck is constrained to seven cervical vertebrae in almost all mammals, making it a gripping subject for evolutionary biologists. Research in this specific field is generally focused on the developmental and evolutionary origin of the fixed number of cervical vertebrae. However, less attention is given on how high functional diversity and morphological disparity evolved in the mammalian neck after the occurrence of meristic limitations. Strong developmental constraints on cervical number and the patterning by highly conserved Hox genes resulted in a strong integration of the neck with other body parts as well as within cervical modules (i.e., upper, middle, and lower cervical module). This modularity of the neck is expressed on different levels of integration (developmental, structural, functional). The fossil record of early mammals, however, shows that not all cervical traits of modern mammals evolved at the same time. Post-Triassic modifications and regionalization of the cervical spine in the lineage leading to modern mammals increasingly allowed to cope with the developmental constraints and biomechanical determinants in the neck. Whereas the specialized head junction (atlas-axis complex) consolidated shortly after the fixation to seven cervical vertebrae, the morpho-functional integration of the lower cervical module (forming the cervicothoracic junction) significantly postdated its putative developmental integration. The developmental and morphological modularity eventually allows for regional specialization through the autonomy of the modules and enables the diversity of neck morphologies seen in modern mammals. Thus, the neck's morphological evolution has not been completely 'limited' at all, but was channeled to new solutions and unique integration patterns during mammalian history.

He Would Forget his Head if it Wasn't Screwed On: The Neck as Key Innovation in Tetrapod Evolution

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In tetrapods, a number of cervical vertebrae form a functionally distinct neck that attaches the head to the trunk. This biomechanical innovation allows for moving the head independently of the trunk and facilitated the radiation of animals as diverse as amphibians, non-avian reptiles, birds, and mammals. Although the vital importance of the neck is clear, reconstructing its evolutionary changes is extremely complex. The wide variation in numbers of cervical vertebrae (CV) across different clades (from one CV in many amphibians to 76 CV in extinct reptiles) makes it difficult to identify homologous elements among species. *Hox* genes are involved in defining anatomical limits, such as the cervicothoracic transition in the vertebral column. The statistical assessment of shape changes between successive vertebrae enables the establishment of the morphological subunit patterns in the neck that reflect the underlying *Hox* code. Thus, the morphological modularity allows homologizing vertebrae among organisms with variable cervical count. Here, I present recent results from collaborative work on the variability and constraint in the cervical vertebral column of three groups of tetrapods: birds, turtles, and mammals. In contrast to birds, which are variable in the number of vertebrae in the neck (10 - 26 CV), turtles and mammals are highly constrained in cervical count. Both stem and crown turtles have eight CV and evidence suggests that the 'fixed' number occurred after the formation of the complete carapace. Non-mammalian synapsids display a variable cervical count, whereas extant mammals virtually always have seven CV. Sloths are one of only two exceptions to the mammalian 'rule of seven' vertebrae in the neck, but the explanation for breaking the evolutionary constraint is still under debate. Overall, the studies presented here aim at contributing to the understanding of the mechanisms responsible for the diversity in the tetrapod 'body plan'.

Comparing the Incomparable: Anatomical Network Analysis to Study the Evolution of Phenotypic Integration of Disparate Forms

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Non-homologous structures pose a problem to the quantification and traceability of phenotypic integration and modularity during evolution. Such difficulties scale up when comparing phenotypic integration during evolutionary transitions, such as the fins-to-limbs transition, or when comparing the phenotypic integration of different body parts, such as head and limb. Anatomical network analysis has recently emerged as a tool to overcome the problem of comparing (seemingly) incomparable forms, by working at a level of abstraction independent of biological correspondences. The utility of a network-based approach to quantify phenotypic integration is illustrated here with examples of comparisons between mammalian and non-mammalian skulls, between fins and limbs, and between heads and limbs.

Disparate Integration Patterns Shape the Evolution of Cranial Disparity across Archosaurs

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An important prediction in the study of phenotypic integration is that the strength of covariation among traits will bias the evolvability and disparity of those traits. However, evolutionary shifts in integration have rarely been examined outside of Mammalia. Here, we quantify patterns of integration in the archosaur skull to test how trait covariances differ among taxa with distinct cranial function and ontogeny. We quantified skull shape and phenotypic integration using high-dimensional 3D-morphometrics across a broad taxonomic sample composed of extinct and extant crocodylomorphs (n = 53), non-avian dinosaurs (n = 37), and birds (n = 352). We find that there are major differences in integration patterns across Archosauria. Crocodylomorphs primarily show strong integration among the rostral elements. In non-avian dinosaurs, the strongest correlations are observed between cranial elements related to jaw articulation and muscle attachment (e.g., squamosal, quadrate, jugal). In birds, correlations among individual bones are more challenging to parse due to the highly fused nature of the skull. Nonetheless, it is clear that skull regions that are highly integrated internally in birds are composed of elements with high between-element integration in non-avian dinosaurs. We hypothesize that these shifts in integration are the result of differences in cranial function and development. We also quantified Procrustes variance in each skull region, finding that all archosaurs exhibit high disparity in the anterior face and low disparity in the occipital region. Uniquely, crocodylomorphs show high disparity in the pterygoid (related to variation in the secondary palate) and the cranial vault is highly variable in non-avian dinosaurs (related to ornamentation). These findings illustrate that differences in cranial integration have evolved across archosaurs, and that such differences have facilitated the evolution of phenotypic variation along different axes of variation.

Dissecting Phenotypic Integration and Connecting Micro- and Macro-Evolutionary Time Scales

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How do micro-evolutionary processes produce macro-evolutionary patterns? How does phenotypic integration affect evolution across the micro-/macro-evolutionary continuum? These are current, pressing and largely unanswered questions in evolutionary biology. We address these questions using a large morphometric dataset of Old World monkeys, an iconic clade with remarkable disparity in morphology, ecology and geographical distribution. We use 3D-geometric morphometrics on over 3,000 skulls of Old World monkeys, followed by analyses of trait evolution informed by quantitative genetic thinking and species diversification. We identify low-dimensional projections of high-dimensional shape data based on quantitative genetic considerations and study their relationship with the evolution of species and phenotypic diversity in this clade. Overall, patterns of covariance show poor association with phylogenetic distance and with diversification rates. However, the main patterns of phenotypic change that are observable at the micro-evolutionary level are, indeed, transferred to the macro-evolutionary scale. These include substantial allometric variation. Our work identifies areas of continuity between time scales (micro-/macro-evolution) that have contributed to the remarkable phenotypic diversity of Old World monkeys. For instance, intra-specific allometric patterns are largely shared across species and account for a large proportion of macroevolutionary variation. Phenotypic integration can be thought of as a series of distinct – but interacting – axes, which respond to distinct pressures (e.g., selection on body size, selection on ecologically-relevant features) and result in a variety of patterns at different time scales.

Assessing the Macroevolutionary Consequences of Phenotypic Integration with Dense Phenomic Data from Living and Extinct Tetrapods

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Interactions among morphological traits, or phenotypic integration, reflect genetic, developmental, and functional relationships among traits and can significantly bias morphological evolution. Simulations using theoretical and empirical trait covariance matrices confirm that integration can result in both, more and less disparate organisms, and most often the latter, than would be expected under unconstrained evolution. However, high rates can persist even when morphological disparity is constrained by trait integration. Similar to a "fly in a tube", trait integration may restrict evolution to particular regions of possible morphospace, but it doesn't necessarily limit the pace of evolution within those regions. Importantly, high evolutionary rates within restricted regions of morphospace would be expected to result in a high degree of convergence and homoplasy. Here, we discuss the patterns and consequences of cranial phenotypic integration using a dataset spanning living and extinct tetrapods. While most large-scale studies of phenotypic integration and morphological evolution utilize relatively limited descriptors of morphology, hindering comparisons across clades, surface sliding semi-landmark analysis allows for detailed quantification of complex 3D-shapes, even across highly disparate taxa. We analyzed cranial integration and morphological evolution using a dense dataset of 700-1500 landmarks and sliding semi-landmarks for over 1000 species of living and extinct species spanning over 300 million years of evolution. While patterns of cranial modularity are generally conserved across large clades (e.g., within mammals, birds, squamates, caecilians), there are clear shifts in patterns of integration across these clades. Tempo and mode are similarly highly variable across cranial regions and clades. While some clades show evidence that high integration constrains morphological evolution, there is not a consistent pattern of constraint across tetrapods.

Evolutionary Constraint of the Diversification of Avian Limbs

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Genetic and developmental factors (e.g., traits influenced by the same gene), and functional factors (e.g., traits of the same bio-mechanical apparatus) may integrate an organism's traits so that selection cannot optimize its form for a given environment, creating tension between processes that promote anatomical diversification versus integration. In this study, we used geometric morphometric methods to assess the extent to which integration has constrained the diversification of limbs during the evolution of birds. Flightless birds have evolved many times, producing unrelated species that share similar limb morphologies, especially in the forelimb. In this study, we compared patterns of covariances in limb bones of flying and flightless birds as a measure of integration using geometric morphometrics, Mantel tests, Two Block-Partial Least Squares, and several other analyses to determine whether patterns of integration are different in flying and flightless birds because of reduced functional demand or whether the two groups have a shared pattern of integration that is consistent with shared genetic and developmental constraints across all birds. A majority of analyses showed that flying and flightless birds have similar integration patterns within elements of both the fore- and hind limb. However, a number of the analyses showed that patterns of integration between elements are different for flying and flightless birds. The results support the hypothesis that integration patterns within elements of avian limbs are constrained by developmental and genetic factors, regardless of flight ability. However, integration between bones may be influenced by functional factors. Therefore, the disparity of functional selection acting on the limbs of flying and flightless birds may promote diverse integration patterns within the limbs of the two groups, while shared genetic and developmental factors constrain the evolution of individual limb elements across all birds.

Insights from Genotype: Phenotype Mapping the Mammalian Postcanine Dentition

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Heterodonty is widely recognized as a key innovation to the evolutionary success of the mammalian clade. Recent advances in Genotype: Phenotype (G:P) mapping offer an opportunity to assess dental variation with fidelity to the underlying genetic architecture. We employed a dataset of extant and extinct mammalian taxa to investigate the evolution of two genetically-patterned dental traits in the postcanine dentition, the Molar Module Component (MMC) and the Premolar-Molar Module (PMM), in comparison to molecular phylogenetic relatedness, diet, and life history. Our sample includes 1,523 individuals spanning six orders, 14 families, 36 genera, and 49 species within the terrestrial Boreoeutheria (Euarchontoglires and Laurasiatheria). We first explored MMC and PMM variation across orders, and then focused on primates to explore variation within and among families, genera, and species. We find that across orders, variation in MMC is more strongly associated with phylogeny than variation in diet. The incorporation of a few paleontological data points suggests that MMC is slower to change than is dietary specialization. Within Primates, a more detailed set of fossil data reveals that a significant shift in MMC corresponds with the major shift in taxonomic diversity observed at the end of the Miocene. Our analysis of genera within the Hominidae indicates that MMC is more evolutionarily stable than PMM, and therefore, may elucidate paleobiological distinction across genera. We find a more variable, species-level pattern for PMM. Clade-based approaches to phylogenetics currently dominate evolutionary biology. As the relationship between genotype and phenotype is discovered, should phylogenetics shift to incorporate the biological etiology of characters? MMC and PMM enable the identification of taxa with similar genetic architectures, and therefore the opportunity to take a more paleobiological approach in taxonomy and phylogenetics.

The Evolution of Phenotypic and Genetic Integration: Field and Laboratory Experiments

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Phenotypic and genetic integration refers to how traits are associated (correlated) within populations of organisms. From a genetic perspective, integration results from pleiotropy and linkage disequilibrium and both properties are potentially labile through time. Genetic integration, in turn, contributes to the phenotypic association between parts. Both genetic and phenotypic integration are important for evolution since the former mediate the evolutionary responses under selection (unit of selection) while the latter along with the traits averages are on the receiving end of selection (targets of selection). Genetic and phenotypic integration can change through time because linkage disequilibrium tends to disappear due to recombination (unless actively maintained by selection) and pleiotropy can change either because different alleles of a gene can have different degrees of pleiotropic effects or because modified loci (epistasis) might change those pleiotropic effects. Here, we discuss how phenotypic and genetic integration can be investigated in laboratory and natural settings. Our laboratory experiments with mice (*Mus musculus*) demonstrate that directional selection increased the magnitude of integration and the proportion of variation associated with size. Our results from natural populations suggest that climatic changes in the past 100 years altered phenotypic integration, and these changes are consistent with the direction of selection.

Hierarchical Variability in Patterns of Integration within the Anthropoid Torso

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Researchers have long considered anthropoid torso evolution to occur as a "package deal," where the entire torso region evolved as a unit because of biomechanical constraints. The common dichotomization of body form in this group into monkey-like and ape-like is linked to this idea of a unified response to locomotor selective pressures and suggests a shared pattern of strong covariation across the anthropoid trunk skeleton. However, recent studies have found greater torso shape variation among anthropoids than previously appreciated, calling this hypothesis into question, as have new considerations on the potential conflicts between locomotor and non-locomotor selective pressures such as postural behavior, obstetrics, and ecogeography. Here, I test the hypothesis that monkeys and apes share a pattern of strong torso integration and its underlying assumption that torso form became canalized into one or the other. With four representative anthropoid taxa (macaques, n=107; gibbons, n=97; chimpanzees, n=109; and modern humans, n=371), I explored patterns and magnitudes of integration as well as calculations of evolutionary responses to selection. My results indicate that magnitudes of covariation vary significantly across taxa, with macaques in general exhibiting stronger integration across elements than do the ape species. Humans in particular exhibit the weakest torso integration but also exhibit unique patterns with respect to the obstetric pelvis. Across all taxa, integration patterns within smaller torso units such as the ribcage and pelvis appear to be conserved, but higher-order patterns among these regions are more variable. These results suggest that selection has not acted upon the anthropoid torso in a uniform manner but rather has affected different elements in different ways and led to variable patterns of relationships among the ribcage, spine, and pelvis. Ethical statement: This research is based on human remains from museum anatomical collections. Research protocols and access to specimens were approved by curatorial staff from all institutions. Human remains were treated respectfully and ethically during data collection, and the research protocol did not include any invasive or destructive techniques.

Conservative Evolution and Integration Continua in the Primate Cranium

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Primates occupy a large variety of ecological niches, and have adapted their craniofacial skeleton to a variety of diets, environments, and behaviors. They have also developed large brains linked to the complexity of their ecology. Researchers have long posited the importance of integration relationships in shaping primate craniofacial evolution. However, although multiple researchers have assessed patterns of integration and modularity in the primate skull, the way that these are influenced by, or in turn influence, evolutionary processes such as natural selection are not well understood, and past research has come to mixed conclusions. Here, I discuss factors linked to integration in the primate cranium in a sample of 11 primate genera including humans (n=1009). My results suggest that although there is a weak phylogenetic component to integration patterns, and potentially some role of posture and locomotion in cranial integration, the major factor affecting the strength of integration in the primate cranium is related to brain size and shape. Despite these influences, however, the overall range of evolutionary change in primate cranial integration patterns and magnitudes is quite small, and the strength and pattern of primate cranial integration is relatively conserved across taxa ranging from lorises and galagos to modern humans. New evidence of the patterns of change observed in six platyrrhine species (n=197) undergoing character displacement also show that, rather than breaking down integration, natural selection is acting on the crania of these monkeys by following 'paths of least resistance' along integration continua towards one of a handful of integrated phenotypes. Together, these results suggest that, although substantial change in patterns and magnitudes of integration have occurred in the postcranial skeleton, the primate cranial skeleton is highly conserved and evolves within an integrated set of possibilities. Ethical statement: All data collection procedures were non-destructive and were carried out with all required permissions, as determined by the local institution and government. Human data were collected in an anonymized fashion.

The Biomechanical Adaptations of Limb Bones – Organizers: Alexandra Houssaye, John Hutchinson

Investigations into the Biomechanics of the Legg-Calvé-Perthes Disease

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Legg-Calvé-Perthes' (Perthes') is one of the most common diseases in paediatric orthopaedics, and affects children between the ages of 4-8 years old. The condition is more common in boys and is characterized by avascular necrosis of the femoral epiphysis and collapse and flattening of the femoral head. The shape of the femoral head may be regained in some individuals, but where it isn't, the result is usually degeneration of the articular cartilage and early osteoarthritis. Despite many years of research, the cause of this disease remains unclear. Many factors have been suggested including: ischaemic events, vascular deficiency or obstruction, coagulation disorders, deviations in geometry, growth impairment and skeletal immaturity, socio-economic conditions and social deprivation, and genetic factors. As a result, different hypotheses describing the possible mechanics that lead to Perthes' have been proposed, varying from simple biomechanical overload to vessel obstruction. Interestingly, a number of different nonhuman animals also appear to suffer from Perthes'-like conditions. We used a series of finite element (FE) models to investigate these different hypotheses, including a model that includes the blood vessels that supply the developing epiphysis. In a first step, a finite element model of a juvenile hemi-pelvis and femur was used to simulate single-leg stance and drop landing. These nodal displacements were then mapped onto a high-resolution FE model that incorporates the blood vessels. The results suggest that direct collapse of the femoral head is unlikely even with high impact loads and a skeletally immature epiphysis. It does appear however that a skeletally immature hip may experience a significant reduction in the cross-section of the blood vessels supplying the femoral head even in single-leg stance loading. This reduction of the blood flow may be sufficient to lead to necrosis, collapse of the femoral head, and onset of Perthes' disease.

Body-Mass Related Variation in Bone Structure and Function at the Tissue Scale

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Bone organs are well known to scale allometrically with body mass, in length and cross-section. The scaling relationships identified across diverse taxa show that bones do not become as monstrous as Galileo predicted for the simplistic isometric case. Adaptations such as more erect postures and ambling fast gaits reduce bone stress in larger animals. Bone tissue is a hierarchical composite material that exhibits dynamic changes in geometry (modelling) in the face of changes in mechanical load. Bone continuously self-repairs through secondary osteonal remodelling. Using X-ray microtomography on bone from 90 mammal and bird species we showed that trabeculae in larger animals are thicker and fewer per unit volume than in smaller animals, while the amount of bone per unit volume does not vary as a function of animal size. Finite elements analysis indicated that larger trabeculae may result in lower strains, under equal applied apparent stress. We accessed the Quekett collection of bone sections at the Hunterian Museum and imaged 39 mammal species' secondary osteons using widefield fluorescence microscopy. Secondary osteons are wider in larger than in smaller taxa, regardless of phylogenetic effects. Osteonal resorption area may be limited by the need to avoid fracture in smaller mammalian species, but the need to maintain osteocyte viability in larger mammalian species. To determine the cellular basis of bone's microstructural scaling, we prepared primary osteoblast cultures from a series of 30 dogs from small to giant breeds, and from 14 mammal species ranging from 0.03 to 45,000 kg. From the small number of species tested to date, osteoblast behavior in culture displays strong individual variation along with pronounced phylogenetic clustering, and a weak to zero correlation with body mass (R^2 = 0.0007 to 0.240, p = 0.004 to 0.86). The cellular and molecular mechanisms underlying bone's microstructural scaling remain obscure.

Comparison of Salamander Limb Bone Mechanics to Model Locomotor Function across the Water-to-Land Transition

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Once tetrapods invaded terrestrial habitats, the limbs experienced new functional demands to support body weight during posture and locomotion. Salamanders are often used as functional analogues for early tetrapods that experienced such evolutionary transition and, because most salamanders possess a generalized tetrapod Bauplan, they are often inferred to have been ecologically and functionally similar to early tetrapods. However, salamanders span a range of habitats and life histories, providing an opportunity to model different stages during the evolution of terrestrial locomotion. For example, the semi-aquatic salamander *Pleurodeles waltl* displays limb kinetics that are generally intermediate between the pectoral fins of mudskipper fish (*Periophthalmus barbarus*) and the limbs of terrestrial salamanders (*Ambystoma tigrinum*) during terrestrial locomotion. The orientation of the ground reaction force suggests that *P. waltl* may experience greater bending moments that would elevate limb bone stresses compared to terrestrial salamanders, potentially imposing a functional trade-off in the shift from water to land. Beyond differences across species, the forelimbs and hind limbs also play distinct functional roles. For example, the humerus of the terrestrial *A. tigrinum* has stiffer mechanical properties, load-reducing features, and a greater margin of safety during terrestrial walking than the femur. These differences may reflect more variable loading regimes resulting from the multiple functions that the forelimbs demonstrate for locomotor and non-locomotor (e.g., burrowing, breeding) behaviors. Further comparisons of mechanical properties and geometries of limb bones in salamanders, ranging from aquatic to terrestrial, will provide a framework for more ecologically realistic models of musculoskeletal function in stem tetrapods spanning the water-to-land transition, and enhance insights for modeling how bone mechanics predict locomotor function.

Signals of Locomotion and Manipulation in the Internal Trabecular Bone Structure of Extant Hominoids and Fossil Hominins

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The enhanced dexterity of the human hand is unique among primates, an ability that is traditionally thought to have evolved in response to tool-related behaviors and a release from the biomechanical constraints of locomotion in our bipedal hominin ancestors. However, recent fossil and archaeological evidence, as well as novel analyses, suggest that dexterity-related morphology and abilities evolved earlier than traditionally thought and that fossil hominins used their hands for locomotion until much later than presumed. Behavior evolves faster than morphology, and it is not yet clear how these different functional demands were potentially accommodated within the morphology of the hominin hand. We aim to improve our understanding of how our fossil ancestors used their hands for both locomotion and manipulation through the investigation of plastic aspects of bone morphology – internal trabecular (cancellous) bone – that can better reflect behavior during life than external morphology alone. We interpret variation in trabecular structure, focusing on metacarpals, within a comparative great ape context via pressure analyses of bonobo (*Pan paniscus*) arboreal locomotion and human tool-use. We then incorporate these biomechanical data into validated musculoskeletal models of the bonobo and human third digit to estimate *in vivo* metacarpophalangeal joint loads. Finally, using microFE-based inverse bone remodeling, we demonstrate how metacarpal trabecular structure reflects differences in joint loading across great apes, which can ultimately inform our reconstructions testing if and how different fossil hominins used their hands for both tool use and climbing. This research is funded by the European Research Council Starting Grant 336301, as well as the Fyssen Foundation (AB), British Academy (AK) and the University of Kent Vice Chancellor Fellowship (EEB, KD).

In vivo Bone Biomechanics and Functional Adaptation in Long Bone Geometry and Tissue Microstructure

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As functional morphologists, much of our interest in the vertebrate skeleton lies in its contributions to accomplishing daily tasks, such as locomotion and feeding. Where the study of skeletal function becomes particularly difficult is in fossil taxa for which we may only have partial skeletons or poor modern analogs. In these cases, features inherent to even a single bone can become important for developing hypotheses regarding skeletal function and life history traits. Given the hierarchical structure of bone tissue, there are a number of microstructural and macrostructural features that could potentially be used in the interpretation of the evolution of skeletal function. But which skeletal features are the best correlates of skeletal function? How do we establish different features as correlates of musculoskeletal function? How far can we trust them? And, are there differences in the sensitivity by which different features adapt to changes in mechanical function during ontogeny or through evolutionary changes in mechanical loading? Very often bone geometry (circular *versus* eccentric cross-sectional shapes) has been associated to different modes of skeletal loading (torsional *versus* bending loads). However, changes in loading during growth or in altered loading regimes do not necessarily result in the predicted changes in skeletal geometry. Relationships between limb bone mechanics and microstructural features, such as collagen fiber orientation or vascular canal orientation, remain equivocal as well. More correlative work is needed to link skeletal features and their changes with growth and remodeling to *in vivo* measures of changes in limb mechanics in order to fully understand relationships between skeletal form and function across diverse vertebrate taxa. Advances in remote methods for collecting skeletal mechanics data and for characterizing fossil and extant skeletal tissues at multiple length scales might help us to achieve these goals.

Curved Bones: Ulna Curvature in Arboreal and Terrestrial Primates

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Recent studies suggest that limb bones are curved as an adaptation to habitual loading. Studies comparing the strains in curved *versus* straight versions of the same guanaco radioulna show that the curved model is less strained. This phenomenon has also been demonstrated for the quokka femur. Furthermore, the direction of curvature also varies with function: in terrestrial marsupials the ulna is caudally curved (concave on the caudal side) like the radioulna of obligate quadrupeds (e.g., guanaco), but in arboreal marsupials the ulna is cranially curved. This seems to be because forelimb extension is vital for terrestrial species, while forelimb flexion is necessary for arboreal species. The present study examines the primate ulna, and tests the hypothesis that the most arboreal/suspensory primates' ulna will have cranial curvature and that the most terrestrial species will have caudally curved ulnae. We also evaluate the olecranon length and sagittal plane robusticity of the ulna shaft. Strict lateral photographs were taken of ulnae representing 95 primate species. Species were assigned to one of seven locomotor categories including suspensory, clingers and leapers, arboreal quadrupeds, and savannah primates. Results corroborate the predicted strong correlation between curvature (cranially curved through straight to caudally curved bones) and locomotor category. In addition, cranially curved ulnae were found to have small olecranon processes, while caudally curved ulnae had a larger olecranon for the attachment of triceps. Some more generalist arboreal species had large olecranon processes associated with a more robust ulnar shaft. The most specialized terrestrial and suspensory primate ulnas have more slender shafts and small to medium olecranon processes. This presentation will include a discussion of the issues related to the formation of bone curvature and the ways that individuals may regulate bone stress through muscle action.

Mechanical Properties of Human Cortical Bones in Upper and Lower Limbs. Is There Any Difference?

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Cortical bone plays a major role in case of fracture of long bones such as radius, femur and tibia. The mechanical properties of bones are related to their daily loading. It is assumed that upper limbs (non-load-bearing bones) and lower limbs (load-bearing bones) in humans have different mechanical and structural properties. To have a deeper insight into the mechanical characteristics and structural features of human cortical bones, the goal of the present study was to evaluate paired anatomical specimens from upper and lower limbs. Thirty-two subjects (50 – 98 y.o.) were included in the study. Cortical bone specimens were extracted in each subject from distal radius, femoral neck, femoral diaphysis and tibial diaphysis. The specimens were loaded in quasi-static mode until failure to determine the toughness properties. Specimens from 8 subjects, among the 32, were selected to perform synchrotron radiation micro-computed tomography (voxel size 0.7 μm3). Haversian system, osteocyte lacunae and linear micro-cracks were quantified. Surprisingly, the cortical bone from the radius was found to have a higher resistance to crack propagation in comparison to cortical bone from the femur and the tibia, under quasi-static loading (Gauthier et al., 2017, J. Mech. Behav. Biomed. Mat 71: 223-230). As the femur and the tibia are load-bearing bones, we thought that they should present higher mechanical properties compared to a non-load-bearing bone. The analysis of the samples' microstructure using synchrotron radiation showed differences between the radius and the femur (e.g., a lower volume fraction of osteonal canal in the radius compared to the femur; Gauthier et al., 2018, J. Struct. Biol. 204:182-190). When analyzing the volume fraction of micro-cracks in samples subjected to the mechanical tests, a higher micro-crack density was measured in the radius compared to the femur (Gauthier et al., 2019, J. Biomech. 85: 59-66). These results suggest that the higher resistance to crack propagation (toughness) in the radius compared to the femur is partly due to the tissue capacity to form micro-cracks to dissipate energy before failure. Ethical statement: The bones were provided by the Departement Universitaire d'Anatomie Rockefeller (Lyon, France) through the French program on voluntary corpse donation to science.

Stepwise Changes in Pectoral Appendicular Muscle Anatomy and Function over the Water-to-Land Transition in Tetrapods

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While the origin and early evolution of the limb skeleton are fairly well studied, those of the muscles remain largely unknown. We sought to fill this gap by reconstructing changes in osteological range of motion (RoM) and muscle leverage over the tetrapod water-to-land transition. To do so, we built 3D-biomechanical models of the pectoral appendages of three fossil taxa: the tetrapodomorph fish *Eusthenopteron*, the Devonian stem tetrapod *Acanthostega*, and the Carboniferous stem tetrapod *Pederpes*. We also built similar models of four extant taxa – a coelacanth, a lungfish, a salamander, and a lizard – and compared the leverage of various muscle groups over a range of limb postures. Our results suggest a series of functional changes across the water-to-land and fin-to-limb transitions, from *Eusthenopteron*, whose RoM and leverage appear very similar to extant lobe-finned fish, to *Acanthostega*, which shows restricted long-axis rotation and increased leverage of shoulder rotators, possibly functioning to stabilize the limb for station-holding, and finally *Pederpes*, which shows increased RoM in flexion/extension and increased leverage of elbow supinators and extensors, which may have helped to support and propel the body forward on land. The actions of individual muscles in the forelimb of *Pederpes* appear very similar to those of the salamander, but with less RoM for the extensive shoulder rotation associated with salamander-like gaits. Similarly, previous studies of the stem tetrapod *Ichthyostega* showed extremely restricted long axis rotation at the shoulder. Together, these findings imply that the earliest tetrapods employed very different locomotor strategies compared to those observed in extant vertebrates. Combined with experimental observations, these types of models can give insight into the paleobiology of extinct tetrapods and the ways in which animals adapt to novel environments.

Changes in Relative Bone Strength through Hominin Evolution in Relation to Mechanical Loadings and Metabolic Trade-Offs

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Previous studies have suggested a possible trade-off between energy expenditure devoted to brain and muscle development during hominin evolution. Limited comparisons of long bone diaphyseal strength to articular size in several early hominin specimens, including A.L. 288-1 ("Lucy"), appeared to support this proposition. In the present study, we extend these analyses to a larger number of fossil hominin specimens and include comparisons of bone strength to estimated body size. The polar section modulus, an index of average bending and torsional strength, was determined using computed tomography or multi-plane radiography in 36 Plio-Pleistocene hominin midshaft femora and 24 mid-distal humeri. One hundred modern humans and 20 chimpanzees and female gorillas of known body mass were used as comparative samples. Body mass in hominin specimens was estimated from femoral head size using recently developed equations or from bi-iliac breadth, and estimated stature when possible. The product of body mass and femoral or humeral length was used as the most mechanically relevant body size parameter. Results show that chimpanzees and gorillas have consistently stronger femora and humeri relative to body size than modern humans, with a greater difference in the humerus because of its locomotor functions in non-human taxa. The earliest hominins in the sample, including *Orrorin tugenesis* (BAR 1002'02, 6 Ma), *Australopithecus afarensis* (A.L. 288-1, 3.18 Ma), and *A. africanus* (StW 431 and 99, 2.4 Ma), are very similar in relative strength of both bones to chimpanzees and gorillas (except the StW 99 femur). All *Homo* specimens, from the Early through Late Pleistocene, fall within the modern human range of strength versus body size, although generally within its upper half for the femur. Thus, prior to the transition to *Homo*, early hominins exhibit relative long bone strengths more typical of non-human taxa, supporting the metabolic trade-off scenario.

From Axolotls to Athletes: How Loading Affects Bone Shape during Growth

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Altered loading during growth can affect joint and bone morphology. In this presentation, we will explore the tools, experiment, and models we have used to examine the role of mechanical loading in bone growth. We have used the Mexican axolotls to examine the effects of mechanics during limb regeneration, in particular joint morphogenesis. We used click-chemistry to label cell proliferation and protein output during regeneration, and imaged the limbs with light sheet microscopy. Blocking muscle contraction via neurectomy or blocking mechanosensitive ion channels in the cells of the developing limb resulted in altered joint morphology, reduced cell proliferation, and altered chemical signaling (Ihh and PTHrP) involved in limb bud differentiation. This study shows how we can examine the cellular and molecular pathways of altered loading *in vivo*. Elite adolescent athletes also suffer alterations during joint development; in particular, the condition femoroacetabular impingement affects the hips of ice hockey, soccer, and basketball players. We used sensors to measure the motion of the hips during practice to identify stereotypical motion patterns. We measured athletes in a motion capture lab and found these motion patterns carried over into activities of daily living, particularly anterior pelvic tilt. We used finite element modeling to evaluate the effects of altered loading on the growing bone and simulate formation of femoroacetabular impingement. Understanding the role of loading during growth may inform prevention strategies that ensure normal bone growth. Ethical statement: All human data was collected with Internal Review Board approval from the associated institution.

The Evolution of Skull Form and Function: Finite-Element Solutions to Infinite Problems? – Organizers: David Button, Laura Porro, Marc Jones, Jen Bright

Challenges and Solutions for Structural Modelling of Ultra-Thin Bone: a Case Study in Bird Skulls

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Resolving fine features in tomographic scans becomes increasingly difficult as specimen size goes up, thanks to a trade-off between manageable data sizes and resolution. Bird skulls exemplify this problem, as even the largest specimens (with head lengths in the tens of centimeters) have highly curved bones a few hundred microns thick, which may blur out if data is down-sampled. It is therefore difficult to reconstruct the geometry of relatively thin bones from microCT-scans. Furthermore, flaws in a geometric reconstruction (such as holes in the surface where bones have been smoothed, or discontinuities between voxels that fail to capture highly curved structures) compound in finite element (FE) models. Such flaws may violate the mathematical assumptions of the FE-method, as the resulting elements are rarely equilateral (in surface-based meshes) or adequately connected (in voxel-based meshes) throughout the model. In industry, thin-walled structures are often modelled with two-dimensional (2D) shell elements, simplifying the geometry to preserve the mathematics. We tested the sensitivity of bird skull FE-models to different segmentation and meshing methods, constructing four surface-based models with linear and quadratic 2D-shell or 3D-tetrahedral elements, and a voxel-based hexahedral mesh from the same CT-segmentation. Additionally, we present a new method combining automated segmentation with mesh-free modelling. Mesh-free methods, while often overlooked in engineering due to their longer solve times, provide an attractive solution to biological problems: firstly, by removing the need for time-intensive manual mesh editing; and secondly, by circumventing the mathematical errors encountered when coercing a mesh to a complex geometry. We find notable differences between the methods, with 2D-meshes in particular creating abnormally high stresses. Further validation work is vitally needed to examine the best approaches for modelling thin, biological structures.

Using Biomechanical Modelling to Investigate an Adaptive Radiation: a Case Study in Dinosauria

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Adaptive radiations – rapid diversification of clades as they colonize new ecospace – are central to our understanding of the history of life, uniting concepts from ecology and evolutionary theory. Information from the fossil record is critical, but paleontological studies of adaptive radiations have often been restricted to qualitative comparison of characters of presumed mechanical and ecological significance. Empirical case studies comparing direct measures of performance through clade history have been lacking, precluding a comprehensive perspective of the dynamics of an adaptive radiation. The early evolution of dinosaurs, between 240-190 Ma, provides a case study of an adaptive radiation. During this interval dinosaurs greatly increased in size, diversity and abundance. Their myriad craniodental morphologies have raised hypotheses linking this radiation to diversification in feeding ecology. However, biomechanical studies of dinosaur crania have largely been restricted to deeply-nested taxa. Consequently, the functional morphology and feeding behavior of early dinosaurs remains poorly understood. Here, we reconstruct the cranial osteology and myology of multiple early dinosaur taxa, and quantify functional performance through finite-element analyses (FEA) replicating feeding behaviors. Results demonstrate differences between theropods and ornithischians consistent with early specialization towards carnivory and herbivory, respectively. However, early sauropodomorph taxa exhibit mechanical compromises leading to more generalized performance. This suggests the rapid diversification of sauropodomorphs in the Triassic was linked with dietary flexibility, rather than specialization. These data permit quantitative comparison between functional performance and diversity dynamics during an adaptive radiation. They highlight the utility of FEA in elucidating patterns preserved in the fossil record, and present solutions to problems inherent in modeling fossil taxa.

Using Finite Element Analysis to Assess the Impact of Gape on Cranial Biomechanics

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Finite element analysis (FEA) has been used extensively over the last two decades to further understanding of vertebrate feeding biomechanics. One aspect of feeding that has been often neglected in FE-studies, however, is gape. The angle to which the jaws are opened during biting can greatly impact stress and strain patterns across the skull. In this case study, biting across a range of gapes was simulated in the skulls of two primates, an aye-aye (*Daubentonia madagascariensis*) and a ring-tailed lemur (*Lemur catta*). It was hypothesized that the aye-aye skull would perform better than that of the lemur at wider gapes, as the aye-aye habitually uses a wide gape when stripping bark from trees during feeding. FE models of aye-aye and lemur skulls were created in Avizo and Vox-FE. The models were loaded with muscle forces derived from published PCSA data and constrained to simulate biting on the anterior teeth. Muscle force vectors were rotated caudally to simulate a range of different gapes between occlusion and 90 degrees. Stress, strain, deformation and bite force were extracted from the solved models. Results showed that, in both species, as gape increases, cranial stress, deformation and biting efficiency all decrease, and strains become more concentrated in the temporal region of the skull. The aye-aye and the lemur show a similar median stress across the skull at gapes up to 45 degrees, but the aye-aye is able to reduce stress more than the lemur at wider gapes. Similarly, aye-aye and lemur skulls deform to a similar degree at occlusion, but as the jaws open, the aye-aye skull deforms less than the lemur. Overall, the results suggest that the aye-aye skull may be better adapted to biting at wide gapes than the lemur skull, as was predicted from feeding ecology. This case study has shown how gape can be incorporated into FE models in a relatively simple way, and has demonstrated the insights that this can bring to form-function analyses of the skull.

The Effect of Naturally Occurring Palate Clefts on Feeding Performance in Bats: Insights from Finite Element Analysis and Comparative Phylogenetics

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How does the evolution of novel morphological traits impact skeletal function and performance? This is a challenging question to answer, especially in the case of traits that are widespread within a lineage but deleterious in others. Cleft palate is a rare congenital condition in mammals in which the incisor-bearing premaxilla bones of the upper jaw develop abnormally. However, naturally occurring, non-pathological cleft palates have evolved multiple times in bats (Order Chiroptera), and are present in over 50% of all bat species. In this study, we used the largest bat family, Vespertilionidae, as a model system to explore evolutionary patterns in cleft morphology, and test if variation in cleft morphology is correlated with skull shape in this group. To do so, we applied linear and 3D-geometric morphometric analyses within a phylogenetic framework. Then, we used finite element analysis (FEA) to experimentally test how the presence of a cleft palate impacts skull performance during biting in a species with extreme cleft morphology (hoary bat, *Lasiurus cinereus*). We constructed and compared the performance of two FE models: one based on the hoary bat's natural skull morphology, and another with a digitally filled cleft that approximated a complete dental arcade. We found that anteroposterior length and mediolateral width of the cleft are correlated with skull shape in Vespertilionidae, with narrower, shallower clefts seen in more gracile skulls and broader, deeper clefts observed in more robust skulls. Results from FEA indicate that the model with a natural cleft was less efficient at transmitting muscle force into bite force, had higher stress, and higher strain than the model with a filled cleft. These results demonstrate that cleft palates in vesper bats reduce biting performance, and that bats with larger clefts may compensate for reduction in performance by evolving more robust skulls.

Correlation between Shape and Biomechanical Indicators in the Armadillo Skull Complex (Cingulata: Xenarthra)

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Xenarthrans are an American mammal clade that had a huge diversity in the past, reaching its maximum of disparity in the Pleistocene, with bizarre forms as ground sloths and glyptodonts. Armadillos are the most diverse extant xenarthran group, comprising 21 species. Together with the extinct pampaterids and glyptodons, they constitute the Cingulata, characterized by the presence of a carapace. Contrary to the general belief that armadillos are basically insectivorous, different species have a wide range of diets that can include items as diverse as roots or carrion. This is expected to have implications in cranial and mandibular biomechanics, because while social insects do not need to be chewed, other items (including other invertebrates) need to be processed before the animal swallows it. Despite the dietary specializations (namely specialist insectivores, generalist insectivores, and omnivores), their teeth, as in all xenarthrans, are not specialized but reduced, and lack enamel. Therefore, their teeth are bad indicators of their diet, and their mandible is the most used anatomical element in ecomorphological studies. On the other hand, the skull, and the mandible through its interaction with it, have constraints different from those imposed by feeding behavior, so those structures are expected not to be fully optimized for chewing. In this work, we aim to disentangle which parts of the skull and the mandible correlate with the biomechanical functions, and which parts vary in relation to other factors, combining different variables obtained from a Finite Element Analysis (as a biomechanical proxy) with shape analysis. This work was supported by the CERCA Programme/Generalitat de Catalunya, the Ministerio de Economía, Industria y Competitividad (project CGL2017-82654-P) and 2014 SGR 1207.

Comparisons of Biomechanical Performance between Phorusrhacid (Aves, Cariamiformes) Skull Types

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The extinct, predominantly South American Phorusrhacidae comprise small to gigantic Cenozoic terrestrial predators without close functional analogues, making reconstruction of their feeding behavior particularly challenging. Two skull morphotypes have been described: terror-bird type and psilopterine type. In the present study, an integrative finite element analyses (FEA) was performed on the skull and jaw of *Andalgalornis steulleti* (terror-bird type), and *Llallawavis scagliai* (psilopterine type) to assess the cranial performance during trophic item capture. Anteroposterior, dorsoventral and lateromedial forces were simulated, applying published bite forces on 3D-models generated from CT-scans. The occipital condyle and articular area of the jaw were constrained in space. Both skulls show higher stresses under lateral loadings, but lower under dorsoventral and "pullback" simulations, meanwhile the jaw shows higher stress under dorsoventral and lateromedial loadings. Larger phorusrhacids such as *Andalgalornis* have sturdier skulls and jaws, which results in lower stresses when compared with *Llallawavis*. The palatal region and the craniofacial hinge (absent in *Andalgalornis*) are particularly sensitive in smaller phorusrhacids. While the "terror-bird" type could be considered as an evolutionary specialization, these two morphotypes may have had a similar performance when handling prey. Phorusrhacids´ craniomandibular complex indicate that prey handling based on rapidly catching the trophic item and tearing it apart through caudally directed movements of the head would not pose risk to the beak. It is inferred that all phorusrhacids had similar functional biomechanical performance, playing the role of active cursorial predators with a very particular type of hunting: using their beaks with precise dorsoventral strikes and pullbacks to kill their prey.

Integrating Hard and Soft Tissues in Studies of Cranial Biomechanics

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The quintessential image of a skull is that of a dry bony shell with empty cavities that once contained soft tissues. Similarly, biomechanical modeling has tended to focus on the bone and its response to loading generated in feeding or locomotion. However, there is a close integration of hard and soft tissues during ontogeny and throughout life. This close association has long been understood by craniofacial clinicians and biomedical engineers, but has received less attention in broader comparative studies. The inclusion of non-muscular soft tissues in biomechanical models has been hindered in part by technical limitations because finite element (FE) modeling of soft tissues can be challenging. Thin structures such as sutures require high resolution tomographical data, and their proper representation between cranial bones necessitates the generation of ultrafine and therefore much larger FE meshes. In addition, measuring reliable material properties of soft tissues is experimentally more difficult, and modeling their non-linear behavior requires computationally more demanding non-linear solutions. Yet, our work has shown that adding soft tissues in the FE model can bring interesting insights to our understanding of cranial biomechanics. Soft tissues such as sutures, ligaments, and fasciae can impact the deflection and strain in the cranial bones generated by feeding loads. For example, we found that the inclusion of the quadratojugal ligament in the ornate monitor lizard decreased strain in the quadrate, but the inclusion of the temporal and palatal fasciae had little effect in a mammalian model like the rat. Finally, the inclusion of soft tissues in FE-models can also bring important insights to our understanding of the biomechanical constraints acting on important non-skeletal structures during ontogeny and throughout life, or in pathological conditions.

Cranial Form and Function on Late Triassic Giant Aquatic Amphibians

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Finite Element Analysis (FEA) is currently widely used to disentangle different controversial form-function biological relationships based on inductive, deductive, or both approaches. Validation and sensitivity analysis are of special interest, but difficult or impossible to assess in some cases. In this sense, FEA has been previously correlated with histology and suture morphology. Herein, we merge FEA with histological results, suture morphology, but also microstructural characters (i.e., thickness and compactness), as a helpful tool to correlate and validate FEA results. Of particular interest, microstructural characters could be used as a proxy to estimate the biomechanical loadings and the latter correlated with FEA results to better understand tensile-compressive regime on fossil tetrapods. We used the well-known Late Triassic group of metoposaurids as a case-study. These animals were very large aquatic anamniotic temnospondyls with a worldwide distribution. FEA, cranial and mandibular suture morphology as well as cranial microstructural characters, together with other information sources (i.e., sedimentology) suggest that these animals were capable to adapt to the seasonal changes of water level in their environments (lake and rivers). During wet season and high water levels, metoposaurids possibly used two foraging techniques: ambush (using bilateral biting) and active predators (using lateral strikes of the head) while during the dry season, their swimming behavior was less active. This influenced the animals' feeding mode, particularly using only ambush strategy (under bilateral biting). However, biomechanical behaviors are still open to debate and suggest that the loading regime on the most posterior part of the skull is more complex than previously thought. Future research on these animals should focus on the muscles connecting the skull with the vertebral column to test the biomechanical capabilities of this region.

The Biomechanical Role of the Predentary Bone for Feeding in Billfishes

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Billfishes are a group of fast, pelagic fishes characterized by the elongation of their upper jaw into a bill or rostrum, giving the name to the group. This structure has a relevant role in feeding, and species-specific rostrum morphologies have been linked to a range of different feeding behaviors and biomechanics. While the bill plays a major role in prey processing, the lower jaw also presents distinct features that have not yet been considered in previous works. Perhaps one of the most interesting characteristics of the lower jaw in billfishes is the presence of the predentary, a distal bone seen in Istiophoridae (marlins and sailfishes) but absent from their sister group, Xiphiidae (swordfishes). We investigated the role of the predentary in billfish feeding using Finite Element Analysis, hypothesizing that the predentary reinforces the symphysis of the more robust istiophorid jaws to prevent torsion and "wish boning", thus allowing istiophorids to withstand the larger bite forces they are known to exert relative to the xiphiids. Finite Element models of the lower jaws of a blue marlin (Isophoridae: *Makaira nigricans*) and a swordfish (Xiphidae: *Xiphias gladius*) were constructed from CT-scans, and Von Mises stresses were compared. Models were scaled to avoid size differences and loaded at the insertion point of the adductor muscles using values from muscle cross-sectional areas. Results show lower stresses along the lower jaws of the blue marlin during unilateral loading, indicating that the predentary could help resist torsion. Indeed, virtual removal of the predentary bone in the blue marlin modified the patterns of lower jaw stress. The functional implications of the predentary, in addition to other morphological differences between the lower jaws of these two families of billfishes, give further insight into the differences in the group's feeding biomechanics and behaviors.

When Things Get Bendy - Evolution of Vertebrate Skull Kinesis

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Although we are intimately familiar with our robust, akinetic mammalian cranium and mandible, the vertebrate tree offers abundant evidence of strong selective pressures driving the evolution of skull kinesis. The lower jaw, for instance, shows impressive convergent evolution of additional articulations, but the function of these intramandibular articulations has only been studied comprehensively in aquatic biters. In contrast, suction feeders tend to stiffen the mandible and acquire elaborate suspensorial articulations to aid jaw protrusion. Kinesis between the lower jaw and cranium is also common with new data suggesting convergent evolution of propalinal as well as transverse jaw movements. Additional innovations in articulation are found between the upper jaw and cranium, and within the cranium itself. Quantifying functional variation associated with skull kinesis requires data enrichment in two key areas: Developmental data is needed to define articulation (how do we distinguish flexible sutures and joints?). Understanding how articulations are actuated requires data on muscle-tendon action driving orofacial behaviors. Due to technique limitations we have only recently begun to measure force from disparate craniofacial systems across the vertebrate tree. Coincidentally, finite element modeling validations via strain-gauge measurements may be an untapped source for data on the evolution of craniofacial kinesis across vertebrates.

Fossil Replicants - Integrating Preserved and Theoretical Morphology in Biomechanical Analyses

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New methods in digital visualization, reconstruction and computational biomechanical analysis have significantly transformed the way in which fossils can be studied in the past decade. Facilitated by the advent of new hard- and software tools, these techniques are now becoming routine techniques in vertebrate paleontology. However, by their very nature, vertebrate fossils are often incomplete, broken or distorted when they are found. Furthermore, the comparatively small sample size of most vertebrate taxa makes it difficult to account for effects of intraspecific variation, sexual dimorphism, ontogeny and allometry. This presents a significant problem for functional analysis of specific morphologies or anatomical structures and the respective comparability of biomechanical behavior. The integration of theoretical morphologies provides a versatile solution to this problem. Using digital modeling techniques a wide range of theoretical morphologies can be created, which can subsequently be subjected to biomechanical analyses to test the functional significance of morphological features. This approach not only permits the overcoming of limitations posed by the incompleteness of the fossil record and preservation but can also increase sample size significantly. Comparing theoretical models with actually preserved vertebrate morphologies allows ground-truthing this approach and testing hypotheses on morphospace occupation and convergence. Different case studies (including mandibular morphology of herbivorous dinosaur, locomotion in marine reptiles) will be presented and the advantages, disadvantages and possibilities of this approach will be discussed.

Interaction of Sutures, Dural Folds, and Muscle Forces on Cranial Loading Studied through Finite Element Analysis

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Sutures as an essential site of bone growth have been studied in many finite element analyses. Sutural growth is influenced by mechanical forces and suture stiffness affects mechanical stresses on the skull. The aim of the present study is to investigate the interaction of sutures and forces on mechanical loading of the human skull. A three dimensional CT-based finite element model of the mature skull including sutures is created. Masticatory and neck muscles forces, and forces created by falx cerebri, falx cerebelli, and tentorium cerebelli are separated in four load cases: bite and lateral pulling during mastication and inertia forces of the brain taken by the dural folds. Stresses with open and fused sutures are calculated. Results show that open sutures contribute to higher compressive stresses in the skull possibly stimulating additionally periosteal growth. Applied forces lead to dynamic loading of open sutures stimulating further growth. Lower, but still physiological loading in the superposition of the four load cases of the skull is observed with closed sutures. The main purpose of sutures is to allow cranial growth and early fusion leads to deformations and possible neurological impairments. In the mature skeleton, persistent open sutures allowing micro movements may have a positive protective function against fractures by reducing tension. Calculated physiological stresses in the model with fused sutures agree with the absence of clinical implications associated with closed sutures in the adult skull. Interactions of mechanical forces and suture stiffness as shown by finite element analysis play an important role in loading of the skull and should therefore be incorporated in simulations of cranial growth. For a potential clinical application, the consideration of further genetic and epigenetic factors as well as validation by *in vivo* models are essential.

Mandibular Biomechanics as a Key Factor to Understand Dietary Adaptations in Mammals

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The main function of the mammalian mandible is to transmit the forces generated by masticatory muscles to the teeth for food processing. Thus, trying to understand the interaction between the mammalian feeding mechanism and the ingesta that is being processed represents an opportunity to study ecomorphological adaptations in extant species. This potentially generates valuable tools for the reconstruction of oral behaviors in extinct taxa. Finite element analysis (FEA) has been conducted in a wide spectrum of mammalian jaws providing new insight into functional constraints and the adaptive value of morphology and structure of the jaw, which can be generally considered as a force transmission system. Results from FEA has been analyzed broadly in different ways that can be mainly divided into two main categories: 1) qualitative methods involving the analysis of the stress (or strain) distribution maps and 2) quantitative methods that involve the use of the numerical results. Recently, we proposed some powerful and innovative approaches to post-process the FEA outputs in a quantitative manner that were specially designed to compare several different models. These post-processing methodologies involved new concepts such as "mesh-weighted" values or the "quasi-ideal mesh", as well as introducing novel techniques such as "the intervals' method" which opened the possibility to analyze FEA outputs using, for example, multivariate statistics and/or machine-learning algorithms. The use of these new methodologies was tested by applying them to the study of chewing performance in mandibular FEA models. These models belonged to different mammalian families such as armadillos, ungulates and primates. The obtained results successfully showed that using biomechanical data it is possible to effectively discern dietary preferences. Moreover, the use of machine-learning algorithms allowed advancing a dietary classification of the fossil taxa studied.

Modelling Calvarial Development in Mice Using Finite Element Method

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During the early stages of postnatal development, in concert with the radial expansion of the skull, the mechanical properties of the calvarial bones change and the visible gaps at the sutures reduce to micro/nanometer gaps where the sutures differentiate to bone. Our understanding of the level of loading that sutures experience during the development is limited. The aim of this study was to develop a validated finite element (FE) model of a normal mouse calvarial growth to estimate the level of mechanical strain that sutures undergo during the development and to predict the pattern of bone formation at these joints. First, a series of ex vivo studies based on micro-computed tomography were carried out on wild type mice (*Mus musculus*, C57BL6/J) at 11 postnatal (P) ages from P3-42 to quantify the morphological changes during the calvarial development. Second, mechanical properties of the calvarial bones (frontal and parietal) were characterized in a total of 11 mice (over 3 age ranges) using nanoindentation. Third, the FE-method was used to model the postnatal radial expansion of the mouse skull from P3-P10 and to model the bone formation at the sutures using a bone formation algorithm. Calvarial length, width and height all gradually increased until ~P20. The elastic modulus of the frontal and parietal bones gradually increased from 5.32±0.68 and 4.33±0.18 GPa at P10 to 7.14±0.79 and 6.30±0.47 GPa at P20, and then to 9.4 and 8.7 GPa at P70 respectively (one specimen at P70). The FE-models predicted the radial expansion of the skull from P3 to P10 and suggested the calvarial sutures may experience hydrostatic strain in the range of 1.25-2.5% during early postnatal growth. The validated FE-models developed in this study offer significant potential to enhance our understanding of the mechanobiology of the craniofacial system, and further highlight the great opportunities offered by the FE-method in predicting morphological changes that occur during musculoskeletal development.

How Valid are Skull Finite Element Models and Does it Matter?

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Finite element analysis (FEA) is increasingly applied to studies of simulated biting in mammals. The aim is to predict cranial skeletal deformation, to assess covariations between performance in resisting loads and related factors such as skeletal form, remodeling activity or diet and feeding. But how valid are the results of cranial FEA and to what degree do errors impact model performance? Validity is not assessed in every study because it is not possible with museum or fossil material. Further, validation studies require considerable investment of time and resources as well as access to specialized equipment. Sensitivity studies are more common and these are useful to understand the effects and relative contributions of different modeling parameters to model performance, but they do not tell us if predictions mirror reality. This presentation addresses the validity and sensitivity of primate cranial FE-models by reviewing a series of ongoing studies detailing the impact of variations in model geometry, material properties, loads and constraints on subsequent predictions of cranial deformations. On the whole, predicted deformations are sensitive to all of these parameters and errors in their estimation impact validity to greater or lesser extent. Practical limitations in estimating parameters mean that it is unlikely that, with current technology, cranial FE-models will reliably predict strains, especially when detailed experimental data are not available to refine modeling. These studies suggest that FEA is best applied to understanding the consequences of variations in anatomy and loading, through experimental manipulation of single models. Where differences in performance among individuals are of interest, modeling should be undertaken in as controlled a manner as possible and the results interpreted cautiously, acknowledging, and where possible quantifying, the effects of modeling simplifications and errors.

The Effect of the Relative Timing of the Muscle Force on the Biomechanics of the Primate Mandible

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Morphological variation in the non-human primate mandible has been linked to variation in mandibular strain, stress and deformation regimes during feeding. In a validated finite element model (FEM) of a rhesus macaque mandible (*Macaca mulatta*), simulated unilateral chewing from two loading conditions resulted in: lateral transverse bending of the balancing-side corpus; high tensile strains in the lingual symphysis; compressive strains on the buccal surface of the balancing-side corpus and negative sagittal shear in the symphysis. However, strain patterns in the corpus likely vary throughout the power stroke *in vivo*: in particular, strains in the lingual symphysis probably peak late in the power stroke, as the balancing-side deep masseter wishbones the mandible. To investigate variation in mandible strain regimes during the power stroke, we modelled the mandibular stress and strain regimes as loading regimes vary through the power stroke. Our results show that peak principal and shear strains in the lingual symphysis and balancing-side corpus occur towards the end of the power stroke (i.e., between 40-50% of the gape cycle), when the activation peaks of the working- and balancing-side superficial masseters and medial pterygoids have started to decline, and the balancing-side deep masseter force peaks. These results yield a more complete understanding of the full range of loading, stress and strain regimes acting on the macaque mandible during chewing. Future comparisons with these regimes during other behaviors will shed light on the full range of stress and strains experienced by the mandible during feeding. Funding was provided by: ERG-MACACA 267207; CIHR MOP-4918; NIH RO1DE023816 and R24 HD050837-01; Brain Research Foundation; Monash University, NSF BCS0962677.

Suture Shape and Skull Function across the Water-Land Transition

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The emergence of vertebrates from the water and their conquest of terrestrial environments was a key moment in the history of life marked by dramatic skeletal evolution. Profound changes in skull shape, a reduction in the number of cranial and mandibular bones, shifts in the size and distribution of the teeth, and presumed changes in jaw muscle architecture have been associated with the development of new feeding mechanisms and diets, and/or differing environmental constraints. Experiments on living animals have demonstrated that sutures – fibrous joints between skull bones – impact overall skull mechanics, and different suture shapes are associated with particular load regimes. High-resolution micro-computed tomography (CT) was used to capture skull shape in fossil tetrapod skulls spanning the transition – from the Late Devonian to the Early Triassic – as well as in extant relatives, including visualizing and characterizing suture shape to predict load regime within the skull. The predominance of overlapping contacts suggests highly variable load regimes in the skulls of *Polypterus* and tetrapodomorph fish such as *Eusthenopteron*, perhaps associated with suction feeding and an aquatic lifestyle. In contrast, the skulls of later stem tetrapods such as *Acanthostega* and *Crassigyrinus* feature interdigitated sutures associated with compression; their distribution appears to have channeled forces from the teeth to the skull roof, suggesting a more consistent load regime dominated by biting. After correcting for taphonomic damage and distortion, 3D-reconstructions from CT-data served as the basis for finite element models of the skulls of early tetrapods and their extant relatives. We compare skull mechanical response under simple feeding loads in finite element models to load regimes predicted by suture shape, including validation of model results using experimental data from living taxa.

How Valid do Our Models Need to Be, and What Use is Stress and Strain Anyway?

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Finite element analysis (FEA) is a method to estimate how a structure mechanically responds to the application of external loads. It is commonplace in engineering analysis and over the past 15-20 years has been used increasingly in paleontological and zoological studies. Despite this, we still lack a broad comparative consensus on how accurate FE models of biological structures can be, and indeed the degree to which this matters, and how the metrics generated by FE relate to organismal performance and evolution. This talk addresses these two key questions. Firstly, how valid are our models, and indeed how and at what level do we determine model validity? A framework for hierarchical levels of accuracy is proposed, which also applies to comparative studies of extant and extinct taxa. Secondly, explicit or implicit to FE studies is the expectation that output metrics such as stress, strain or deformation are in some way related to the performance of the organism, and, that variation in these parameters may confer a fitness and hence selective advantage to the bearer. What is the evidence for selection or optimization of mechanical parameters in evolutionary morphology, and how may we address this question further in the future?

Joint Loading and Transformation in Suchian Evolution

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Modern crocodylians employ immense forces during feeding. Many characters that enable crocodylians to generate and resist these forces are not found in their ancestors, and thus the evolution of crocodylians involved a substantial reorganization of the feeding apparatus. Once this suite of changes was in place, crocodyliforms radiated into forms with derived diets and craniodental modifications. To assess the biomechanical effects of changing configurations of muscles and cranial joints, we used CT-data to create 3D-models of extant and fossil suchians that demonstrate the evolution of the crocodylian skull, using osteological correlates to reconstruct muscles. Muscle forces were distributed with the computational package Boneload and used as input for finite element analysis and 3D-lever analyses. We found that jaw muscles expanded and shifted attachments throughout suchian evolution: muscle orientations became more mediolateral as the skull flattened, the pterygoideus ventralis muscle began inserting on the lateral mandible, and the depressor mandibulae muscle expanded its attachment on the enlarged retroarticular process. Changes to cranial joints accompanied muscular changes: the pterygoid buttress expanded, the articular surfaces of the jaw joint changed, and the quadrate and palate sutured to the braincase. Our results showed that joint force orientation tracks with articular surface metrics. We found that as bite location moves caudally, working side joint force decreases in magnitude; it is likely that in feeding events such as shaking bites or death roll, the jaw joint is loaded in tension. This study depicts a feeding apparatus that defies traditional understanding. The combination of dual craniomandibular joints and jaw joints loaded in tension is unknown from the rest of tetrapods.

Interspecific Variation in Mechanical Performance of the Hominid Mandible

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Mandibular morphology varies among hominin species but the mechanical significance of this variation is not well understood. Variation in symphyseal depth and inclination, corpus thickness, height and orientation of the mandibular rami and divergence of the posterior tooth row have all been hypothesized to be functionally related to feeding. According to previous work, these features should serve to reduce bone strains, increase biting efficiency, or both. However, whether these features function together to produce species-specific deformation patterns and strain regimes or to bolster feeding performance has not yet been evaluated. Here, we use finite element analysis to examine the biomechanical implications of mandibular shape variation within and across species of extant great apes and humans. Geometric morphometric methods were used to analyze mandibular shape variation in male and female *Pan* (10 F,16 M), *Pongo* (9 F,10 M), *Gorilla* (9 F,13 M) and *Homo sapiens* (24 F,28 M). Eight FE models (FEMs) were constructed from the CT-scans of the specimens identified as closest to the mean male and mean female morphology for each species using shape-space principal coordinates analysis. FEMs were assigned the material properties of bone, loaded with equivalent muscle forces and constrained to simulate maximal bites at multiple locations along the tooth row. FE results indicate variation in strain magnitudes but broadly similar deformation and strain regimes across taxa. Primary deformation and strain regimes include sagittal bending, axial twisting and sagittal shearing of the mandibular corpora and lateral transverse bending ('wishboning') and frontal shear at the symphysis. Overall, our results accord with previous FE and *in vivo* strain studies of the macaque mandible and suggest basic similarities in primate mandibular mechanics. The extent to which mandibular variation impacts feeding performance is the focus of our ongoing work. Ethical statement: All procedures (i.e., CT-scanning) utilizing skeletal material were non-destructive and performed according to ethical standards of the American Museum of Natural History and the International Council of Museums.

Simulated Evolution Suggests Selection-Mediated Generation of Complex Structure-Function Mapping in the Primate Cranium

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Redundancy, a prominent feature of complex biological systems, is thought to represent a primary factor characterizing structure-function relationships in the vertebrate cranium. Although many studies have demonstrated the presence of redundancy in complex structure-function mapping of the vertebrate masticatory system, the mechanisms by which selection generates or acts on redundant systems have only been speculated. Here, we use a new functional morphological simulation framework to demonstrate that strength and duration of selection, standing morphological disparity, and evolutionary starting point all can interact to generate substantial functional morphological redundancy in the primate skull. We modeled simple structure-function relationships in primate bite biomechanics and subjected the hypothetical primate ancestor skull shape to biomechanics-driven, iterative selection-based evolution. Results indicate that even when selection is modeled to occur in simple, planar adaptive landscape surfaces in all shape components, evolutionary outcomes exhibit significant many-to-many structure-function mapping. Redundant structure-function linkages are present over a range of selective pressures, and maximal selective pressure generates predictable morphological outcomes that are sub-optimal in functional attributes. These simulations suggest the presence of moderate to high selective pressure could generate functional redundancy in primate cranial shapes; cases of one-to-one structure-function linkages are consistent with short-duration, very-high selective pressure that favors local, rather than regional or global, functional optima.

Functional Morphology of the Zygomatic Arch and the Zygomatico-temporal Suture in Primates

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By means of finite element solutions we found that the zygomatic arch in primates is stabilized during biting by a synchronized tensioning of the temporal fasciae acting to oppose masseteric contraction forces. During temporalis muscle bulging the forces generated within the tensioned temporal fasciae are large enough to oppose the pull of m. masseter with minimized bending in the parasagittal plain of the z. arch. The frontal MRI-section through the head of a chimpanzee shows aside the skeletal structures running lines of action of the temporal fasciae and the masseter muscle. The vector sum of both forces results in a medially directed load on the z. arch. A more or less curved form of the z. arch depends on the magnitude of bite muscle forces. The zygomatic and temporal bones including the zygomaticotemporal suture are working during muscle activities under compression in a stable connection. Lateral pulling on the frontal jaws during biting will impose bending moments in the skull inducing compressive stresses in the z. arch on one side and tensile stresses on the other. A spatial addition of bite and lateral pulling stress vectors in the z. arches define the suture orientation. In the case that a z. arch will have to bear tensile stress the zygomaticotemporal suture forms a small gap with a definite stop on this sliding movement. The slipway is formed by a number of lamellae for a guided movement. Under critical tensile stress the facet of the zygomatic bone leaves the alinement with the temporal bone allowing additional movement to preserve the zygomatic arch against fractures. Finally the finite element structure synthesis (FESS) can be used to generate a zygomatic arch out of a homogeneous volume as its bauraum only by loading through variable resultant vectors of tensioned tissue. That sheds light on variable stress conditions and resulting structures during ontogenesis and phylogenetic adaptations.

Evodevo of the Vertebrate Mouth: An Exploration of the Relationships of Oral Organs – Organizers: Abigail S. Tucker, Maria Hovorakova

Linking Teeth and Taste Buds to the Evolution of Tooth Regeneration

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The shark dentition is continuously regenerative. Teeth form from a continuous and permanent epithelial dental lamina. Previously we discovered an intriguing link between the regenerative potential of the shark dentition and the oral taste bud field, both emerge from a common epithelium during development. RNAseq analyses on specific cell compartments within the continuous dental lamina and cells from the taste-tooth junction, have uncovered a common set of candidate genes involved in the initiation and maintenance of continuous dental regeneration. Our data provide new information on novel markers associated with tooth regeneration, timing and cyclicity of the shark tooth system, and the origins of dental regeneration. With these data we can start to construct gene regulatory networks as a tool to further investigate the functional role of these potentially important candidate genes. Our findings shed light on the regulation of both the timing of continued dental redevelopment and the maintenance of stem progenitors for rapid tooth turnover in an exciting and emerging EvoDevOmic model, the shark.

Quantifying Morphogenesis in Ectodermal Placodes and Skull to Link Molecules to Phenotypes

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The craniofacial region is one of the most complex parts of the body and although there is a large body of literature on evolution and genetics, knowledge of the cellular processes that generate it is surprisingly limited. We are analyzing morphogenesis processes at two different scales using highly quantitative methods. We present an analysis of the formation of ectodermal placodes, specifically the teeth and salivary glands based on cellular measurements. We show that both involve a common and unexpected cellular behavior that we have named "vertical telescoping" in which epithelial cells create an invagination through active vertical migration. To understand gene-morphogenesis relationships more broadly, we have developed a novel landmark-free morphometrics pipeline that will be suitable for analysis not only of adult phenotypes (such as skull shape) but also for landmark-sparse shapes found in embryos. We have applied this method to the analysis of the craniofacial phenotype of a model of Down Syndrome.

Relationship of the Vestibular and Dental Laminae in Mammals: Cheek and Tooth Relations

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The oral vestibule in humans is the area located external to the dentition and lined by the gums, lips and cheeks. It is frequently a place where pathologies appear that show the presence of dental tissue, such as peripheral odontomas or dentigerous cysts.

Non-erupted or erupted tooth-like structures may also be involved. The oral vestibule forms from the vestibular lamina (VL) during development. The VL is composed of several epithelial structures that appear discontinuously in the vestibular area during early odontogenesis. These epithelia develop in close association with the dental epithelium of both the upper and lower human embryonic jaws and at certain stages appear similar to the shape of a tooth germ in histology. Using tamoxifen inducible Cre-LoxP system, we traced the progeny of early Shh expressing cells associated with the forming dentition located in the anterior of the lower jaw in mice at E12.5. Shh is normally expressed in the forming dental lamina but not in the vestibular lamina, and is associated with odontogenic potential. Interestingly, lineage tracing showed that Shh expressing progeny were shared between the developing incisor tooth germs and the adjacent vestibular lamina (24/48/72/96/120 hours after the tamoxifen injection activating recombination in Shh expressing cells). Strikingly, the Shh progeny only contributed to the inner epithelial layer of the vestibular anlage, suggesting unappreciated differences between the labial and lingual sides of the VL. Thus the early developmental events in the embryonic anterior mouse mandible are common to the vestibulum oris and the prospective incisor primordia. Our findings help to explain the developmental background of pathologies where dental tissues develop in the vestibular area, since the original odontogenic potential of epithelial cells in the embryonic anlage of the oral vestibule could be awaken under pathological conditions. This might lead to the formation of dental pathologies in the area external to the dentition. Funding: Grant Agency of the Czech Republic (18-04859S).

The Turing Instability of Teeth and Palatal Ridges Signaling Centers during Oral Development

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Teeth and palatal ridges (also called rugae) are epithelial appendages in the oral cavity of mammals that may share a common phylogenetic origin. As other epithelial appendages, they develop through epithelio-mensenchymal interactions and their arrangement in periodic patterns is controlled by Turing-type mechanisms. One shared specificity is that their patterning takes place sequentially, as the jaw grows. In this talk, I will draw comparisons between the sequential formation of molars and rugae in mouse, but also in shrew. In particular, I will focus on an intriguing phenomenon, the instability of tooth and rugae signaling centers over the course of development. Using a combination of mathematical modeling and experimental data, we have shown that in mouse the formation of the first molar signaling center destabilizes the older neighboring signaling center known as R2. Because this signaling center is most likely the vestige of a premolar lost during mouse evolution, this phenomenon may at first glance be seen as a peculiarity of mouse molar formation. However, I will also show that a similar phenomenon is observed during shrew rugae formation, and therefore argue this likely reflects a common property of the development of (oral) epithelial appendages.

Pathologies of Oral Patterning - Odontogenic Tumors and Cysts

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The oral cavity is an area of numerous pathologies present not only within, but also outside the dental arch. The presence of supernumerary ectopically located teeth in non-dental areas or pathologies with dental tissue formation in non-dental areas evokes the questions how these pathologies are formed and what their origin is. One of the tissues maintaining an odontogenic potential is the prospective oral vestibule located externally to the developing dentition. In case the signaling is awoken, it might explain the presence of pathologies externally to the dentition with signs of possible tooth-associated structure formation. Also during successional dental lamina disintegration, some lamina cells remain in small islands known as the rests of Serres or as epithelial pearls. These epithelial remnants are of general interest for human clinicians because they can give rise to cysts or odontogenic tumors. Odontogenic cysts are enclosed epithelial sacs with a distinct membrane derived from the rests of the odontogenic epithelium. Odontogenic tumors are pathological lesions derived from the epithelial and/or mesenchymal remnants of tooth germs. In addition, dental hard tissue may or may not be included in these lesions. The precise mechanisms controlling the initiation of odontogenic cysts or tumors are however still unknown. Uncovering the signaling pathologies and altered cell communication between epithelial and mesenchymal components could explain the mechanisms driving the initiation of tumors or cysts in our patients. As this field is largely unexplored, an association of clinical findings with molecular events in individual patients could help us to predict the patient's prognosis and to plan directly targeted treatment. This research was supported by the Czech Science Foundation (18-04859S), the Institutional support of RVO-FNOs/2018 and by the Ministry of Education, Youth and Sports of the Czech Republic (CZ.02.1.01/0.0/0.0/15_003/0000460) to MB and EH.

The Relationship of Fangs and Glands in Snakes

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In most squamate reptiles the dental lamina, the epithelial organ producing tooth germs, develops adjacent to a dental gland. Both the dental lamina and gland primordia differentiate from the oral ectoderm, and appear to develop from a common thickening, which then splits into the two distinct fates. In venomous snakes a similar single placode appears to form both the dental lamina and the venom gland, uniting these two essential components of the venom delivery system. We have been investigating the relationship between the dental lamina and venom gland in the Egyptian cobra (*Naja haje*) and the Monocled cobra (*Naja kaouthia*) using histology, soft tissue microCT and immunofluorescence. In both species the dental lamina in the fang region undergoes branching to create a labial and lingual sheet producing multiple synchronous fangs. These two dental lamina sheets remain connected to each other throughout development by epithelial anastomoses. The fangs also remain physically connected to the forming venom gland via epithelial connections. Immunofluorescence for epithelial markers highlights distinct patterns of gene expression in the forming fang lamina and associated gland, along with distinct patterns of innervation. Our results highlight novel features of the dental lamina specific to the fang region that appear to have evolved to allow frequent fang replacement. We also establish the close connection between fang and gland, suggesting coordinated development of these two structures to create a functional unit.

Developmental Morphology and Evolution of Amniote Eggs and Embryos – Organizers: Daniel G. Blackburn, Matthias Starck, James R. Stewart

Early Development of the Amniote Embryo from a Reptilian Perspective: a Study on Chick, Turtle and Chameleon

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Animals as diverse as avians, reptiles and mammals constitute the amniote clade. With the aim of describing a putative evolutionary path for amniotes, we studied the early developmental stages of the chicken embryo, a well-established experimental system, and compared it with members of the reptile class. We focused on gastrulation, that specific window of time during development when a three-layered embryo forms and the basis of the body plan is laid out. Amniote gastrulation has always been described with respect to human, mouse and chick development by the presence of the primitive streak, a posterior-to-anterior midline morphological cell ingression feature that has come to define amniote gastrulation. How this midline, ingression-based strategy of gastrulation evolved from the ancestral internalization via a blastopore, a circumferential involution event seen in anamniotes, is unknown. However, within the amniote clade there exists a more diverse range of gastrulation strategies than the primitive streak. We analyzed the gastrulating embryos of two reptile species, *Chameleo calyptratus* (chameleon) and *Trachemys scripta* (turtle), using diverse staining approaches. Our study suggests that reptiles undergo gastrulation utilizing strategies that stand mid-way between anamniotes on the one hand, and birds and mammals on the other: cells internalize via an incomplete blastopore, adopting a combination of involution and ingression to achieve mesoendoderm formation. Investigating the mechanisms of gastrulation in a wider range of amniotes provides a way to understand the changes that occurred during evolution from blastopore to primitive streak and gain insights into the amniote ancestor.

How Turtle Embryos Process Yolk: Evidence from Ultrastructural Analysis

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Recent studies have revealed two distinct patterns by which sauropsid amniotes cellularize and digest yolk for embryonic development. The situation found in birds traditionally has been thought to be shared by all extant reptiles. However, our lab has documented a more elaborate pattern of yolk processing in lizards and snakes. To expand these investigations to chelonians, we studied how yolk is processed in two North American species: the snapping turtle, *Chelydra serpentina* (Chelydridae) and the pond slider, *Trachemys scripta* (Emydidae). Scanning electron microscopy revealed a developmental pattern in these turtles that is very similar to that of squamates. The yolk sac cavity becomes filled with a compact mass of "spaghetti-like" strands, each formed by endodermal cells clustered around a blood vessel. This arrangement provides an effective means by which yolk is cellularized and digested, and by which its metabolic products are delivered into the blood for transport to the embryo. In contrast, in birds the endodermal cells that process the yolk are confined to the lining of the yolk sac. Existence of a similar form of yolk processing in squamates and in turtles suggests that this pattern is ancestral for extant reptiles.

Functional and Evolutionary Morphology of Yolk Processing Patterns in Reptiles

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Evolution of the amniotic egg required new ways to process yolk for embryonic development. Due to meroblastic (incomplete) cleavage, the yolk material of the early embryo is extracellular. It must be cellularized and digested before its metabolic products can fuel embryonic development. In birds, endodermal cells that line the yolk sac take up and digest yolk and release its metabolites into the vitelline circulation. Our studies of diverse reptile species have revealed a pattern of yolk processing that is very different from that of birds. In lizards, snakes, and turtles, the yolk sac cavity is filled by clumps of proliferating endodermal cells that phagocytose the yolk. Blood vessels invade the yolk sac cavity, and the endodermal cells become arranged in monolayers around them. They thereby form a compact meshwork of "spaghetti-like" strands of cells that fills the yolk sac cavity. The overall developmental pattern is well-designed for uptake, digestion, and provision of yolk nutrients to the embryo. The fact that this unexpected pattern is shared by squamates and chelonians indicates that it is probably ancestral for extant reptiles. How, when, and why this pattern was abandoned in archosaurian ancestors of birds is a subject of ongoing investigation.

How do Fetal Membranes Support Mammalian Embryogenesis? Lessons from Marsupials

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Marsupial fetal membranes support the development of a highly atricial neonate. They function well before dissolution of the shell membrane and before the choriovitelline placenta is formed. In many eutherians, the earliest stages of development likewise depend on yolk sac membranes, although this changes after establishment of the chorioallantoic placenta. Uterine secretions are the principal source of nutrition in marsupials and absorption occurs mainly through the non-vascular part of the yolk sac. Exemplified by the equine blastocyst, this can be an important route even in eutherians. The vascular portion of the yolk sac and a choriovitelline placenta appear rather late in marsupials and are often ascribed a role in gas exchange. Comparison across mammals is problematic, however, since the oxygen dissociation curve is left shifted in eutherians (facilitating gas exchange), but right shifted in marsupials. Therefore, as in eutherians, a more important role for the vascular yolk sac and choriovitelline placenta could be nutrient exchange (hemotrophic nutrition). An additional function of the membranes in marsupial and early eutherian gestation is secretion of steroids, peptide hormones and growth factors for pregnancy maintenance and maternal adaptation to the pregnant state.

Specializations for Calcium Uptake from the Eggshell of Corn Snakes: Implications for Evolution of the Reptilian Egg

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A calcareous eggshell is a shared derived trait for Reptilia and eggshell calcium is an important embryonic nutrient source for oviparous reptiles. The chorioallantoic membrane lies adjacent to the eggshell and regulates calcium mobilization and transport. Calcium transport by the chorioallantoic membrane has been most extensively studied in chickens and corn snakes. Studies of protein expression (immunoblotting) of the chorioallantoic membrane of corn snakes indicate similarities to chickens in a mechanism for calcium release from the eggshell but differences in the calcium transporting mechanism. Carbonic anhydrase II, which is implicated in a mechanism to enhance calcium solubility, is expressed in chorioallantoic membranes of both species. In contrast to chickens, the chorioallantoic membrane of corn snakes expresses calbindin-D28K, a marker for intracellular calcium transport. We report an analysis of transcriptomes from chorioallantoic membranes of chickens and corn snakes that supports data from protein expression and reveals additional candidate proteins of a functional model for the corn snake chorioallantoic membrane. We also report functional specialization among cells within the corn snake chorionic epithelium based on differences in immunohistochemical localization of either carbonic anhydrase or calbindin. These findings support the hypotheses: 1) specializations for calcium extraction and transport from the eggshell evolved soon after the evolution of a calcareous eggshell, and 2) mechanisms for calcium transport by the chorioallantoic membrane diverged in the lineages leading to either birds or snakes.

Maternal-fetal Signaling and the Origin of Novel Placental Morphologies in Amniotes

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Studying the origin and evolution of vertebrate organs is difficult because many have ancient origins and have only evolved once in the history of vertebrates. The placenta is a great model to study the evolution of novel organs because it has evolved repeatedly in many vertebrate clades, it has evolved relatively recently in some lineages, and exists in intermediate forms in extant taxa. By studying a range of vertebrates we investigated the evolution of maternal-fetal interactions in the placenta. In terrestrial vertebrates, placentas form following the interactions of two distinct tissues, the luminal surface of the uterus, and the epithelial surface of an embryonic membrane. Using transcriptomics of the uterus and embryonic membranes from oviparous and viviparous vertebrates we show that the chorioallantoic membrane of amniotes (reptiles, birds, and mammals) was ancestrally an endocrine organ. We then show that the uterus of oviparous reptiles expresses receptors for the hormones and signaling molecules produced by the chorioallantoic membrane. We argue that the novel apposition of uterine tissues with embryonic membranes is sufficient for the generation of novel maternal-fetal signaling networks. In a second example, we show that key components of implantation in eutherian mammals are the result of an ancestrally inflammatory interaction between the uterus and the apposed embryonic tissue. We argue that the interaction of placental tissues, is not merely a consequence of placenta formation, but that novel interactions form the basis of new placental regulatory networks, functions, and patterning mechanisms.

Impact of Reproductive Mode on Skeletal Development in a Reproduc-tively Bimodal Squamate

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The calcareous eggshell of oviparous lizards is an important source of calcium for embryonic development. Eggshell calcium is greatly reduced or absent in viviparous eggs resulting in a potential cost to embryonic nutrition. Previous studies of the reproductively bimodal lizard, *Zootoca vivipara*, reported larger mass and higher calcium content in oviparous hatchlings compared to viviparous neonates. We cleared and stained embryos to reveal bone development of embryonic series from oviparous and viviparous populations of *Zootoca vivipara* to test the hypothesis that skeletal development is delayed in viviparous embryos. Photographs (high magnification, calibrated to size) were used to obtain measurements of lengths of the body, humerus, femur, skull and lower jaw, and of ossified portions of limb bones. Percent ossification was scored for targeted skull bones. Results were analyzed using general linear models and revealed no differences in ossification in either limbs or skull. However, overall size of oviparous neonates was significantly larger. Findings do not support our hypothesis and indicate that reduction in eggshell calcium in embryos of viviparous populations does not negatively impact limb or skull ossification during development but does influence hatchling size.

Functional Morphology of the Avian Yolk Sac and Avian Egg Evolution

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The avian yolk sac is a multifunctional extraembryonic organ that serves several transitory functions during embryogenesis. The yolk sac develops from the extraembryonic endoderm and mesoderm. It is the site of early formation of blood cells, formation of blood vessels, and nutrient absorption. The yolk sac membrane is specialized to function as an extraembryonic absorptive organ, but it is neither morphologically nor functionally part of the embryonic gut; at least during later developmental stages, there is no open connection between the lumen of the embryonic gut and the yolk sac. Yolk absorption is largely by phagocytic activity of the cells of the yolk sac epithelium. Despite its pivotal role during development, analysis of its evolutionary history and its functional morphology have been neglected. – I have used cryo and resin embedding histology of complete developmental series of domestic quail and domestic duck to document the development of the avian yolk sac and pertinent changes of the microscopic anatomy/cytology throughout development. During embryogenesis, the yolk sac endoderm forms large villi that increase the absorptive surface and reach deep into the yolk ball. The histology of the absorptive epithelium is unique and structurally specialized for phagocytic absorption of yolk. Large epithelial cells are filled with lipid droplets. During early developmental stages, the epithelium of phagocytic cells is single layered but it eventually becomes several layers thick during later stages. Below the yolk sac epithelium is an extensive layer of hematopoietic tissue; deep in this tissue lie the yolk sac capillaries. Yolk that was phagocytosed by the epithelial cells is transported through several layers of cells before it comes to the capillaries that finally transport the nutrients to the embryo. The yolk sac epithelium is becoming apoptotic before hatching. Results are discussed in the light of evolutionary history and phylogeny of the vertebrate egg.

Fetal Membranes and Intrauterine Gestation in Viviparous Reptiles

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Placentation has evolved multiple times in Squamata, coincident with the evolution of viviparity, yet structural and functional diversity of the maternal embryonic relationship is largely unexplored. Embryonic tissues define two general types of placentation; chorioallantoic membrane and omphalopleure. A primary function of the highly vascularized chorioallantoic membrane in oviparous species is respiration. This function is retained in the chorioallantoic placenta. The omphalopleure participates in two placental arrangements, omphaloplacenta and omphalallantoic placenta. The foundation for these placental types is a unique feature of the squamate yolk sac, the yolk cleft isolated yolk mass complex. The function of this tissue in oviparous species is unknown but a distinctive characteristic is the absence of direct vascular support for the omphalopleure. In contrast to oviparous species, the omphalopleure persists to later embryonic stages in viviparous species, which suggests a novel function in viviparous species. Models for the evolution of placental specializations, which are dependent on comparative data, are limited to few lineages. In two lineages of scincid lizards, comparisons with oviparous sister taxa suggest independently derived similarity in specializations of both the chorioallantoic placenta and omphaloplacenta. Gerrhonotine lizards provide a second model for evolution of placental specializations. Yolk sac placentation is prominent and supported by a vascular system unique to this lineage. Structural specializations include similarity to both the chorioallantoic placenta and the omphaloplacenta of skinks. The chorioallantoic placenta is a highly vascular organ with thin epithelia, suggesting a respiratory function. These three lineages reveal that placental structural similarity can arise through either similar or different developmental pathways and that ancestral traits of oviparous species contribute importantly to diversity.

Evolution and Morphological Diversification of Vertebrate Appendages – Organizers: Karen Crow, Igor Schneider

Are Tetrapod Digits Homologous to Fish Fin Radials? Modulation of Shh Activity in Lungfish Fins Provides Clues

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The digits of tetrapod limbs have been regarded as an evolutionary novelty of tetrapods with no counterpart in fish fin skeletons. While paleontological data and gene expression studies in lungfish suggest that digits evolved from distal fin radials of sarcopterygian fish, strong evidence in support of this homology is lacking. Among modern lungfish, an elaborate array of distal radials is present in the paired fins of Australian lungfish, whereas African lungfish have a reduced number

of distal fin radials and South American lungfish have lost distal radials entirely. SHH signaling is crucial to digit development, as *Shh* knockout mice demonstrate digit loss while ectopic activation of SHH signaling results in polydactyly. *Shh* expression during appendage development is controlled by a highly conserved enhancer element termed ZRS. Here, we investigated the role of SHH signaling in lungfish fin radials during fin regeneration. Cloning and sequence comparison of lungfish and vertebrate ZRS revealed a 17 bp deletion of a key ETS transcription factor binding site in the African and South American lungfish but not in the Australian lungfish. Pharmacological inhibition of SHH signaling impaired regeneration, whereas its ectopic activation led to early formation of additional bone elements compatible with distal radials. Overall, our data suggests that SHH signaling, a key pathway underlying digit development in tetrapods, also controls distal radial development in lungfish fins, providing support for the homology of digits and distal radials.

How the Devil Ray got its Horns: the Genetic Basis of Body Plan Remodeling in Manta Rays and their Relatives

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Compared to sharks, the skates and rays exhibit highly modified body plans that are adapted to life on the benthos, including dorso-ventral compression with pectoral fins that extend anteriorly and fuse to the head. Patterns of morphological evolution in the pectoral fins of most batoids are constrained due to their dual use in feeding and swimming. Skates use their pectoral fins to capture prey by "tenting", and employ undulatory swimming for locomotion. However, the manta rays and their relatives (Myliobatidae) have evolved distinct pectoral fin domains that are functionally dedicated to feeding (cephalic lobes) or swimming (modified pectoral fins). Due to the presence of cephalic lobes, the mobulids have been referred to as the only vertebrate with three paired appendages. However, we found no evidence that cephalic lobes develop independently from pectoral fins. In an analysis of differential gene expression from comparative RNASeq data and *in situ* hybridization, we uncovered expression of several patterning genes that are shared between the anterior pectoral fin of skates and cephalic lobes. We found no evidence of independent posterior patterning by HoxD in cephalic lobes, and conclude that cephalic lobes are neither independent nor novel appendages. That said, both cephalic lobes and pectoral fins of myliobatids exhibit adaptations associated with specialized feeding or the evolution of the oscillatory swimming, including a redistribution of pectoral fin rays in the Myliobatidae and Gymnura that arose multiple times independently in association with pelagic flight and oscillatory swimming. Batoid fin rays are specified by HoxA11 early in development, and unique domains in anterior pectoral fin and posterior pelvic fin are specified by HoxA13. Finally, we identified candidate genes that are likely associated with subtle changes in paired fin development that may be responsible for morphological disparity among batoids.

Evolution of Skeletal Patterning in Tetrapod Limbs

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Research on the tetrapod limb is one of the best examples of how data from different disciplines – molecular biology, embryology, morphology and paleontology - have come together for a broad understanding of how appendages initially evolved and diversified. Despite the great variety in form and function of adult limb structures, comparatively late events in tetrapod limb development (e.g., skeletal patterning) seem to be conserved across different clades. Interestingly, among extant tetrapods salamanders are unique in showing a reversed, preaxial polarity in patterning the skeletal elements of the limbs, deviating from the postaxial pattern observed in amniotes and frogs. While the basic preaxial polarity is observed in all salamanders, some variation can be recognized between salamander taxa with different ecologies and life histories with respect to timing and details in the sequence of establishment of skeletal elements. Gene expression data of classic limb development genes indicate that expression is conserved compared to other tetrapods during early phases of limb development. However, notable differences occur in later phases of limb development, especially during formation of the autopod. While preaxial polarity was classically presumed to be a derived featured of salamanders, the fossil record shows that preaxial polarity in limb development was present in various Paleozoic temnospondyl amphibians. These include the 290 Ma old dissorophoids *Apateon* and *Micromelerpeton*, likely stem representatives of modern amphibians, as well as the coeval but more distantly related stereospondylomorph *Sclerocephalus*. This suggests that preaxial polarity in limb development was widespread among members of the temnospondyl lineage and may indeed be plesiomorphic for tetrapods. Hence the postaxial polarity observed in the majority of living tetrapods may represent the derived pattern of skeletal development in the tetrapod limb.

Limb Diversification in Microteiid Lizards: Morphology, Ecology and Development

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The tetrapod limb comprises a synapomorphic feature, the autopodium, whose evolution is a key event in the evolution of vertebrates. After its single origin, this structure has morphologically diverged in several lineages, leading to a myriad of limb shapes and sizes. The evolutionary history of Tetrapoda comprises many cases of limb reduction encompassing digit loss, and non-pentadactyl autopodia are widespread among lineages. Recurrent events of digit loss are particularly notable in Squamata such as microteiid lizards (Gymnophthalmidae). In microteiids, non-pentadactyl autopodia independently evolved in two fossorial lineages: Cercosaurini and Gymnophthalmini. In addition, the microteiid literature also provides evidence for the reversal of digit loss. While published data describe a unique muscle anatomy in the autopodia of the Cercosaurini *Bachia*, with the arrangement of both the manus and pes being very similar, our CT-scan images suggest the autopodial bones are in fact distinct. Within Gymnophthalmini, there are two genera of monodactyl species each characterized by a styliform autopodium that resembles the single-digit phenotype of sonic hedgehog knockout mice. We characterized the osteology of these styliform autopodia using CT-scan imaging, and we sequenced the ZRS limb enhancer of *sonic hedgehog* in Gymnophthalmini, and compared these sequences with data from pentadactyl species. We conclude that: 1) in Cercosaurini species, the effects of reversals in digit loss are more extreme in muscles than in bones, 2) in Gymnophthalmini, transitions from the plesiomorphic pentadactyl limb morphology to a spine-like appendage dramatically affect the configuration of bones and muscles, and 3) the sequence patterns in the ZRS limb enhancer provide interesting insights about developmental pathways involved in the evolution of styliform autopodia in microteiids.

The Evolutionary Mechanisms of Neuromuscular Systems in Batoid Appendage

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Batoids have evolved the unique body plan for benthic adaptation: exceptionally wide pectoral and pelvic fins, gills covered by epithelial tissues, and flat body. Although some studies have revealed molecular mechanisms underlying the evolution of the batoid body, the evolutionary and developmental mechanisms of neuromuscular systems in batoids have not been studied sufficiently. Here, we present the neuromuscular development of skate (*Leurcoraja erinacea*) by immunohistochemical staining of muscles and nerves. The hypaxial muscles and associated motor neurons bifurcate and invade into the body wall and pectoral fin at the same axial level which supports movements of the body wall and pectoral fin. Importantly, this bifurcating pattern of muscles and nerves observed in skates is somewhat conserved in chain catshark (*Scyliorhinus retifer*), suggesting that the bifurcating muscles and nerves into the body wall and pectoral fin are the ancestral state of finned animals. To understand the genetic basis underlying this bifurcating pattern, we investigated the expression pattern of Hox genes during embryonic development of skate and compared them with those of shark. In skate embryos, the expression domains of several Hox genes are shifted posteriorly compared to those of shark in the lateral plate mesoderm, paraxial mesoderm and neural tube, implying that dynamic posterior shifts of Hox expression led to the evolution of batoid neuromuscular systems as well as the expansion of the width of paired appendages. Our analysis of skate neuromuscular systems highlights the ancestral neuromuscular patterns and their evolutionary origins as well as the molecular mechanisms underlying evolutionary diversity in appendages.

Developmental Timing of Mammalian Limb Diversification

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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 and ChIPSeq to compare the transcriptomes and regulomes of the developing limbs of several mammals, including bats, horses, humans, mice, and opossums. Results suggest that the transcriptome and regulome varies more during later than earlier stages of limb development, both within and among species. This study also identified key differences in the putative regulation of genes associated with key differences in gene expression. We are currently investigating the role of these regulatory changes in the evolution of gene expression and morphology.

Functional Characterization of Bat Wing Development

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Bats are the only mammals capable of powered flight, but little is known about the genetic determinants that shape their wings. We used a combination of whole-genome sequencing, RNA-seq and ChIP-seq (H3K27ac, H3K27me3) on *Miniopterus natalensis* developing forelimbs and hindlimbs at three sequential embryonic stages (CS15, CS16, CS17) to decipher the molecular events that underlie bat wing development. We first generated a genome for the *Miniopterus natalensis* at 77X coverage which allowed us to align RNA-seq and ChIP-seq reads. RNA-seq analyses found over 7,000 genes and several lncRNAs to be differentially expressed between forelimb and hindlimb and among stages. ChIP-seq identified thousands of regions that are either active or silenced in forelimb versus hindlimb, with selected sequences showing differential limb enhancer activity in mouse. Comparative genomics found 2,796 bat-accelerated regions (sequences with an accelerated number of nucleotide substitutions specifically in the bat lineage) within H3K27ac peaks, several of which cluster near limb-associated genes. Mouse enhancer assays of a selected number of bat accelerated sequences showed differential forelimb enhancer activity for the bat versus mouse sequence. To select additional candidate wing-genes and enhancers for functional characterization, we carried out RNA-seq and ChIP-seq (H3K27ac, H3K27me3) on matching developmental stages in mouse embryonic limbs and used comparative analyses to tease out sequences that show differential activity in bat forelimbs. Combined, our work outlines multiple genetic components that contribute to bat wing formation, providing a genomic blueprint for this morphological innovation.

Digit Loss and Re-evolution in the Philippine Skink Genus *Brachymeles*: Morphology and Development

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Variation in digit number is one of the main modes of limb variation in tetrapods, where digit loss is a broadly recognized trend in a variety of lineages. More controversial is a model, where digits can re-evolve. The Philippine skink genus *Brachymeles* is an ideal model system to study both digit loss and digit re-evolution because of its wide variety of limb phenotypes and the strong statistical evidence of digit re-evolution. We performed a survey of limb phenotypes and evolution and find strong statistical support for the re-evolution of digits in this clade, which is associated with changes in the musculature similar to what has been found in *Brachymeles*. The embryology of digit reduced limbs shows evidence of retained digit condensations, i.e., a larger number of digit condensations than the number of adult digits. This finding supports a model where digit re-evolution is made possible through the retention of digit anlagen in early limb development and the re-activation of these condensations once digits re-evolved. Finally, gene expression studies suggest that digit reduction in this group might be related to delayed maturation of the limb mesenchyme.

Educating the Vertebrate Morphologists of the 21st Century: Technology, Pedagogy, and Core Concepts – Organizers: Nicole Danos, Katie L. Staab, Lisa B. Whitenack, John Hutchinson

Museums, Students, Anatomy and the Public: Bringing Them All Together

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Many natural history museums, particularly those in universities, were originally founded as resources for comparative anatomy. However, in recent decades one could argue that this foundational topic has become less visible in public galleries. At the same time, the teaching of 'traditional' morphology and whole organismal biology was diminished in many university curricula. Happily, this latter trend is on the reverse. This presentation will explore examples from university museums which have sought to thoroughly embed student learning within museum collections, spaces and public programs. It will also discuss the principles by which anatomy is included in museums' public content through their interpretation and learning programs. Providing access to extensive and comprehensive museum collections can be transformative for undergraduate students, who typically arrive from school thoroughly naïve of the discipline. Teaching in museums can act as the key pedagogical step in understanding difficult scientific concepts and in preparing students for postgraduate research. The incorporation of assessed real-world public engagement around comparative anatomy in undergraduate teaching in museums will also be discussed. The integration of public engagement, based on the students' own collections-based research, provides opportunities for museums' public audiences to understand the science behind the collections. It also introduces students to the responsibility that museums and researchers have to working with the public, and the science communication skills required to do so.

Using Peer-to-Peer Teaching to Improve Learning Outcomes, Student Engagement and Inclusion

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Peer-to-peer teaching has been shown to be effective in improving learning outcomes in science classrooms. I employ this technique during systems-based dissections in the comparative anatomy classroom. In any given laboratory session pairs of students dissect one of four animals. In this arrangement, students have other partner pairs who are dissecting the same animal to consult with; they also then have the responsibility to teach the rest of the classroom the anatomical features of interest in the animals that only they dissected. I found that giving students the responsibility of teaching others increases their engagement during the dissection and provides ownership of the material they learn. However, such a classroom rearrangement requires critical thinking of the core concepts that need to be reinforced in the laboratory classroom. For example, students cannot be expected to learn in a single classroom all the features traditionally taught for all four specimens. Therefore, learning outcomes and core concepts need to be prioritized. Two concepts that I focus on are form and function and descent with modification.

3D-Technology and Animation: Key Tools in Educating Future Morphologists

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Humans are visual creatures: about 30% of the neurons in the cortex are devoted to visual processing and at least 65% of the people are considered "visual learners". While education in functional and evolutionary morphology generally is provided as a combination of theoretical background and practical skills labs, which can include histological sectioning and microscopy or dissections, these techniques are limited by their "static" nature. 3D-visualization can play a crucial role in overcoming the limitations of current education in comparative vertebrate anatomy. 3D-images already provide more information than "old-school" 2D-images, as they capture the morphology and/or architecture of cells, organs or functional systems at a more detailed and realistic level. Furthermore, to fully comprehend how a cell, organ or organism functions, there is a need to see these structures or organisms at work. 3D-technology allows the visualization of actual movements, such as how the combined contraction of circular and longitudinal muscle cells in the intestine results in peristalsis or how the contraction of jaw muscles causes mouth closure. Furthermore, short 3D-animations where the shapes, organization or interaction of cells, organs and functional systems are being altered can allow us to visualize how such changes result in differences in a structure's performance and/or efficiency. By subsequently comparing the anatomy of different (groups of) species, core concepts such as adaptation, homology and convergent evolution can be explained. Next to providing a more efficient way to transfer information to young biologists, such short animations are more likely to stick in the mind. As such, the rise of 3D-technology and animation allows the education of morphologists at a more advanced level than ever before.

Build Your Body (No, Seriously, Actually Make it): Integrating 2D- and 3D-Maker-Culture into a Comparative Vertebrate Anatomy Course

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Skeletal articulation - assembling a complete but completely disarticulated skeleton - has long been a rite of passage for anatomists. I employ this in my Comparative Vertebrate Anatomy course: each group of three students gets a complete skeleton of, e.g., a fox, owl, seal, or dolphin, which they articulate over the span of six three-hour lab sessions. This humbling, detail-oriented, frustrating experience fosters a deep respect for the intricacies and complexities of vertebrate form. Questions of function, performance, and connective tissues inevitably arise. These newly-generated questions provide serious buy-in from students, and the finished articulation is a source of pride. This culmination of positive outcomes is in part a result of the fantastic diversity of forms across vertebrates, in part because of the endless combinations of skeletal tools used to solve innumerable problems, and also in part because of the simple, tactile act of building. Hands-on building – making – is well known to stimulate and deepen learning & retention. One pitfall is that students become frustrated if even a single bone is missing. Obtaining a real replacement for a seal metacarpal is not tractable, but new technologies allow us to build good replicas. Many photogrammetry applications exist that can be used on a mobile phone to generate accurate 3D-surface models and 3D-printed. Therefore, an existing left third metacarpal can be scanned, digitally flipped and 3D-printed to replace a missing right third metacarpal. Maker Culture can be employed in schematic biomechanical modelling, to build physical models of relatively simple, yet not-completely-intuitive systems. Future endeavors such as Arduino-controlled, servo-driven animatronic skeletons are no doubt coming. In short, the tools emerging from 21st century Maker Culture can aid in making vertebrate morphology more engaging, both by enriching 'old-school' techniques such as skeletal articulation, and opening new avenues.

Comparative Anatomy: An Integrative, Multidisciplinary and Multispective Discipline, and a Foundational Course for the Health and Bio-logical Sciences

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Comparative vertebrate anatomy (CA) is the foundational discipline of organismal and evolutionary biology. By comparing representatives of different vertebrate classes, CA integrates a wide range of biological fields, synthesizes the theory and practice of organismal, comparative and evolutionary biology, and provides evidence for concepts and principles, such as individual variation, structure-function causality, selection, adaptation, homology, homoplasy, evolutionary change, etc. CA is also unendingly fructiferous for research, because its methodology is applicable to all levels of biological organization and can enrich and test phylogenetic hypotheses based on molecular data. Because of its integrative, multidisciplinary and multispective nature, CA is also one of the more challenging teaching assignments. Students need to be taught a broad range of skills, such as how to dissect a specimen conservatively; mentally visualize 3D-configurations; formulate inferences from indirect evidence (e.g., function from structure, evolutionary change through comparisons of individual observations); test working hypotheses; synthesize seemingly disparate data; learn scientific terms; and memorize a voluminous amount of information. In this way, CA provides students with a solid foundation for critical and creative thinking that is indispensable for health care practitioners and research scientists alike. CA challenges students to rise to their potential and, therefore, has been one of the "trials by fire" for those aspiring to enter graduate programs in healthcare or biology. Because students are in general academically less well prepared than even some years ago, teaching CA requires not only expertise in one of the more complex disciplines, but also the humane and emotional capacity to motivate students and lead them to experience the incomparable thrill of being in possession of knowledge and the capacity to use it for problem-solving in clinical settings and research.

Getting Pre-University Students Excited about STEM via 3D-Modelling of Dinosaur Anatomy in Teaching

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Dinosaur paleontology is famous for exciting students of many ages and for providing leverage to get them more interested in STEM topics. Three-dimensional computer (and physical) modelling is likewise appealing to students for its visually intuitive and technological natures, and yet can convey a wide variety of concepts of varying degrees of complexity. Thus it is popular to combine these approaches in educational and outreach work. Here, we present a multi-pronged, multi-disciplinary approach that we have been refining in local schools with substantial numbers of underrepresented students. This approach spans the full breadth of our current archosaurian evolutionary biomechanics research (https://www.dawndinos.com), using the diversity of topics to reach students with different interests. Our school-based "dinosaur club" sessions cover: (1) Triassic-Jurassic paleontology, ecosystems, macroevolution and extinction; (2) Osteology and limb proportions; (3) Joint morphology and mechanical advantage; (4) Body dimensions and computer models of center of mass and (5) Dynamic computer simulations of locomotor balance. Here, we explain our approach and lessons learned from testing it with students, plus comparisons/contrasts with similar club sessions run with students whose major interest is art rather than science. We then expound upon how our approach also introduces students to major concepts in morphology, showing how morphology is central to the study of organisms, biomechanics, behavior, ecosystems and evolution, as well as being fascinating in its own right.

Inclusivity in Vertebrate Morphology: What are the Barriers and What Can We Do About Them?

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Science can be a creative endeavor that benefits from diverse perspectives, experiences, and opinions. If so, then both science in general and vertebrate morphology in particular suffer from an inclusivity problem. In the United States, professional participation in vertebrate morphology does not reflect the actual demographics of the population. The reasons for such disparities cannot always be disaggregated and addressed easily because they are evident simultaneously for many undergraduate students. For example, undergraduate biology is known for "gatekeeper" introductory courses that are often high-enrollment, assume unrealistic levels of college preparedness, and do not take advantage of evidence-based methods of instruction. As evidenced by rates of graduation from the biology major, a lack of success in such gatekeeper courses can stifle in a student any preexisting desire to study the form and function of vertebrates. Even as the tenets of scientific teaching are implemented by more and more biology departments, vertebrate morphology may still not receive adequate support from academic administrators or funding organizations. In addition, biology students and their personal support networks (consisting of, for example, family members and close friends) may not be aware that the study of vertebrates can actually lead to rewarding careers. In other words, a career in medicine is not the only logical conclusion to earning a baccalaureate degree in biology. The above assertions are supported by the literature, as well as the author's experiences as a first-generation college student and as a faculty member at a Historically Black University.

Becoming Biologists: Using Social Media, Service Learning and Outreach to Build Student Identity

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Students incrementally become biologists through experience. However, experiences in the classroom and lab have traditionally been limited to unidirectional flow of information from professor to student. Social media is easy to include in classes with convenient platforms like Facebook that allow text posts, photo submission and links to the internet while image-based content platforms like Instagram may be part of their established routines. Including social media into classes can allow students to connect to the material and their fellow students in many ways. This practice can help students develop a biologist's voice as they learn to communicate their observations, ideas and experiences with their peers. Since most college-age students are still developing socially, this practice can contribute to student identity construction in a virtual space where they feel comfortable. Beyond the digital extensions of the classroom, social interactions help students communicate in the language of science. Service learning is ideally suited to promoting this type of identity construction because it typically occurs outside of an often competitive academic environment. Opportunities abound with communities of professionals who work with animals at nature and rehabilitation centers, zoos and aquariums, veterinarian offices and research labs. Similarly, working with researchers and organizations on science-based outreach programs allows students to engage in applied problems facing the animals they are studying. All these options for increasing engagement provide adaptable opportunities for students to care and learn about others and organisms while developing socially in locally meaningful contexts. As the problems facing organisms and environments are increasingly overwhelming and dire, students may respond better to opportunities to actively help rather than simply learning about the facts and problems facing the planet.

Specimen Preparation Projects and Visual Study Guides Exhibited as Art: Engaging Undergraduates and the General Public in Vertebrate Morphology

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Educational psychology research shows that arts training affects cognitive processes in part by increasing motivation and attention span. Furthermore, strong observational skills are essential to students of anatomy and the act of drawing augments scientific observational study. Here, I highlight two examples of assignments in an undergraduate comparative vertebrate anatomy course that reinforce the material learned in lecture and lab and can be exhibited as art. Students prepare a specimen of their choice using one of three techniques commonly employed by vertebrate morphologists. Options include 3D-printing bones from open-source digital repositories of CT-scans, clearing and staining a small preserved fish or frog available in the lab's collection, or preparing a skeletal specimen using a dermestid beetle colony. I provide resources and training for each type of preparation in the syllabus, on the course website, or in the first week of class so that students have the entire semester to take ownership of the independent project. The resulting specimens remain in the anatomy lab and are used as teaching tools for future classes. Students also create visual study guides, labeled drawings associated with each major lab exam, detailing the structures that they are required to learn. Not only do these assignments enhance student learning, but also the results are quite beautiful. Most colleges and universities feature an art gallery on campus, and gallery directors or curators are often eager to cross disciplines and exhibit art inspired by science. By collaborating with galleries on or off campus through formal exhibitions, morphologists can share student work with interdisciplinary colleagues, other students, and the general public, generating interest in, awareness of, and appreciation for the field of vertebrate morphology.

Stereotype Threat in Organismal Biology: Small Intervention, Big Impact

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Stereotype threat can be defined as distress associated with the prospect of confirming a negative stereotype about a group to which one belongs. Previous work has shown that stereotype threat is associated with lower performance in science courses in several groups including underrepresented minority groups and first-generation college students. At UW Parkside just over half our students are first generation college students. Our proportion of underrepresented minority (URM) students is over 25%, which is the highest in the University of Wisconsin System. Our students are potentially at risk for stereotype threat in large science courses like introductory organismal biology. I implemented a one-time, brief (15-minute) values-affirmation writing intervention and a control exercise in the first week of an organismal biology course over two semesters, with two different instructors. This values-affirmation writing exercise has been shown to positively affect performance in first-generation and underrepresented minority groups. I found that students who had the opportunity to affirm their values in writing in the first week of classes showed a 7% better performance on their average exam scores for the semester than those in the control group. In contrast to previous work, all students benefitted, on average, from participating in the values affirmation compared to control, not just first generation students. This includes males and females, continuing and first-generation students, URM students and non-URM students. Although there was still a gap between URM and non-URM students, URM students participating in the intervention had an 8.5% increase in exam performance overall compared with those in the control group. Including this type of short intervention can have a significant impact on student performance and help support students that have traditionally had higher rates of leaving STEM fields.

Integrating Active Learning Strategies to Engage Students, Promote Inclusion, and Maximize Learning in Vertebrate Anatomy

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Research from a variety of disciplines suggests that how students personally experience learning environments strongly influences their engagement, motivation, sense of belonging, and conceptual learning. Active learning strategies have been repeatedly demonstrated to produce superior learning gains with large effect sizes compared to lecture-only teaching approaches. Additionally, teaching diverse populations of students requires instructors to construct learning environments that are purposefully inclusive and highly structured to provide access to learning for all students. Yet, few scientists have experienced these types of learning environments themselves or had opportunities to learn about these research-based teaching strategies that promote active learning, foster inclusion, and maximize student success. In this series of interactive sessions, attendees will experience multiple examples of active learning strategies to teach biology concepts, including those relevant to vertebrate anatomy. Participants will experience how to integrate active learning in 1-minute, 5-minutes, or 10-minutes into existing lecture-only teaching approaches for classes of any size or cognitive level. In addition, participants will explore how to use results of active learning to assess students' understanding and plan next steps for teaching. Attendees will explore and discuss how different students may experience the same classroom environment differently from one another, as well as have the opportunity to self-assess their current awareness and frequency of use of 21 common inclusive teaching strategies that require minimal skill or preparation to implement. Finally, attendees will identify those active learning and inclusive teaching strategies that could be immediately implemented not only in their classrooms, but also in their laboratories, group meetings, or other professional settings to maximize learning and promote inclusion for all students.

Identifying Core Concepts in Vertebrate Morphology

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Although there are entire journals dedicated to the teaching of medical anatomy, the pedagogical literature on teaching comparative vertebrate anatomy is lacking. This has created a situation where new instructors are lacking research into best practices and core concepts to teach. In addition, recent reports calling for change in science education ask that learning objectives focus on proficiency of core concepts. Focusing on core concepts, or big ideas, is thought to help students achieve meaningful learning, as they are transferable across sub-disciplines, foster retention, build problem-solving skills, and provide scaffolding for learning new concepts later. However, before we can employ these core concepts, we must define them. This interactive talk will discuss the pedagogy of core concepts, present data gathered at the Society of Integrative & Comparative Biology annual meeting, and serve as place to gather input on the core concepts in comparative vertebrate anatomy and morphology from ICVM attendees.

Integrating a Virtual Dissection Table in Anatomical Education

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There is an overall trend to reduce anatomical dissection hours during medical, veterinary, and biological education. This has many reasons, e.g., financial burden of obtaining specimens, maintaining the lab and specimens, space for laboratory courses, focus on more 'modern' technologies (genetics, CT-scans, etc.). However, detailed anatomical knowledge is still necessary in many disciplines as basis to understand biomechanics, physiology, pathology, and many more. Despite the increasing use of genetics to understand phylogenetic relationships, analyzing morphological characters is still an important tool in phylogenetics. Several different approaches were discussed over the past years. One is the addition of life-size virtual dissection tables to improve the learning success in general anatomy. The advantages are that less cadaveric material is needed, students are less exposed to chemicals (e.g., fixed tissues), the material can be used over and over again. However, there are clearly also disadvantages, as students do not have any hands-on experience of the dissection process if the dissection tables replace the laboratory experience. Here, I would like to discuss the advantages and disadvantages of virtual dissection tables in anatomical education.

New Insights into Chiropteran Evolution: Fossil Record, Development, and Function – Organizers: Daisuke Koyabu, Laura A.B. Wilson

How the Nose Grows: Nasal Fossa Function, Airway Anatomy, and Ontogenetic Oddities in Bats

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How the various functions of the nasal fossa (e.g., respiration, olfaction, echolocation) relate to its anatomy remains something of a black box in the form-function paradigm. Recent work has begun to uncover the mysteries of nasal airway and function, especially in the realm of olfaction. One important recent finding has been showing that some parts of the bat nasal fossa are well-suited for enhanced olfactory capabilities. In particular, many species contain a blind pocket of the nasal fossa called the olfactory recess (OR), which functions to slow down odorant-laden air, allowing more time for odorant sampling. The benefits of the OR in olfaction have been in part elucidated by computational simulations of airflow, supplementing morphological and histological techniques. In this project, we extend our previous work investigating the OR and other anatomical contributions to olfactory function by studying the nasal fossa of prenatal, juvenile, and adult bats, focusing on the developmentally unique vampire bats. Existing work has shown that nasal anatomy, especially the ethmoidal region, undergoes a prolonged postnatal transformation. Ossification of the turbinals (an important scaffold for olfactory mucosa) is relatively delayed, becoming elaborated postnatally with additional bony lamellae. However, anatomical heterochrony of the nasal fossa may or may not have much bearing on functional utility. We examine this hypothesis by performing functional analyses on bats of different ontogenetic stages, and we find species-specific effects of development on airflow correlates of olfactory function. In particular, vampire bats show advanced early development of olfactory structures and airflow, which may correlate with their ecology and social dynamics. Our study highlights the need to take a nuanced approach to considering structure-function relationships of the nasal fossa, especially with respect to the ecological and social environments of pre-adult individuals.

Peculiar Cranial Morphology in Nasal-Emitting Bats (Chiroptera: Rhinonycteridae) from Miocene Forests in Northern Australia

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Old World leaf-nosed (Hipposideridae) and trident (Rhinonycteridae) bats emit pure-tone echolocation calls through the nostrils that allow detection of fluttering prey around vegetation, and have expanded nasal chambers and cochleae that are associated with energy transmission and reception. They have an Old World tropical to subtropical distribution, with a fossil record extending back to the middle Eocene of Eurasia. In the Riversleigh World Heritage Area of northern Australia, these bats are the most speciose and abundant taxa in late Oligocene to middle Miocene karst deposits, with 20-plus species identified. Many taxa are represented by hundreds of well-preserved skulls each, and show a diversity of cranial forms thought to be correlated with ultrasound emission and reception. We used 3D-geometric morphometrics to examine cranial traits in one of the most distinctive of these lineages – the *Xenorhinos* group. These bats are characterized by a broad, deep rostrum, voluminous nasal cavities, incomplete nasal septum, broad interorbital region, extremely short palate, splint-like sphenoidal bridge, and conspicuous rostral rotation. A 3D-GMM approach enabled recognition of two new species referable to this group, reappraisal of the lineage's probable phylogenetic relationships, assessment of their likely echolocation call attributes and ecology, and a possible developmental pathway for their unique skull form. Members of the *Xenorhinos* group represent ecomorphs that have been completely lost since the middle Miocene, possibly as a result of a shift in paleoenvironments in the Riversleigh region, from closed-canopy forests to today's open woodlands and grasslands.

Comparative Postcranial Skeletal Development in Bats (Chiroptera)

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Understanding differences in ontogeny is important in comparative research on functional morphology, ecology, or evolution. There have been efforts to define developmental stages in some bat species, but the record is far from complete. From shortly after birth, a juvenile bat needs to hang on to its mother by its feet and thumbs, and by attaching to a nipple with its milk teeth. In many bat species, juveniles are initially carried on foraging flights or moved between roosts by their mothers. During flight, the bat pup has to hold on without help from its mother. This accounts for considerable weight bearing demands on the bones of the hindlimb and parts of the forelimb (humerus, radius, and thumb). The rest of the forelimb, however, is bearing weight much later, when the juvenile bat learns to fly. In this ongoing study, the pre- and postnatal development of the postcranial skeleton are compared between species of vespertilionid insectivorous bats (*Pipistrellus pipistrellus* and *Miniopterus schreibersii*) and species of pteropodid fruit bats (*Eidolon helvum* and *Cynopterus brachyotis*). The bones of ethanol preserved specimens from museum collections are analyzed nondestructively in 2D and 3D, using X-ray microtomography (microCT) imaging. Digital photographs are taken to document key features for exterior staging. We aim to place bone development and ossification into an ecological and behavioral context. Preliminary results show different patterns of ossification, reflecting the species' differences in foraging and roosting ecology, juvenile bat behavior, litter size, and lifespan. Reference data on bat developmental stages will be useful in comparative research on functional morphology and ecology of bats. It will also enable researchers to better estimate embryonic ages in field- and museum-studies.

Prenatal Development of Echolocation-Related Traits in Bats and the Origin of Laryngeal Echolocation: Single Origin or Convergence?

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Bats are phylogenetically classified into two major clades: yangochiropterans and yinpterochiropterans. In terms of the echolocation ability, bats can be behaviorally categorized into non-echolocators, laryngeal echolocators, and tongue-click echolocators. All members of yangochiropterans are capable of laryngeal echolocation, whereas yinpterochiropterans include all three types. The origin and evolution of echolocation in bats has been highly disputed, and currently, there are two competing hypotheses. One hypothesis argues that laryngeal echolocation evolved only once in bats, and then the ability was secondarily lost in pteropodids (the so-called Old World fruit bats) among yinpterochiropterans, and then tongue-click echolocation evolved later in some members of pteropodids (i.e., *Rousettus*). The alternative hypothesis suggests that laryngeal echolocation evolved twice convergently in yinpterochiropterans and yangochiropterans. Some researchers studying the quantitative growth of the cochlear in some bat species reported that non-echolocating pteropodids show a common growth curve to laryngeal echolocators. This apparent resemblance of cochlear growth pattern was proposed to be a vestigial signal of echolocation ability in the last common ancestor of bats and thus as supporting evidence for the single-origin hypothesis. However, our recent comprehensive μCT observations on prenatal cochlear development of widely-sampled bat species revealed that early-stage fetuses were not sampled broadly enough in this previous investigation. We demonstrate that non-echolocating pteropopids show a distinctive developmental pattern compared to other echolocating bats, rebutting the results reported by previous investigators. Our ongoing work also reveals the unprecedented variation of cochlear development among bats. Together with these results, we discuss the possible scenario regarding the origin and evolution of laryngeal echolocation.

The Morphogenetic Basis of Mammalian Flight: Allometric Trajectories and Ossification Heterochronies in Prenatal Skeletogenesis of Bats

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Vertebrate flight evolved independently in three clades: pterosaurs, birds, and bats. Of the three, given the limited bat fossil record, the evolutionary history of mammalian flight remains mostly unknown. Development determines whether it is possible to evolve from one morphological state to a different one that might be more adaptive. Therefore, studying the morphogenesis of bats can potentially shed light on how morphological adaptations associated with flight have evolved. In order to better understand the evolution of extreme morpho-physiological adaptations for flight in bats, we assessed the presence of an ontogenetic basis in the evolution of the postcranial skeleton of bats. We quantitatively compared ossification sequences and metric growth data for the prenatal development of 24 postcranial bones between bats (14 species), non-volant mammals (11 species) and birds (14 species). In order to evaluate how variable the ontogenetic trajectories are among bats, we also reconstructed the allometric trajectories of nine bat species, representing both suborders. Ossification sequences in bats were more similar to those of other non-volant mammals, showing a general mammalian developmental pattern. However, sequence heterochronies were detected in bones adapted for flight-specific biomechanical needs in bats and birds. Modularity analysis revealed an axial-appendicular partition in both volant and non-volant mammals, indicating that mammalian postcranial covariance patterns are constrained prenatally. Suborders were clearly separated across allometric space, revealing shifts in the growth rates of specific bones for each. Our results revealed a strong phylogenetic signal in the allometric trajectories of bats, indicating an ontogenetic basis for the postcranial morphological diversity in modern bats.

Anatomical Multifunctionality and the Diversification of Skull Morphology in Bats

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The vertebrate skull performs multiple functions, such as feeding, protecting the brain and supporting the sensory organs. Dietary demands are considered a major evolutionary driver of skull diversity in mammals, but only a few, large-scale, quantitative studies have tested the impact of various functions on skull morphological diversification.

Bats are an ideal system to investigate this issue because they are extremely diverse in species richness, skull morphology, diet, and major sensory modalities. Here, we explore the potential impacts of both sensory and dietary functions on the evolution of skull shape across the bat radiation. We used micro-Computed Tomography scanning to generate 3D-geometric morphometric datasets of the cranium and mandible of 203 bat species, spanning all families, diets and sensory modalities. We used these data in phylogenetic comparative analyses to uncover macroevolutionary patterns and potential functions shaping skull diversity across bats. These included: (1) estimation of adaptive landscapes of skull shape evolution, (2) quantification of skull shape disparity across the evolutionary history of bats, and (3) tests of associations between shifts in modularity of the skull and sensory or ecological transitions. We found that early divergences in skull shape across major bat lineages are best explained by selective regimes based on echolocation, including transitions between echolocators and non-echolocators, and between oral and nasal emitters. Echolocation type also seems to have strongly influenced cranial morphological disparity, and may be associated with changes in skull modularity, allometry and lability. More recent shifts in skull shape evolution are associated with dietary diversification primarily within Phyllostomidae, and may have been driven by increased morphological integration in the cranium. These results illuminate potential drivers and mechanisms of morphological and ecological diversification across bats.

Understanding Evolutionary Novelty: An Example from Bats

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How do we explain the evolution of a novel morphological structure? A complete answer to this question requires integrating hypotheses and experimental methods across disciplines; the origin and subsequent diversification of a novel structure might be both the result of alterations in developmental programs and the consequence of natural selection on functional attributes of the structure. To advance our understanding of the interplay between these intrinsic and extrinsic causes of evolutionary novelty, we describe how various methodological approaches can be linked through a comparative morphology research program that capitalizes on existing natural anatomical variation. Our focal structure is the calcar, a bony or cartilaginous spur found in the feet of bats (Chiroptera) that constitutes a discrete morphological novelty dating to the earliest bat postcranial fossils. Through detailed anatomical studies of the calcar and associated structures across many bat species, we demonstrate that the calcar takes on extraordinary anatomical diversity among bats. Critically, this diversity has allowed us to test models of morphological evolution, examine anatomical parameters that likely affect calcar function, and most importantly, design ongoing studies of calcar development and function. This integrative research program illustrates the importance of comparative anatomy in understanding broader questions in evolutionary biology.

The Complex Architecture of Bat Wings: Diverse Morphologies Integrate Actuation and Sensing

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During more than 58 million years of bat evolution and diversification, a remarkable range of flight performance has evolved in the nearly 1400 extant bat species. These capabilities are supported by great diversity in overall wing shape, details of musculoskeletal architecture, the capacity to sense the internal and external environment of the wing, and patterns of motor control. Full understanding of bat evolution requires that we assess the diversity of the structural components of bat wings, and improve our abilities to interpret the functional significance of this variation. In addition to common elements, bat wings possess several traits that distinguish them in mammalian limb design: muscles that have no direct attachments to the bony skeleton, a prominent network of large elastin bundles, and a distinctive array of specialized sensory hairs. We demonstrate that all three of these characteristics vary among bat species, and that this variation has strong phylogenetic signal. Intramembranous muscles, elastin networks, and sensory hair arrays likely all play critical roles in supporting flight capabilities, particularly by tuning the three-dimensional shape of the wing to the dynamic demands of flight.

Morphological Variation and Molecular Origination of Chiropteran Wing Membranes

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Through the evolution of novel wing structures, bats became the only mammal to achieve powered flight. This achievement led to an unprecedented adaptive radiation and diversification in membrane structure, such that today bats employ diverse flight styles and account for over 20% of all mammalian species. However, despite the importance of the evolution of the bat wing to the group's success, the mechanisms that drove the origination and subsequent diversification of the novel components of the wing remain largely unknown. Bat wings are comprised of several, novel membranous structures that are supported by elongated forelimb and digit bones. Our research specifically investigates the evolutionary origination and diversification of two novel membranes of the bat wing: the plagiopatagium which connects the 5th digit to the body and hind limb in all bat species, and the uropatagium which connects the hind limbs in many species. We characterize differences in adult membrane phenotype among bat species with diverse flight styles. This is achieved by performing geometric morphometrics on specimens housed at the American Museum of Natural History (AMNH). Additionally, we seek to determine when during development and from what tissue sources the membranes initially form, and when differences in membrane form arise among species. The geometric morphometric approach is also extended to embryonic and juvenile bats from a range of developmental stages. Embryonic specimens are obtained from AMNH fluid collections and newly captured bats. Lastly, we establish a general cellular and molecular framework for plagiopatagia and uropatagia development in bats, and establish how this framework differs among species with divergent membrane development. This is achieved by visualizing cellular processes, gene expression, and protein localization in developing embryos.

Holding on: The Evolution of Arboreality in Tetrapods – Organizers: Anne-Claire Fabre, Michael Granatosky, Dionisios Youlatos

Convergent Evolution of Humeral and Femoral Functional Morphology in Slow Arboreal Mammals

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In this work, various levels of bone organization are studied for a comprehensive understanding of the traits related to convergent evolution of slow arboreal locomotion. Within mammals, this behavior was independently acquired in at least six phylogenetically and geographically distant lineages: the two genera of Central-South American tree sloths, the African-Asian lorisids, sub-fossil sloth-lemurs and koala-lemurs from Madagascar, and the Australian koalas. In the first part of the study, the relationship between locomotor repertoire and long bone morphology is investigated in order to identify a potential pattern of phenotypic convergent evolution. For this purpose, bone functional morphology is studied analyzing both the external (using 3D-geometric morphometrics) and internal (trabecular architecture and diaphyseal cross-sectional properties) anatomy of the humerus and femur. MicroCT-scans of a mammalian sample comprising xenarthrans (tree sloths, anteaters, armadillos), primates (lorisids, galagids, lemurs, sloth-lemurs, koala-lemurs) and marsupials (koalas, wombats) are analyzed with phylogenetically informed methods. The second axis of the study focuses on xenarthrans: humerus and femur in the two lineages of tree sloths are studied with the same multi-pronged approach for uncovering further common features associated with their widely recognized convergence. With the aim to gain insights into this pattern of convergent evolution and how it occurred in the past, Neogene and Quaternary sloth fossils will also be included. The third part of the project focuses on the bone histological level. Low humeral cortical compactness (CC), recently found as a convergent trait of tree sloths, likely relates to their low metabolism. Since this trait was never studied in other slow arboreal mammals, CC will be quantified for them and their sister-taxa, in order to understand the functional significance of low CC. Preliminary results and trends are presented and discussed.

Grip it or Stick it: Frog Adaptations to Arboreal Environments

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Adaptation to arboreal environments requires special anatomical features. Moving on the ground does not impose the same physical constraint as moving on a branch or a trunk. The arboreal milieu is discontinuous, unstable, and consists of complex substrates that differ in flexibility, orientation and width. Despite the functional challenges imposed by the arboreal environment, several species have independently colonized it. In this study, we investigate the multiple adaptations to the arboreal environment in frogs. We predict that arboreal species will have a stronger grip (exerting more centripetally directed) force than terrestrial species. Our sample consists of 127 specimens belonging to 26 species of frogs with differing locomotor adaptations, including arboreal jumpers, slow arboreal quadrupedal climbers, and terrestrial species. We acquired data on grip forces of the forelimb from frogs holding longitudinally and perpendicularly oriented branches, and with and without sand paper. We took measurements of each segment of the forelimb for each specimen. The relationships between grip forces and morphological data were assessed using regression methods taking into account the phylogeny. Our results show that arboreal species have a stronger grip than terrestrial species. Species walking on thin branches have a stronger grip when they are grasping longitudinally compared to all other species. Radioulnar morphology seems to be the most impacted by grip force in general.

The Mechanical Origins of Arm-Swinging in Primates

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Arm-swinging is a locomotor mode observed only in primates, in which the hindlimbs no longer have a weight bearing function, and the forelimbs must propel the body forward and support the entirety of the animal's mass. It has been suggested that the evolution of arm-swinging was preceded by a shift to inverted quadrupedal walking for purposes of feeding and balance, yet little is known about the mechanics of limb use during below branch walking. In this study, we test whether the mechanics of inverted quadrupedal walking make sense as precursors to arm-swinging and whether there are fundamental differences in inverted quadrupedal walking in primates compared to non-primate mammals that would explain the evolution of arm-swinging in primates only. Based on kinetic limb-loading data collected during inverted quadrupedal walking in primates (seven species) and non-primate mammals (three species), we observe that in primates the forelimb serves as the primary propulsive and weight bearing limb. Additionally, heavier individuals tend to support a greater distribution of body weight on their forelimbs than lighter ones. These kinetic patterns are not observed in non-primate mammals. Based on these findings, we propose that the ability to adopt arm-swinging is fairly simple for relatively large-bodied primates, and merely requires the animal to release its grasping foot from the substrate. This study fills an important gap concerning the origins of arm-swinging and illuminates previously unknown patterns of primate locomotor evolution.

How Arboreal Tetrapods Visually Navigate the Spatial World

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The three dimensionality of arboreal substrates combined with environmental variability due to seasonal changes in vegetation, weather conditions, and daily shifts in ambient light create an information-dense visual environment from which an animal must encode, among other variables, spatial form for visually guided locomotion, navigation, and spatial cognition. Integrated locomotor control in many vertebrates combines visual motion, vestibular, and kinesthetic information for motor planning. A number of arboreal tetrapods that travel across relatively distant and discontinuous substrates provide potentially fruitful case studies for visual motion specializations. Gliding, flying, jumping, and leaping tetrapods all must compute: (1) depth, distance, size, and orientation of target landing substrates prior to takeoff; (2) the heading and acceleration of movement in order to adjust while in air; and (3) body position for landing. The neural computations of visual motion, such as optic flow and static and motion parallax, rely on factors that vary among vertebrates, including the sensitivity and resolution of the eyes and the shape and orientation of the visual field. In this study, I model the limitations imposed by resolution, sensitivity, and visual fields as these vary by environmental light conditions on distance and heading perceptions. Results suggest that, with some notable exceptions, optical and retinal resolution limitations constrain the visual motion sensitivity of arboreal mammals when compared to non-mammal arboreal tetrapods.

Arboreality Constraints on Forelimb Shape Evolution in Carnivorans and Primates

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We focus on the relationship between form and function of forelimb long bones in the context of arboreal adaptation. Arboreal environments are challenging because they require peculiar morphological modifications. Indeed, moving through the tree does not impose the same functional constraints as moving on the ground. However, several mammals have independently colonized the arboreal environment. In this study, we compare the morphological adaptation of the humerus, radius, and ulna within two mammalian lineages that exhibit independent adaptation to the arboreal and terrestrial environments: carnivorans and primates. To do so, we used high-dimensional geometric morphometrics on each long bone of the forelimb for over 200 species of carnivorans and primates. Phylogenetic multivariate analyses of variance as well as test of convergence were used to assess the relationship between morphological shape of the long bones and lifestyle (arboreal versus terrestrial) independent of phylogeny. Results indicate that there is a strong phylogenetic signal for each bone. Nevertheless, several arboreal species of carnivorans (e.g., kinkajou) have a forelimb morphology that is convergent with some primates (e.g., strepshirrhines and platyrrhines). Thus, similar constraints seem to act on the long bones of the forelimb in arboreal carnivorans and primates and result in similar morphological adaptations, especially in the humerus. This provides us with further insight into how environments affect morphological adaptations.

The Procyonid Paradox: Comparative Biomechanics of Locomotion of the Coati and Kinkajou (Mammalia: Procyonidae)

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Primates and thin-branch arborealists like woolly opossums are distinguished from most other mammals in having unusual locomotor characteristics such as diagonal-sequence walking gaits and relatively higher vertical peak substrate reaction forces on the hind limbs. In order to strengthen the functional link between thin-branch arborealism and primate-like gait characteristics, we compared in the laboratory the locomotor biomechanics of a pair of closely-related mammals with very different ecologies: the coati (forages preferentially on the forest floor) and the kinkajou (forages exclusively in the trees and preferentially on smaller branches). Two individuals per species were recorded with a high-speed camera while moving freely on a runway and on a raised 25-mm pole (kinkajous only) with a midsection of each substrate instrumented onto a force platform. Like primates, kinkajous displayed trots and diagonal-sequence walking gaits on both runway (57.5% limb phase) and pole (58.7% limb phase). Vertical peak substrate reaction forces were not significantly different between limbs on both substrates. However, vertical impulses were significantly higher on the hind limbs relative to the forelimbs on the runway and pole (0.43 and 0.47 ratios showing a hind limb bias for both substrates, respectively). Kinkajous achieve a primate-like pattern of hind limb biased weight support by modulating timing of limb contacts rather than altering force magnitude. Like most mammals, coatis relied on lateral-sequence walking gaits (22.5% limb phase). Vertical peak substrate reaction forces were significantly higher on the hind limbs relative to the forelimbs (0.44 ratio showing a hind limb bias). Vertical impulses were also significantly higher for the hind limbs relative to the forelimbs (0.43 ratio showing a hind limb bias). The combination of lateral-sequence gaits and primate-like limb force patterns observed in coatis is unexpected and unique among mammals. Funded by NSERC.

New Analyses on the Navicular of the Middle Eocene Adapiform *Anchomomys frontanyensis* (Primates) Reveal Implications for Early Primate Locomotor Behavior and Navicular Morphology

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Anchomomys frontanyensis is important for understanding adaptive tendencies of adapiforms relative to omomyiforms due to its small size: it is one of only two adapiform taxa known from postcrania that can be compared with omomyiforms in a narrow allometric context. We compared navicular elongation as well as relative articular facet areas of *A. frontanyensis* to more than 90 specimens (fossil adapiforms and omomyiforms, as well as extant strepsirrhines and anthropoids). Our results reveal that *A. frontanyensis* has a more elongated navicular than other adapiforms, and that unlike other adapiforms its navicular relative length overlaps with that of some omomyiforms (*Teilhardina* and *Tetonius*). The relative length of the navicular of *A. frontanyensis* is also comparable to that of some cheirogaleids. The relative proportions of the different navicular facet areas of *A. frontanyensis* most closely resemble those of *Tetonius*, and they both most closely resemble lemurids in this aspect. Both the calcaneus and navicular of *A. frontanyensis* bring support to the idea that it was more specialized for leaping than other adapiforms. In fact, it is the only adapiform that has a morphology unambiguously similar in its functional signal to at least some omomyiforms. *Microcebus* and *Mirza* are again proposed as good analogues. The contact between mesocuneiform and cuboid facets of the navicular (a strepsirrhine synapomorphy) in *A. frontanyensis* confirms its strepsirrhine status. We propose this correlates to a tendency for habitual foot inversion. Therefore, the presence of this trait in *A. frontanyensis* implies a greater reliance on smaller diameter supports than in similarly sized omomyiforms which all lack mesocuneiform-cuboid facet contact. Funding: NSF BCS 1317525, 1440742, 1440558, 1552848; MINECO/FEDER, UE: CGL2017-82654-P, IJCI-2015-26392; CERCA Programme/Generalitat de Catalunya (2017 SGR 86, CLT009/18/00069, 2017 BP 00003); Plan Propio de Investigación, Universidad de Granada.

The Haramiyidan (Mammaliaformes) Experiment of Arboreality in the Jurassic Forests

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Well-preserved skeletal material of several euharamiyidan species has been reported from the Jurassic Yanliao Biota, China. These discoveries provide important new information about the anatomy and biology of haramiyidans, a group whose phylogenetic placement remains controversial. The Yanliao Biota fossils unequivocally show that euharamiyidans were adapted to arboreal life, with a number of convergent features commonly present in extant arboreal mammals. For instance, nearly all known euharamiyidan species had gracile skeletons, with long, slender limbs. Evidence of grasping and climbing adaptations includes the phalanges (of both the manus and pes) that are proportionally more elongate than the metapodials. Moreover, fossil impressions of fur and patagium (gliding membrane) convincingly show that gliding locomotion was developed in at least some species. In general, these arboreal/gliding features are similar to those of the distantly related gliding species *Volaticotherium antiquum*, also from the Yanliao Biota, as well as extant arboreal mammals. However, euharamiyidans show differences in limb proportion and patagium shape. The poor fossil record of haramiyidans is attributable to their gracile skeleton and arboreal lifestyle, characteristics that are unfavorable to preservation. The extinction of this highly specialized group of tree dwelling Mesozoic mammaliaforms may have been influenced by environmental factors such as the change from gymnosperm dominant forests to angiosperm dominated ecosystem during the Jurassic-Cretaceous transition.

Effects of Support Inclination and Diameter on the Locomotion of Swinhoe's Striped Squirrels

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Sciuromorph rodents are an ecologically diverse clade with more than 300 species and a body size range spanning three orders of magnitude. Although sciuriomorphs include fossorial, scansorial, and even gliding members, an arboreal lifestyle is considered the ancestral condition. Therefore, sciuromorphs present an interesting radiation to investigate locomotor adaptations of mammals. In addition, a comparable morphology (small body size, claws on all digits, limited prehensility), and scansorial or arboreal lifestyle had also been assumed for the earliest Euarchontoglires. Thus motion analyses of extant sciuromorphs could shed light on the early evolution of the Eurachontoglires "superclade". In this study, we investigated how Swinhoe's striped squirrels (*Tamiops swinhoei*; Sciuromorpha) adjust their locomotion when faced with inclinations on broad supports and simulated small branches. Four individuals were available for the study. We simultaneously recorded high-Hz videos and support reaction forces during 240 trials of squirrels running on two types of instrumented trackways installed at either a 45° incline (we recorded locomotion on inclines and declines) or with a horizontal orientation. Striped squirrels almost exclusively used asymmetric gaits such as bounds, half bounds, and gallops. Locomotion on simulated branches differed substantially from the locomotion on the flat runway. We interpreted several of the quantified adjustments (in comparison to horizontal supports) on declines and inclines as mechanisms to increase stability by minimizing toppling moments and as adjustments to the differential loading of fore- and hind limbs on inclined supports. Our data, combined with previously published comparative studies on the locomotion of other small arboreal rodents, treeshrews, and primates, tentatively suggests that asymmetric locomotion is ancestral for Euarchontoglires.

Influence of Substrate Type on Hand and Foot Postures in Arboreal Mammals: Implications for the Origin of Grasping in Primates

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The possession of an opposable hallux, flat nails, and elongated digits are among the defining features of primates and are central for understanding their origins and early evolution. The manual and pedal grasping abilities of primates have long been associated with the use of a complex arboreal environment and foraging in fine branches. However, other arboreal mammals occupy similar niches. Thus, it remains unclear how substrate type may have exerted a selective pressure toward the acquisition of nails and a divergent hallux/pollex in primates, and in what sequential order these unique adaptations evolved. To tackle these questions, we quantified the effect of substrate orientation (horizontal, oblique, vertical) and diameter (large, medium, small) on hand and foot postural repertoire during locomotion in 11 primate species (6 strepsirrhines and 5 platyrrhines) and 11 non-primate arboreal species (1 scandentian, 3 rodents, 3 carnivorans and 4 marsupials). Our results indicate that hand and foot postures are phylogenetically constrained. All primates exhibit a higher diversity in their postural repertoire compared to other mammals, suggesting a strong capability for postural adjustment. However, strepsirrhines are more specialized for pollical/hallucal grasping, whereas platyrrhines exhibit more zygodactylous and convergent grasps, as well as other mammals studied. Interestingly, we found that small vertical substrates have a strong influence on grasping variability and on the use of the pollex and hallux for climbing in all studied species. However, the possession of nails on the lateral digits does not seem to confer a particular advantage in grasping small substrates compared to other species, unless the animal is large. We propose that the acquisition of nails may not be the result of a fundamental adaptation for arboreal locomotion but of a more complex evolutionary history.

Locomotor Behavior of Small Arboreal Mammals or How to Cope with Twigs, Branches, and Boughs

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Locomotion is a major biological parameter as it provides access to resources and mates and enables escape from potential predators. Moreover, moving within the 3-dimensional arboreal milieu is even more complex, requiring the use of a variety of modes to cope with the particularities of the substrates. Although of paramount importance for fitness, locomotor behavior has been inadequately studied in most arboreal mammals, save for primates. The analysis of the locomotor behavior and substrate use of a variety of small arboreal rodents and marsupials under naturalistic and semi-naturalistic conditions reveals a diversity of modes in association with specific substrate features. Mammals with prehensile extremities tend to employ clambering and suspension to negotiate small and horizontal substrates. In contrast, mammals with functional claws use vertical climbing and avoid leaping. However, as body size increases, claw-bearing species tend to shift to more quadrupedal leaping activities and increased use of horizontal substrates. These preliminary results suggest that arboreal mammals adopt different locomotor strategies across different substrates. In order to fully unravel the locomotor diversity that arboreal mammals have evolved, further studies in both the field and under captive conditions are required.

Prehensile Systems in Vertebrates: Form, Function, and Bio-Inspired Design – Organizers: Dominique Adriaens, Anthony Herrel, Ian Walker

Artificial Hands and Feet: How Modern Robotic Technologies can Enable Bioinspired Design

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Human hands and feet consist of a complex architecture of bones, joints, muscles and ligaments that work together and physically interact with the environment. From a cognitive point of view an important and large area of the brain cortex copes with their sensorimotor functions. Hands and feet are the main interface of humans with the world which they manipulate and the ground on which they walk, but also are perceptual tools for sensing the environment, and are equipped with a rich variety of receptors. Human extremities are an outcome of a long evolutionary process that has made their structure suitable for human loco-manipulation, which differs substantially from the one of our closest living relatives, the African apes, because it evolved specifically for dexterous manipulation and bipedal locomotion. The shape-morphing artificial hands and feet we propose are the result of a scientifically principled biomimetic combination of soft “muscles”, elastic “ligaments”, flexible “tendons”, articular “joints” and rigid “bones” with kinaesthetic and cutaneous “receptors” inspired by the principles that underpin the human architecture and its sensorimotor apparatus and realized through contemporary technologies such as soft robotics. To understand the complexity of the human hand and foot system and extract its fundamental control principles, we build upon the neuroscientific concept of sensorimotor synergies, a theory of how our brain organizes the abundance of the human sensorimotor apparatus into stabilized and uncontrolled manifolds. Sensorimotor synergies are amenable to mathematical descriptions in terms of principal spaces. Therefore, to enable the design and realization of an effective, robust and reliable artificial foot system, we adopt the engineering framework of soft robotics, a set of modern materials and technologies capable of transforming the lesson learned by the observation of how the musculoskeletal system of animals responds and is regulated to mediate physical interactions with the environment in technological achievements.

Manual and Tail Prehensile Systems in Vertebrates: Performance and Morphology

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Grasping is a key fitness-relevant trait in many vertebrates, especially those that have evolved an arboreal life-style. As both climbing and horizontal locomotion on narrow branches require a strong grip (to pull the body against gravity and to maintain stability), grasping ability is expected to co-evolve with substrate use. Moreover, the morphology of hands, feet and tails of animals that excel at grasping can be expected to be modified resulting in increased performance. Here, we test this hypothesis by comparing morphology and grasping performance across species of vertebrates (mammals, frogs, lizards) living in structurally different habitats. We measured external limb measurements and used CT-scanning to study the morphology of the hands, feet, and tails to explore correlations between morphology and performance. Our data suggest a strong correspondence between grip strength, perch diameter and the size of the manus, pes, and tail. Moreover, grip strength varies across species at both the inter- and intra-specific level. In chameleons hand grip strength was correlated with tail strength indicating that selection on the ability to hold on to perches has driven the evolution of many aspects of the unusual phenotype of these animals.

From the Octopus to Robots: Prehensile Capabilities with a Soft Arm

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Prehensile capabilities have always been a major objective in robotics. Robot manipulation has evolved from simple grippers to more dexterous hand-like devices. While vertebrates' prehensile strategies, and especially the human hands, have been the main reference for robot grasping, *Octopus vulgaris* provides an unprecedented model for highly dexterous prehension, at the same time simple to control. More in general, the octopus stands as an ideal model for soft robotics and its reaching arm movement nicely shows the simplifying strategies that allow the control of a virtually infinite number of degrees of freedom, by taking advantage of the physical properties of the arm and its interaction with the environment. The octopus arm dexterity is a combination of water interaction, distributed control and arrangement of the muscular structure. The octopus arm muscular hydrostat is composed of longitudinal and transverse muscles that produce bending in all directions, at any point along the arm, as well as stiffening, in addition to oblique muscles wrapped around the arm, clockwise and counter-clockwise, for respective arm torsions. By adopting the principles suggested by the octopus arm, a soft robot with longitudinal and transverse actuation can reach and grasp objects in water, in the same conditions for environment interaction. Soft robots that adopt the octopus-inspired principles can move, bend, elongate, shorten, stiffen and reach for objects with model-free computationally efficient control systems. The octopus suggested effective strategies for soft robots and opened perspectives for applications in several fields, from medicine to explorations.

Elephant's Trunk: An Extremely Versatile Under-actuated Continuum Robot Driven by a Single Motor

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Continuous-bodied "trunk and tentacle" robots have increased self-adaptability and obstacle avoidance capabilities, compared with traditional, discrete-jointed, robots with large rigid links. In particular, continuous-bodied robots have obvious advantages in grasping objects across a wide range of external dimensions. Not only can they grasp objects using end effectors like traditional robots, but their bodies can also be regarded as a gripping device, and large objects with respect to the robot's scale can be captured by the entire structure of the robots themselves. Existing trunk-like robots have distributed multi-drive actuation, and are often manufactured using soft materials, which leads to a complex actuator system that also limits their potential applications in dangerous and extreme environments. This paper introduces a new type of elephant's trunk robot with very few driving constraints. The robot consists of a series of novel, under-actuated linkage units. With a single motor drive, the robot can achieve stable grasping of objects of different shapes and sizes. The proposed robot simplifies the requirements of the sensing and control systems during the operation process, and has the advantage of accomplishing the capture task without determining the exact shape and position of the target object. It is especially suitable for operations such as non-cooperative target capture in extremely dangerous environments, including those in outer space. Based on theoretical analysis and model design, a trunk robot prototype was developed, and a comprehensive experimental study of the bending/extension and grasping operation functions was conducted to verify the validity of the proposed robot design. The work was supported by the National Natural Science Foundation of China (51605474) and Self-planned Task of State Key Laboratory of Robotics (2016-Z09).

Relating the Form to Function in the Prehensile Tail of Chameleons

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Prehensile appendages represent an adaptation that has evolved in numerous vertebrate and invertebrate lineages. Prehensility is the ability to hold and grasp firmly an object, while combining flexibility and strength. Yet, what it takes to make a tail prehensile remains poorly understood. Among terrestrial vertebrates, chameleons with an arboreal lifestyle evolved prehensile tails, which are used for anchoring and support during feeding. In taking chameleons as a model organism, we aim to decipher the links between the variation in musculo-skeletal anatomy of the tail and the prehensile function. A previous study focused on the morphological variation in tail vertebrae of prehensile and non-prehensile chameleon species using μCT data. Following the detailed description of the tail musculature, we wanted to perform further functional tests of adaptive hypotheses. To do so, we studied the musculoskeletal architecture by collecting data using μCT-scans of PMA stained specimens and performed dissections to reveal the attachment sites of the muscles on the vertebral spine, and how many vertebrae they cross before insertion. These data were combined with virtual 3D-reconstructions of the tail vertebrae to investigate the role of the individual muscles in the movement and function of the tail using multibody dynamic analysis. Furthermore, we analyzed the relation between the variation in vertebral morphology and tail usage based on *in vivo* observations of the veiled chameleon (*Chamaeleo calyptratus*). We filmed 4 male specimens climbing on different set-ups to test the parameters influencing tail use (surface roughness, distance to bridge, grip diameter). Notably, we tested whether there is a differential use between the proximal and distal sections of the tail, as most of the morphological variation was observed in the distal part.

Tail Prehension in Small Mammals

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Among prehensile specializations related to arboreality, the mammalian prehensile tail is the least studied and understood. Although the evolution of prehensile tails has been associated with large body size negotiation over small and fragile arboreal substrates, one-third of prehensile-tailed mammals weigh less than 100g. At this size scale, mechanical constraints may be different from the ones encountered in the well-studied large-sized platyrrhine monkeys and carnivorans. Nevertheless, our study of the external and skeletal characters of small-bodied muroid rodents and diprotodont and didelphid marsupials demonstrates that they are also constrained by the arboreal way of life. The external morphology is variable. Marsupials possess either extended or short distal naked ventral surfaces which apparently enhance frictional forces, whether their tails are scarcely-haired (didelphids) or bushy (diprotodonts). In contrast, muroid rodents lack a distal naked ventral pad in their scaly and scarcely-haired tails. On the other hand, skeletal morphology is convergently uniform, with long proximal caudal regions, a proximally located longest vertebra, and short and robust distal vertebrae. These anatomical features are very likely related to critical functional constraints imposed by specific caudal postures. Unfortunately, the lack of detailed tail use data in relation to positional patterns and substrate use impedes any robust morpho-behavioral links that could eventually elucidate the evolution of this unique prehensile system in mammals.

Bio-inspired Prehensile Continuum Robot Systems

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This talk will provide an overview of research in biologically inspired prehensile robotic grasping by continuous backbone "trunk and tentacle" continuum robots. In particular, robotic grasping inspired by primate tails, elephant trunks, octopus arms, and plants (e.g., vines) will be discussed. The recent emergence of continuum robots inspired by such structures in the natural world offers new modes of machine grasping and manipulation. In particular, the use of their continuous body structure in prehensile grasps provides more stable and versatile capabilities as compared with traditional robotic end effectors. Use of continuum robots in prehensile grasping for novel manipulation applications, targeted towards remote operations, will be discussed.

The Axial Skeleton: Diversity, Patterning and Function - Organizers: Christine Böhmer, Emily Buchholtz

The Neck of the Birds, from Form to Function

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Apart from the neck, the axial skeleton of birds is rather rigid. Most body flexibility arises from the neck. The head supports the basic functions of perception, feeding and grip, but is also involved in specialized behaviors. This imposes different biomechanical demands. The neck (i.e., the cervical musculoskeletal system) that manipulates the head must therefore be versatile. The Avineck project aims to explore the bird's neck anatomical diversity to understand its versatility allowing the richness of the behaviors. We will present here some of the results of the interdisciplinary team working on this project. Depending upon the species, the neck of the birds comprises from ten to 24 vertebrae. Based on differences in intervertebral flexibility, the avian neck is generally organized in three main parts, a cranial, intermediate and caudal part, giving at rest, a typical S-shape under the feathers. In order to quantify the vertebral morphology, we performed a 3D-shape analysis of 195 cervical vertebrae from 17 species. A clustering approach characterized the vertebrae depending on their position along the cervical vertebral column, irrespective of the species. All analyzed birds shared a common pattern. The neck was organized as a modular system, each module comprising different numbers of vertebrae. The modules corresponded to the three main parts. The neck muscles followed another pattern of superimposed layers laying along the different parts. The overall muscular arrangement in the neck was equivalent across different bird species, but the cross-sectional area and the insertions of the cervical muscles differed among the species. The different organization of the osteological and muscular systems permitted complementary adjustments and participated to the flexibility and versatility of the neck system. It allowed its adaptation to different mechanical demands, as we will present in a case study on two closely related vultures with different trophic niches.

When Fish go on Land: Axial Morphology and Locomotor Mode

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The phrase "fish out of water" is widely used as a metaphor for being in a wholly unfamiliar, and unsuitable, situation. Yet many fishes of diverse taxa voluntarily come out of the water and move on land; these brief terrestrial excursions are typically to escape poor water conditions, elude predators, or capture prey on the shore. Depending on body size and shape, fish may use one or more of several strategies for terrestrial locomotion: appendage-based locomotion (e.g., mudskippers;

pectoral fins only, with axial body held straight), axial locomotion (e.g., eels and other elongate fishes; snakelike undulations), axial-appendage-based locomotion (e.g., walking catfishes, snakeheads; pectoral fins and tail used in concert), and tail-flipping (e.g., mangrove rivulus; head and body are lifted over the tail, and the tail pushed against the substrate to propel the fish into ballistic flight). How do axial movements and morphology correlate with locomotor mode? A prerequisite for effective terrestrial locomotion, of all modes, appears to be dorsoventral compression of the body; species with deep bodies thrash on land but are unable to make consistent horizontal progress. Body stiffness limits curvature and horizontal velocity in axial-appendage-based locomotion. Among terrestrial modes, tail-flip jumping is associated with consistently shorter/taller (as a percentage of standard length) vertebrae in the caudal region. The most effective tail-flip jumpers (e.g., mangrove rivulus, *Kryptolebias marmoratus*) also demonstrate the ability to twist the tail about the long axis up to 90 degrees; the mobility allowing this torsion is spread over several caudal vertebrae. Identification of axial morphological features associated with tail-flip jumping may allow interpretation of terrestrial locomotor abilities from fossil taxa.

Homology and Modularity in the Mammalian Sternum

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The mammalian presternum is a keystone structure that links the head, forelimb, and axial skeleton, but its evolutionary history is controversial. Simplification of presternal structure during the synapsid to eutherian transition has been interpreted as the result of either element fusion or loss. Here paleontological, developmental, and comparative evidence is used to support a novel hypothesis that involves both fusion and loss. Homolog identities are established on the basis of conserved lateral articulations and the unique developmental history of each element. Three discrete presternal units with distinctive histology are present in adults of some basal eutherians. An anterior midline element that articulates with the clavicle, a paired lateral element that articulates with thoracic rib 1, and a paired posterior element that articulates with thoracic rib 2 are homologized with the interclavicle, manubrium, and anterior sternal bands of ancestral taxa, respectively. Three elements also occur in early ontogenetic stages of some crown eutherians, but they are fused in adults. Sequential ontogenetic fusion of elements was documented using CT-scans of 350 humans. Fusion sequence of elements varies among individuals, and may extend to sternal ribs and the mesosternum in the elderly. Across taxa, element expression is correlated with the relative size of the articulating structures. Taxa that lack clavicles or an articulating thoracic rib 2 have reduced interclavicles or sternal bands, respectively; this pattern is particularly marked in cetaceans. The manubrium:thoracic rib 1 articulation is universally conserved and defines both the neck:chest and the cervical:thoracic vertebral transitions. This evidence suggests that presternal evolution has been constrained by dedicated articulations between specific lateral structures and presternal elements, and also enhanced by independent responses of each modular unit to different selective pressures.

Evolution of Axial Segmentation Across Vertebrates: Insights from a Cartilaginous Fish

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An axial skeleton with segmented vertebrae is a key feature of the vertebrate body plan, but the diversity of developmental mechanisms that give rise to the axial column remains poorly understood. Vertebral elements derive from a series of mesodermal segments called somites. In tetrapods, somites are polarized, with adjacent somite halves recombining to form a single vertebra through a process known as "resegmentation". However, in teleost fishes, strict resegmentation is less apparent, with cells from one somite half giving rise to numerous vertebral halves. To determine whether the process of resegmentation is restricted to tetrapods, or rather ancestral for jawed vertebrates, we tested the relationship between somites and vertebrae in an outgroup to the bony fishes – a cartilaginous fish, the little skate (*Leucoraja erinacea*). We first demonstrate that skates and tetrapods share molecular markers of somite polarity. Next, using cell lineage tracing approaches, we show that the anterior and posterior halves of single skate trunk vertebrae derive from adjacent somites, as in tetrapods. Interestingly, the tails of cartilaginous fishes exhibit a condition known as diplospondyly, in which two vertebral units correspond with a single body segment. Lineage tracing of adjacent skate tail somites also reveals resegmentation in this region, though each somite gives rise to half of one vertebra, an entire subsequent vertebra, and half of a third, resulting in a complete duplication of the trunk condition. These data demonstrate that the developing skate axial skeleton undergoes tetrapod-like resegmentation, that this process occurs across the entire vertebral column (regardless of the mono- or diplospondylous conditions of the trunk and tail, respectively), and that resegmentation is likely an ancestral feature of the vertebrate axial skeleton.

The Evolution of the Avian Sacrum, and the Transition from Tail- to Hip-Centered Locomotion during the Evolution of Birds

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The avian body plan is unique among all other vertebrates and was assembled over tens of millions of years through their dinosaurian ancestors. The avian pelvis and sacrum in particular is conspicuously different from the ancestral reptilian condition, providing adaptations suited to the biomechanical demands of flight. The ancestrally long tail is dramatically shortened in living birds and the ilium and thigh musculature are greatly expanded, with the main tail-centered adductor muscle (the caudofemoralis [CF]) reduced to a minor band in the avian condition. These changes are complemented with a highly modified sacrum that possesses a far greater number of vertebrae (12–24) than the ancestral archosaurian condition (2). Whereas the evolution of this region is recorded by extinct forms, how development has influenced the formation of the avian body plan is poorly delineated, leaving a major knowledge gap that precludes an integrated understanding of avian evolution. Here, we use a new method of imaging embryonic tissues in three dimensions—immunostaining cleared embryos and stacking the resulting confocal microscope images—to demonstrate that the avian pelvis possesses ancestral archosaurian and dinosaurian states, progressively gaining derived avian character states during prenatal development. We show that the embryonic avian ilium is anteroposteriorly short (5-6 vertebrae) and the tail and CF musculature is well-developed—the embryonic CF is derived equally from the limb and axial muscle masses. Sacral vertebrae are added to the sacrum as the ilium expands, but their homology (i.e., identity of dorsosacrals, caudosacrals, and duplicated elements) remains to be explored. Therefore, in certain key aspects the beginning of pelvic morphogenesis resembles several key ancestral conditions. Using the fossil record and development in unison is a powerful way to understand the transition from ancestral tail-centered to avian hip-centered locomotion in birds.

Growth Pattern and Functional Morphology of Cervical Vertebrae in the Giraffe Antelope, Gerenuk (*Litocranius walleri*)

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Long necks have evolved independently in several different taxa, but the processes underlying the evolution of this trait are not yet fully understood. In this study, we focused on the giraffe antelope, gerenuk (*Litocranius walleri*), which possesses the longest neck in the Antilopini (Bovidae, Artiodactyla), and examined the skeletal mechanism underlying the neck elongation in this tribe. The functional vertebral length of the centrum of each vertebra was measured by calipers in 73 specimens of Antilopini species. We calculated the growth patterns of the cervical vertebrae in the gerenuk from eight skeletal specimens ranging from juvenile to a large mature adult and compared it with those in two related species. The growth rates of the vertebrae were not significantly different between species, suggesting that the long neck of the gerenuk has resulted from the elongation of the cervical vertebrae during the fetal or juvenile stage rather than the high growth rate after birth. The morphology of the cervical vertebrae of gerenuks differed from that of the closely related, relatively long-necked dama gazelle (*Nanger dama*), with protrusions occurring on the dorsal surface of the ventral arch of the atlas. This implies that gerenuks possess a well-developed transverse ligament of the atlas that functions to hold the dens of the axis against the atlas. We also found that the atlas lies in close proximity to the neural spine of the axis in the gerenuk, suggesting that hyperextension of the atlantoaxial joint is osteologically limited in this species. While foraging on high foliage, gerenuks flex and extend their necks freely in a bipedal posture without moving their entire body. Our study suggests that these morphological characteristics peculiar to the gerenuk enhance the rigidity of the atlantoaxial joint and decrease the risk of subluxation of the joint during this unique foraging behavior.

Deciphering the Origins and Functional Implications of Mammalian Axial Regionalization

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The axial skeleton is the ancestral vertebrate locomotor organ and has been coopted in tetrapods to fulfill many functions, from the highly-flexible flamingo's neck to the dexterous spider monkey's tail. In mammals, diversity of axial function has been linked to division of the vertebral column into morphologically-distinct regions. However, subtle morphological regionalization is pervasive across extant amniotes and evolved in the mammal stem prior to strong divergence of region morphology (heterogeneity). Therefore, the relationship between regionalization, morphological diversification and functional diversification of the vertebral column in mammal evolution remains obscure. To examine functional regionalization in amniotes, we measured ex-vivo intervertebral stiffness and range of motion along the entire presacral column of a cat (a regionalized, heterogeneous mammal) and a tegu lizard (a regionalized, homogeneous squamate). Using these data and morphometric measures, we compared patterns of morphological and functional regionalization between the more heterogeneous and less heterogeneous species. The cat exhibited much greater variation in biomechanical properties along the column than the tegu, corroborating assertions of functional diversity in the mammal axial skeleton. Cat columns were also more functionally regionalized: tegus exhibited functional distinction only between neck and dorsal vertebrae, but cats exhibited multiple dorsal regions and stronger correspondence between functional and morphologic regionalization. This suggests that mammals may exploit underlying regionalization patterns to increase heterogeneity and promote functional diversity. Regional variation in regression slopes of morphology versus function in cats imply that this diversity is achieved by modularity of form-function relationships along the column. Implications for the evolution of vertebral function in non-mammalian synapsids will be discussed.

Postcranial Paleoneurology of Pterosaurs and its Relation to Locomotion

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The postcranial paleoneurology of fossil reptiles is understudied, and those studies that exist focus predominantly on crocodyliforms and dinosaurs. The intervertebral foramina of the spine house nerves that exit to innervate surrounding tissues and the extremities. In the heavily fused (and typically distorted or poorly preserved) pterosaurian sacrum, intervertebral foramina can be difficult to observe and are rarely identified. The Lower Cretaceous azhdarchoid *Vectidraco* exhibits large, paired foramina on each sacral vertebra, originally identified as pneumatic foramina. Micro-computed tomography (μCT) imaging reveals these foramina contact the neural canal, suggesting they are intervertebral foramina for sacral nerves. The sacral vertebrae of *Vectidraco* are fused, and intervertebral foramina occur dorsolaterally on the centra. We identified these structures in other pterosaur sacra, including those of the ornithocheiroids *Anhanguera* and *Coloborhynchus*. The sizes of the sacral and notarial neural canals are compared and considered within interpretations of paleoecology and locomotion, following previous studies. The relatively large sacral neural canal of *Vectidraco* implies a sacral enlargement for innervation of the legs and lumbosacral plexus. When compared with *Anhanguera*, this supports indications that azhdarchoids were more hindlimb-proficient than ornithocheiroids. Neural canal size in both ornithocheirid notaria (fused vertebrae where the wings articulate) suggests that ornithocheirids spent less time on the ground, their brachial enlargement and small sacral region indicating enhanced innervation of the wings and poor innervation of the sacrum and legs. The variation in notarial neural canal size between *Anhanguera* and *Coloborhynchus* points to potential ecological differentiation. This is the first study focusing on pterosaur postcranial paleoneurology; more studies on other taxa are currently underway to reveal patterns across Pterosauria as a whole.

Variation and Regionalization in the Axial Skeleton of Saurichthyid Fishes (Actinopterygii; Latest Permian–Middle Jurassic)

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The postcranial axial skeleton of actinopterygian fishes is typically divided into three regions: (1) an anterior abdominal (2) a posterior caudal region (these two are differentiated based on the presence of ossified hemal spines in the latter), and (3) the region with vertebrae supporting the caudal fin rays. However, axial regionalization within actinopterygians can be complex, with these basic regions often subdivided into up to six sub-regions to characterize the range of observed morphologies. Here, we examine variation in axial regionalization within saurichthyid fishes as a case study to assess regionalization in a group of non-teleost actinopterygians with highly variable axial morphology but a conservative body plan related to ambush predation. Saurichthyids lack ossified vertebral centra; however paired neural and hemal arches are ossified, as are dorsal and ventral intercalary elements. In all species, the dorsal intercalaries are expanded and superficially similar to the neural arches in morphology, while the ventral intercalaries show greater variation across the clade. We document up to six morphologically distinct regions (A–F) in the vertebral column of *Saurichthys*: an anterior abdominal region (A), a posterior abdominal region (B), a transitional region spanning the abdominal-caudal boundary (C), a caudal region (D), and precaudal fin (E) and caudal fin (F) regions. Based on both taphonomy and morphology, region C appears to function in axial stiffening, whereas region D is highly flexible. The degree to which regions A–F are differentiated, as well as morphological correlates of these regions, is highly variable across Saurichthyidae. These regions correlate well with those documented in some teleosts and Paleozoic taxa, and also those in potential outgroup genera, suggesting potential deep patterning homology but independent evolution of specific regionalized axial morphologies related to functional demands.

On the Hierarchical Levels of Vertebral Shape Covariation: a Study across Cats

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The mammalian vertebral column is highly constrained in count relative to other tetrapods, despite high ecological and morphological diversification across this clade. This meristic constraint has been hypothesized to be circumvented by increased modular disparification of vertebral shape, driving higher regionalization in the mammalian axial skeleton. Using 3-D geometric morphometrics on >1710 vertebrae of Felidae specimens, we investigated the patterns of shape covariation across three hierarchical levels of organization in the axial skeleton: 1. intravertebral morphology; 2. pairwise combinations of presacral vertebrae; and 3. covariation in the organismal level, between vertebrae and other skeletal components. We tested evolutionarily and developmentally-informed hypotheses of trait covariation and modularity to investigate the drivers of shape integration across the hierarchy of vertebral organization. Further, we assessed the relationship between trait correlations and disparity to test fundamental hypotheses on the evolutionary significance of integration. Results from the three levels of analyses demonstrate that regionalization of vertebral morphology highly correlates with partitioning of function and developmental constraints across the axial skeleton. At the intravertebral level, development strongly regulates vertebral shape, with a two-module model of covariation being highly supported. Moreover, high trait integration promotes vertebral shape disparification. Across the presacral column, whereas the cervical region is phylogenetically conserved, ecological signal concentrates in the highly integrated posterior region between the diaphragmatic vertebra and last lumbar. Finally, at the organismal level, vertebral shape evolution is dissociated from other skeletal components, demonstrating how modularity may have allowed higher diversification of cranial and appendicular structures by decoupling their variation from a more conservative axial skeleton.

Axial Skeleton Diversity across Reptilia: Quantified Regionalization and Developmental Implications

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Axial skeletal diversity and complexity have traditionally been considered to increase linearly through vertebrate phylogeny, from a comparatively homogeneous skeleton basally in gnathostomes to a highly complex, regionalized skeleton in crown mammals. Despite this assumption, there has been almost no comprehensive examination of axial skeleton diversity in Reptilia, the most species-rich and ecologically diverse tetrapod clade. We use both discrete characters and quantitative morphology of the vertebral column in fossil and extant reptiles to test hypotheses of conservation and homogeneity. We also created a quantitatively informed database of regionalization patterns for select reptilian taxa using statistical analysis of 3D-geometric morphometric data of landmarked presacral series. We found a complex variety of vertebral morphologies and regionalization schemes across Reptilia, contrary to their presumed homogeneity. Both Lepidosauria and Archosauria display evidence of increasing vertebral complexity across phylogeny, possibly indicating independent acquisition of highly regionalized axial skeletons. Our results elucidate a greater diversity of form than expected, and do not support a loss of regionalization associated with the repeated evolution of the snake-like body form in squamates. Increased regionalization has been established as a key aspect of mammalian axial skeleton evolution. Our work demonstrates evolutionary trends towards highly regionalized morphologies across Reptilia.

Axial Morphology of Elongate Amphibious Fishes

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Highly elongate body forms have evolved repeatedly across vertebrates through dramatically different modifications to the axial skeleton. Those changes include region specific changes to both vertebral number and shape, a reduction or loss of the limbs, and elongation of the head. In actinopterygian fishes, the general trend is for body elongation to be associated with an increase in caudal vertebral number, although plenty of exceptions can be found to this general rule, and a reduction in pectoral fin size or the absence of the pectoral fins. A main locomotor benefit of body elongation is the ability to move forward and backwards with relative ease. Highly elongate fishes are often found in environments that have increased structure and many are known to leave water to transition onto land for food and/or reproduction. The primary mode of terrestrial locomotion is axial undulation. In this study, we have investigated the relationship between body shape, morphological diversity and kinematic performance of elongate fish moving across different substrates. We focus our efforts in understanding how the morphology of divergent elongate forms may facilitate movement on land. We found that movements along the axial skeleton are relatively consistent despite dramatic differences in underlying axial morphology. For example, *Erpetoichthys calabaricus* and *Anguilla rostrata* use similar patterns of movement when traversing different substrates despite being independently evolved elongate lineages with distinct axial patterning. By documenting how phenotypically similar forms with divergent axial morphologies exhibit similar movement patterns, we have the potential to determine the traits critical for providing sufficient axial flexion to support derived land-based movements.

The Dog-Human Connection: Evolution, Morphology and Behavior – Organizers: Blaire Van Valkenburgh, Adam Miklosi, Greger Larson, Jeffrey T. Laitman, Timothy D. Smith

Scent Hounds, Sight Hounds and Short-snouted Dogs: Does Cribriform Plate Morphology Challenge Our Assumptions of Olfactory Capacity in Dog Breeds?

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The domestic dog is assumed by nearly everyone to be the consummate smeller. Within *Canis familiaris* individual breeds are known as olfactory stars, such as the bloodhound or beagle. These breeds belong to the "scent hounds," one of the functional groupings long used by breeders to sort dog breeds by behavioral or morphological traits. Our first aim is to determine how much variation in olfactory anatomy exists among dog breeds and to test the accepted lore that "scent hounds" are superior smellers. Second, we hypothesize that olfactory anatomy is increasingly restricted in breeds with reduced snouts, as olfactory turbinals must develop in ever-smaller spaces. To test our hypotheses, we use high-resolution CT-scans and 3D-imaging software to measure the areas of snout and cribriform plate (CP), an olfactory skull feature, in 45 dog breeds representing the extreme range of snout morphologies produced by centuries of artificial selection. To best estimate snout, or rostrum, size we include linear metrics that describe the rostral area occupied by turbinals. In this way, we develop a snout index graded from brachycephalic to dolicocephalic that accounts for the lateral expansion of the turbinal chamber in some short-snouted breeds, e.g., English bulldog. Preliminary results suggest that, with some exceptions, the six "scent hounds" we examined have slightly larger CPs on average than other breeds. Notably, two non-scent hounds, German shepherd and English bulldog, have for their body sizes the largest CPs in our sample. Second, we found a positive correlation between relative CP size and relative snout size. Finally, we show that some extremely brachycephalic breeds have "ingrown turbinals" that invade the pharynx from the overcrowded nasal chamber but do not appear to carry olfactory epithelium. Our results suggest that selection for a morphological trait, specifically brachycephaly, may have secondarily driven a loss of olfactory ability in dogs.

Evolutionary Morphology of Canid Facial Mimetic Musculature: Visual Communication in the Evolution of Domestic Dogs

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Domestic dogs evolved from wolves under selective pressures associated with humans and likely included modifications in how they communicate with humans (and possibly one another). Facial displays or facial expressions are a type of communication that is found in a wide range of mammals, both domestic and wild and it is well known that domestic dogs and humans attend to facial displays from one another. However, our understanding of the evolutionary processes and mechanisms in this communication method remains incompletely understood. Facial displays are generated by way of facial (or mimetic) musculature, making mimetic musculature a desirable target in efforts to better understand evolution of the domestic dog. Mimetic musculature was grossly examined in cadaveric specimens from a range of dog breeds and compared to mimetic muscles in gray wolves. Select mimetic muscles were also sampled for histological processing to examine microanatomical and physiological aspects of facial musculature mobility. Results revealed little variation in mimetic musculature among the domestic dog specimens, and the same was true within the gray wolf samples. However, mimetic musculature around the eye differed between the domestic dogs and the wolf samples in two key muscles. Domestic dogs (except for the husky specimen) consistently had musculature around the eye that varied in the wolf specimens. Variation in myosin fiber type percentages was also apparent with the domestic dog sample having a greater percentage of fast-twitch fibers in muscles associated with the eye and mouth. These results may indicate that movements associated with the eye region may have played an important role in domestication of dogs and that increased speed in facial expressions may have been an important variable in dog domestication.

Trabecular Bone Density in Canids: an Analogue for Understanding Human Self- Domestication

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The domestication syndrome describes phenotypic changes arising from the domestication process. Notwithstanding the debate about this process, it is undoubtedly a complex one involving profound morphological, cognitive and physiological changes. Among canids, some of the features and behaviors associated with domestication of dogs compared to their wild-counterparts the wolves, are: prosociality, reduced stress levels, and reduced cranial capacity. Data suggest that selection for prosociality among dogs resulted in morphological by-products such as reduction in cranial capacity, and overall gracile morphology. This concept has recently been applied to understanding the gracilization of the modern human skeleton. One significant event in human prehistory was a morphological shift from robust to gracile skeletons in the Holocene. While this may have been due to sedentism, a competing hypothesis is the effect of self-domestication. In other words, as modern humans settled in communities, there was increased selection for prosociality. Consequently the by-product of this selection was the evolution of a gracile skeleton, i.e., having low trabecular bone density. However, this hypothesis has not been tested between dogs and wolves, which exhibit the effects of domestication (i.e., the domestication syndrome). This study hypothesizes that dogs have a low trabecular bone density as a consequence of domestication compared to wolves. The study compares trabecular density in hind limbs (femur and distal tibia) of dogs and wolves. Results from Kruskal-Wallis tests indicate that indeed the dogs have a lower trabecular density than the wolves. This supports the hypothesis that selection for prosociality may have had an effect in the observed gracile skeletons of dogs. This comparison provides an analogue that may further the understanding of self-domestication and gracilization. Still, more research is needed to better understand whether this is a consistent pattern across breeds.

Comparing Brains from Different Dog Breeds Based on 3D-Endocast Modeling

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Analyzing gross morphology and inter-species differences of the brain can be done in different ways. Direct methods allow to examine the organ either ex situ by removing it or *in situ*, through imaging methods (e.g., CT, MRI). Indirect methods rely on the estimation of the volume of an endocranial cast, obtained by filling the endocranium with a certain matrix (e.g., liquid, beads, stones etc.). Compared to these a more precise procedure is the creation of virtual endocasts, where computer-analysis and comparison can be performed. We used 15 dog (*Canis familiaris*) skulls with different head types (5 brachycephalic, 5 mesocephalic, 5 dolichocephalic) from a private collection, digitalized with high definition computed tomography (CT). Imaging was performed with a Siemens SOMATOM Definition AS+ machine (120 kV, spiral pitch factor= 0.6, convolution kernel= J45s, FOV= 512x512, voxel size= 0.3x0.3x0.3 mm). Image series were exported in NIfTI- (Neuroimaging Informatics Technology Initiative) format, then they were imported into Amira for Life Sciences 6.0 software. Using Amira's Segmentation Editor two separate label fields were generated for each volume: one for the osseous structures, and one for the endocast. Afterwards, surfaces were created from the label fields, and saved in STL- (stereolithography) format. Refining of the 3D-models was obtained with Amira and Autodesk Meshmixer, and photos and video-animations were also recorded. We are currently working on the digitalization process. Preliminary segmentation results indicate that it is possible to measure the total volume of the endocasts and the surface of the models, and make craniometric analysis in connection with these parameters. Creating virtual endocasts from various breeds will also provide a good base for further comparative studies. Research was supported by ERC 680040, Bolyai RS, Bolyai+, and HAS 2017-1.2.1-NKP-2017-00002.

Biomechanics of Different Dog Breeds on Land and in Water

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Dogs have been bred for different sizes and functions, which can affect their locomotor biomechanics. As quadrupeds, dogs must distribute their weight between fore and hind legs when standing. The weight distribution in dogs was studied to determine if the proportion of supported weight on each limb couplet is dependent on body size. A total of 557 dogs from 123 breeds ranging in size from Chihuahua to Saint Bernard were examined. Each dog was weighed on a digital scale while standing, alternating fore leg and hind leg support. Overall mean proportion of weight on the fore legs to the total weight was 60.4% (range: 47.7-70.0). When separated into AKC categories, only the working group (e.g., Newfoundland)) was significantly above the mean. For groups based on genetics, European origin mastiffs and drovers were significantly greater than the mean (e.g., bulldog, Rottweiler), while herders and coursers (e.g., collies, greyhounds) were below the mean. The weight of the head, chest, and musculature for propulsion could explain the weight support differential. When the weight factor was removed during swimming, movement and coordination of the limbs was the same for different breeds. Underwater video of surface swimming dogs was recorded for eight individuals from six breeds, ranging in size from terrier to Newfoundland. Dogs all swam with a similar quadrupedal paddling stroke. The paddling stroke represented a modified terrestrial gait similar to a fast diagonal sequence single footfall. Stroke frequency decreased with increasing body size with the power phase of the stroke cycle shorter than the recovery phase for both fore and hind limbs. However, maximum velocity during the power phase was greater for the hind limb compared to the fore limbs. The modified terrestrial gait used for swimming in the dog paddle appears to be stereotypic among breeds, whereas weight distribution and terrestrial locomotion in dogs shows substantial variation among breeds.

Skeletal Changes through Domestication and Selective Breeding in Dogs: a Developmental Perspective

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Domestic dogs offer an excellent case study of changes in growth and development as a result of the domestication process and breed formation, and their study and comparison with other mammalian domesticates offer insights into patterns and mechanisms of morphological diversification. It has repeatedly been proposed that a single ontogenetic process was responsible for the overall similar skull shape of adult dogs, which resembles that of juvenile wolves (paedomorphism). We tested this by using 3D- geometric morphometric methods to investigate ontogenetic trajectories of skull shape change in different domestic dogs and the wolf. We found that skull shapes of domestic dogs are already different from one another and the wolf at birth, but that skull shapes of juvenile domestic dogs consistently resemble those of absolutely younger wolves at any given age. As opposed to these fundamental changes of skull shape, which likely occurred relatively early during the domestication process, the tremendous morphological variation of domestic dog skull shapes, which are apparent in modern breeds, is more recent. We examined the pace with which morphological changes took place in some phases and forms of domestic dogs and compared rates with the wild relatives and other species. These comparisons show that there is no acceleration of the evolutionary rate of skull shape change in domestic dogs compared to wolves, which contrasts with previous notions that rates of evolution are universally faster in domestication. Further studies of cranial and epiphyseal suture closure and of tooth eruption profit from documentation in important collections and provide insights into the tempo and mode of changes due to domestication and breed formation in domestic dogs and in other species, in which selection but also 'internal' and phylogenetic factors play a role.

Variation in the Shape of the Cribriform Plate between Domestic Dogs and Wild Canids

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The relationship between humans and domestic dogs has dramatically changed in the ~20,000 years since their domestication. In the past 500 years, domestic dogs have increasingly become the focus of intense artificial selection, leading to extreme variation in skull shape. Selection for snout length has been particularly intense, with some dogs having long slender snouts (many sighthounds), and others having almost no snout at all (pugs). This likely impacts the structures within the snout, such as those related to olfactory ability, including the cribriform plate. Using CT-scans from over 40 dog breeds and 11 species of wild canids, we reconstructed the cribriform plate using the Materialise 3D-rendering software and then used geometric morphometrics to quantify how cribriform plate shape varies among dog breeds and between domestic and wild canids. The overall shape of the cribriform plate across domestic dogs varies greatly. A PCA demonstrates that much of the variation in cribriform plate shape is due to variation within the anterior to posterior length of the domestic dog cribriform plate. The variation in cribriform plate shape within the wild canids does not approach that of the domestic dogs, despite having longer divergence times. While dog breeders have not selected for alterations to the shape of the cribriform plate, the intense selection for extreme skull shapes in a relatively short period of time has greatly modified the shape of the cribriform plate.

An Ancient Genomic Approach to Understanding the History of Dog Domestication

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Despite numerous investigations leveraging both genetic and archaeological evidence, the geographic origins of dogs remain unknown. On the basis of an ancient Irish dog genome and an assessment of the spatiotemporal appearance of dogs in the archaeological record, a recent paper suggested that dogs may have been domesticated independently in Eastern and Western Eurasia from distinct wolf populations. Following those independent origins, a mitochondrial assessment suggested that the Mesolithic dog population in Western Europe may have been replaced by a population from the East. To test this hypothesis, we are generating nuclear genomes of ~30 ancient dogs sampled from sites across Eurasia, and mitochondrial genomes from ~400 dogs spanning the last 15,000 years across Eurasia. The results of this analysis will reveal the phylogenetic affinities of dogs that were present across the Old World prior to the introduction of dogs associated with farming communities. This study will also allow us to infer the timing of the European mitochondrial turnover and to assess whether there was a commensurate turnover at the nuclear level, thus directly addressing whether dogs were domesticated from more than one population.

The Sensory Aspects of Dog-Human Communication

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For some ten thousand years, dogs and human typically form social groups, and dogs living in families develop an attachment relationship with their human companions. This relationship is supported by a wide range of communicative signals, involving vision, hearing and olfaction. Some of these signals seem to be related to environmental events, others reflect changes in the emotional state of the sender. Dogs and humans seem to have gone a long way to be able to recognize and process mutually these signals. Dogs have been shown to be sensitive for human pointing signals which help them to perform well in cooperative interactions. However, it seems that dogs' visual abilities may constrain their ability to processing human gestures. Size of the dogs and their head shape may also play a role in what ways dogs attend to signals displayed by the human body. Although dogs have a wider hearing range, both humans and dogs seems to use the same interval of frequencies when it comes to acoustic signaling. In general, mammals share a wide range of (possibly homologue) acoustic signals many of which are also present in humans and dogs. Recent behavioral studies have also shown that dogs and humans are very effective in reacting to each other's vocalizations that express inner states. In addition to mutual learning about the specific meaning of acoustic signals, overlapping communicative signals of the two species contribute significantly to their close relationship.

Positive Selection and Differential Expression of Olfactory Receptors in the Domestic Dog

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Olfaction is the oldest of the vertebrate special senses and yet remains the least understood. We assess positive selection and differential expression of olfactory receptors in dog breeds of enhanced and diminished olfactory sensitivity. Positive (or directional) selection is among the most extensively studied forms of selection, occurring when an allele is favored by natural selection. However, positive selection on olfactory receptors among breeds and wild canids has not been extensively studied. We analyze sequence data from ~800 olfactory receptors (OR) from multiple individuals from 30 breeds with supposed differences in olfactory sensitivity and 10 gray wolves. We used several analytical methods such as Polysel, PAML and HyPhy to detect positive selection. Our second aim is to assess differential expression of olfactory receptors across breeds that have distinct olfactory abilities. We extracted RNA from 24 epithelial tissues across 23 dog breeds. A first exploration, based on gene expression pattern in 344 olfactory genes remaining after filtering for low counts, evidenced a pattern of expression consistent with breed body size rather than the supposed olfaction abilities for the dog. A second analysis based on breed sizes below 20 pounds and above 66 pounds showed that 26 OR genes are upregulated in larger breeds. These preliminary results suggest that breed size might be an important predictor of olfactory abilities in dogs, perhaps due to the greater surface area and likely neurological capacity of the cribriform plate in large dogs.

Whole Genome Sequencing of 722 Canidae Reveal Genomic Regions Under Selection and Variants Influencing Morphology, Behavior and Longevity

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Domestic dog breeds present an unrivaled diversity of morphologic traits and breed-associated behaviors resulting from human selective pressures. Most breeds were created within the last 200 years to fulfill working or aesthetic requirements by either reproductively isolating small number of homogenous founder animals with specific characteristics or by combining founders from multiple breeds of desired phenotypes. This has generated an inimitable system for understanding and identifying genetic variants and their biological consequences on mammalian traits and disease susceptibilities. To identify the genetic underpinnings of such traits, we worked with dog owners, breeders and the kennel clubs to collect DNA samples from dogs of varying breeds and phenotypes. We then analyzed 722 canine whole genome sequences (WGS), documenting over 91 million single nucleotide variants and small indels, creating the largest catalog of genomic variation for a companion animal species to date. We undertook both selective sweep analyses and genome wide association studies (GWAS) inclusive of 144 modern breeds, 54 wild canids and a hundred village dogs. Our results identify new sequence variants of strong impact associated with 16 phenotypes, including ear and tail position, leg length and body weight variation. The latter, when combined with existing data, explains greater than 90% of body size variation in dogs. We further explore the genetic relationship between regulatory mutations, body size and longevity.

We also identify genomic variants that account for differences in breed-specific behaviors. We thus demonstrate that GWAS and selection scans performed with WGS are powerful complementary methods for expanding the utility of companion animal systems for the study of mammalian growth and biology. This work was supported by the National Human Genome Research Institute of the U.S. National Institutes of Health.

The Price of a Cute Face: The Impact of Selection for Facial Reduction in Dogs

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Through artificial selection and longstanding breeding practices, humans have produced a variety of short-faced dog breeds that are desirable for their temperament, iconic appearance, and paedomorphic facial features. However, breeding for these traits has come at a cost. Brachycephalic airway syndrome affects the health and well-being of many brachycephalic breeds, leading to issues with respiration, olfaction, and thermoregulation. The purpose of this project was to analyze the effects of breeding on facial reduction and cranial size and shape in domestic dogs (*Canis lupus familiaris*). We used clinically-obtained CT-scans and geometric morphometrics to analyze three brachycephalic breeds, one normocephalic breed, and a small sample of unknown breed. We recorded 62 cranial and mandibular landmarks that allowed us to analyze differences in shape in the neurocranium, basicranium, and viscerocranium. Unsurprisingly, we determined that most of the cranial shape variance in our sample was associated with cephalic index (ratio of cranial width to length), and that shape changes in the crania and mandibles co-vary. Additionally, there is evidence of localized shape change throughout the skull. In the mandible, there is a uniform shift in proportion involving rostral-caudal shortening and medial-lateral widening. In the hard palate, the majority of the shape change is localized to the maxilla. Here, a pronounced difference in maxillary carnassial orientation relative to the mandibular carnassial orientation results in disruption of the functionally important carnassial complex. Additional shape effects were found in the orbits, zygomatic arch, and foramen magnum. These results support previous studies showing integration within the skull and highlight the deleterious effects of artificial selection for facial reduction in domestic dogs. Localizing the shape effects associated with brachycephaly is necessary for identifying specific mechanisms that result in facial reduction.

What the Dingo (or *Canis familiaris*) Says about Dog Domestication

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Dogs (*Canis familiaris*) were the first and arguably most important species ever to be domesticated. They are certainly the most common domesticate and are often accorded near-human status, both today and in the past. It is widely accepted that the dog is descended from gray wolves (*Canis lupus*), possibly a population now extinct. How can a living canid, the dingo (*Canis dingo* or *Canis familiaris*), whose status as a species and as a domesticate is controversial, improve our understanding of the process of domesticating the dog? The earliest European depictions of kangaroos and dingoes were produced by George Stubbs in 1772. There is still no agreement on what a dingo is. Some feel that the iconic Australian "wild dog" is descended from village dogs that went feral after arriving in Australia. As with the humans, dingoes arrived from Asia by boat. The earliest modern human occupation of Australia is dated to 65,000 years ago, well before dog domestication. Yet, genetics and remains of dingoes suggest they invaded Australia about 5,000 years ago. Dingoes' distinctive traits are either primitive or adaptations to the Australian habitat that evolved over their period of isolation prior to the European colonization. Most recently, Crowther et al. (2014, J. Zool. London 293: 192–203) have argued that the dingo is a distinct primitive species, never domesticated. These scholars point to the dingo's different reproductive cycle (one breeding per year versus two in dogs), different morphological proportions, and unusual physiological and behavioral adaptations to aridity and to human company. Nonetheless, dingoes interbreed with domestic dogs. Only remains pre-dating 1900, when Europeans became widespread in Australia, are likely to represent pure dingoes. Comparing the archaeological and genetic domestication of the dog with that of dingoes highlights important similarities and differences in both the human and canid invasions of the world.

The Unbalanced World of Highly Bred Domestic Dogs: An Examination of the Canid Inner Ear

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The mammalian inner ear houses the organs for hearing (cochlea) and balance (vestibular system). The vestibular system, one the most primitive of sense organs, encompasses aspects of balance, linear and angular acceleration. The bony labyrinth (BL) of the petrous houses the semicircular canals, organs pivotal in detecting angular acceleration. Studies in mammals have shown that semicircular canal orientation at right angles (orthogonality) enhances sensitivity to angular acceleration. Little is known about this region in canids, however, who provide an excellent natural experiment due to their considerable variation in craniofacial form while exhibiting similar locomotion. This study tested the following hypothesis to examine how changes in BL size and cranial base length across dog breeds affects semicircular canal orthogonality: That orthogonality between semicircular canals is significantly correlated to BL size and cranial base length. Materials used (17 BLs of 13 dog breeds) were data derived from the comprehensive study by Schweizer et al. (2017, Sci. Rep. 7(1), 1–8) on canid inner ear metrics. Results supported the hypothesis that orthogonality between the anterior and posterior semicircular canals is significantly correlated with BL size and cranial base length (R^2= .371, p=0.006 and R^2= 0.488, p=0.001, respectively). This suggests a close relationship

between these canal orientations and cranial structure across dog breeds. Of particular note was the observation that highly derived breeds, such as the short-faced pug, had anterior and posterior semicircular canals that deviated the most from orthogonality. Therefore, such highly bred domestic dogs may also have altered vestibular function due to compressed cranial form. Funding Statement: Supported by The Graduate Center, City University of New York; The Anatomical Record; the Center of Anatomy and Functional Morphology at the Icahn School of Medicine at Mount Sinai; and the New York Consortium of Evolutionary Primatology.

"Mucosal Maps" of the Canine Nasal Cavity: Can Micro-Computed Tomography be Used to Identify Olfactory Mucosa?

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The high resolution of micro-computed tomography (μCT) now allows us to describe minute bony structures that were previously only accessible using destructive methods (e.g., histology). Such structures include nasal turbinals, thin scrolled or branched bones of the nasal cavity that support respiratory or olfactory mucosa (OM). Standard μCT currently lacks the capacity to identify OM or other mucosa types without additional radio-opaque staining techniques. However, even unstained mucosa is more radio-opaque than air, and thus mucosal thickness can be discerned. Here, we assess mucosal thickness of the nasal fossa using the cranium of a cadaveric adult dog that was μCT-scanned with an isotropic resolution of 30 μm. The snout was then serially sectioned and stained for histological study to assess within-individual variability of the mucosal thickness. Using ImageJ, mucosal thickness was estimated at four locations on each section (at least 30/region): the roof of the nasal cavity where the nasoturbinal merges with the nasal septum, the opposing side of this region in the frontal recess, and two locations near the apex of the scrolled nasoturbinal. Results based on either μCT or histology indicate mucosa along the roof of the nasal fossa is the thickest and least variable of the three regions, based on the coefficients of variation (CV); histology confirms a uniform lining of OM. Histology also allowed us to assess variation within OM and non-OM. OM on the nasoturbinal (CV = 9 to 25%) is thicker on average and less variable than non-OM (CV = 36 to 74%). OM along the roof of the nasal fossa is less variable (CV = 15%) than in the frontal recess (CV = 25%). High variability of non-OM appears to relate to the varying degree of vascularity of the lamina propria. Results indicate that OM can be distinguished as a thicker and less variable mucosa than adjacent regions that lack OM. Support, in part, by NSF grants BCS-1830919, BCS-1830894, and IOS-1457106.

Introduction: Dogs in the Context of Canid Evolution

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The domestic dog is undoubtedly the best-known member of the family Canidae, living and extinct. Serving as our companions, helpers, defenders, and sometimes as food, dogs have been modified by us for thousands of years. This has resulted in an astounding array of body conformations, from tiny to large, svelte to stout, with an equally diverse collection of head shapes. How does the morphological diversity of dog breeds compare with that expressed over the 40 plus million years of canid history? The fossil record has produced over 130 species of canids in three subfamilies, the extinct Hesperocyoninae and Borophaginae, and the extant Caninae. As background for our symposium, I review the history and diversity of morphological forms within the Canidae, highlighting possible parallels between breeds and extinct taxa, as well as extinct forms that have no modern analogs among living dogs or wild canids. Despite the impressive variety of form exhibited among dog breeds, there are regions of canid morphospace that they have yet to occupy, probably because they descend from a single species. Notably, a hallmark of canid history is evolutionary versatility, a feature that has allowed them to opportunistically adapt to changing environments, successfully invade new continents as well as the homes and lives of *Homo sapiens.*

'*Forever Young*' – Postnatal Growth Inhibition of the Respiratory Turbinals in Brachycephalic Dog Breeds (*Canis lupus familiaris*, Canidae, Carnivora)

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The dog (*Canis lupus familiaris*) comprises different cranial morphotypes. While the facial length in medium (mesaticephalic) to long snouted (dolichocephalic) breeds is similar to the ancestral stage determined by the Eurasian wolf (*Canis lupus lupus*), in short snouted (brachycephalic) breeds diverse genetic mutations cause a postnatal growth inhibition in the dermal bones of the midface (viscerocranium). Affected breeds keep their neonate snub nose and modern extreme brachycephalic dogs (e.g., pug, English bulldog) even suffer from this pattern culminating in severe health issues like asphyxia and thermoregulatory problems. However, detailed morphological studies on dogs regarding how snout length affects associated internal structures like the turbinals within the nasal cavity are still scarce. For the present study eleven breeds covering different snout length types and ontogenetic stages were selected. Adult Eurasian wolves served for outgroup comparison. Based on high-resolution computed tomography (μCT) and virtual 3D-models the morphology and morphometry of the turbinal skeleton, especially the respiratory functioning maxilloturbinal, was investigated. Our analysis proves a complication of the maxilloturbinal in sighthounds, but it does not yet highly exceed the shape of the Eurasian wolf. The shorter the snout becomes, the simpler is the maxilloturbinal, supported by morphometric analyses, namely a proportional decrease in turbinal surface area and surface density. The conspicuous reduction and simplification in the most extreme brachycephalic breeds can be elucidated by including perinatal stages into the morphological dataset. We can conclude that in brachycephalic adult dogs the maxilloturbinal arrests at an early ontogenetic stage. Our results exactly correspond with studies on the dermal bones proving that the growth of the turbinal skeleton is significantly affected by the length reduction of the viscerocranium.

Skeletons in Moving Fluids – Organizers: Pauline Provini, Kristen Crandell

Morphology and Motion of the Axial Musculoskeletal System During Suction Feeding in Rainbow Trout, *Oncorhynchus mykiss* (Actinopterygii: Salmoniformes)

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Many fish take advantage of the viscosity of water to capture food by suction: rapidly expanding the mouth cavity so that water and food are sucked inside. Suction feeding requires not only a deformable mouth cavity, but also substantial power to increase mouth volume with enough speed and force to accelerate a bolus of water. While a mobile cranial skeleton allows 3D-mouth cavity expansion, most of the power for expansion comes from the dorsal and/or ventral body muscles. Dorsally, the epaxial muscles span the length of the body and can contribute to suction expansion by elevating (dorsally rotating) the neurocranium relative to the vertebral column. This feeding role may influence the morphology of these axial structures as much as their locomotor roles. But the dynamics of how the epaxials generate power for suction flows—and to what extent the vertebral column contributes—remain poorly understood. I used XROMM and fluoromicrometry to measure skeletal motion and muscle lengths during suction feeding in rainbow trout (*Oncorhynchus mykiss*) and quantified vertebral shape from CT-scans. Dimensions of the vertebral centra suggest a morphologically distinct cervical region consisting of at least the first five vertebrae. However, during cranial elevation epaxial shortening extended over a much larger region of at least the first 20 vertebrae, as in other suction feeding fishes. The mediolateral width of the epaxials increased during cranial elevation as well, consistent with these muscles bulging laterally as they shorten longitudinally. These results suggest epaxial shortening and power production is not limited to a morphologically distinct region of the vertebral column, and that muscle force and velocity is transmitted cranially to power suction expansion. Understanding the role of 3D-epaxial muscle deformation during suction expansion may reveal how the demands of both suction feeding and swimming have shaped the morphology of the axial system in these fish.

Linking Skeletal Patterns to Swimming Performance in Foot-Propelled Birds

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Within the diversity of birds, numerous lineages have colonized aquatic environments. Because birds that swim using their feet face tradeoffs for walking on land, we expect hindlimb musculoskeletal morphology to vary with the degree of aquatic specialization. Many studies identify avian hindlimb adaptations based on functional interpretations of the skeleton. Here, we combined measurements of hindlimb skeletal elements with detailed muscle dissections, high-speed videography, and engineering experiments to link skeletal patterns to swimming performance. We present three cases. (1) Accounting for phylogenetic relatedness, we find that highly-diving species have a high tibiotarsus to femur length ratio ($p<0.01$), which corresponds to relatively massive hip extensors and "ankle" plantarflexors ($p<0.05$), muscles that power paddling. These skeletal proportions also enable diving birds to tuck the proximal limb next to the ribs and within the abdominal skin, permitting shifts in muscle insertions that increase mechanical advantage. (2) We observed over 90 degrees of lateral rotation at the knee joint in grebes and loons associated with specialized condylar structures. By tracking the limbs of loons while swimming in a rehabilitation pool, we recorded foot movements that require knee rotation. Replicating loon swimming using cadaveric feet attached to an industrial robot enabled measurements of time-varying hydrodynamic forces. We found that by rotating their feet loons produce lift, a force often considered more efficient than drag but previously unrecorded in foot-propelled birds. (3) We quantified digit length ratios and foot shape, finding a significant influence from swimming ability. Upcoming tests measuring drag produced by physical foot models that range in shape will associate digit proportions to swimming forces. Together, these three cases relate skeletal measurements to biomechanical performance with implications for evolution, conservation, and bioinspiration.

Using 3D-Printed Models to Explore the Functional Consequences of Avian Beak Morphology

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The upper and lower mandibles of birds are highly specialized to a variety of tasks, including singing, foraging, and display. While these selective pressures have led to a variety of rostral morphologies, all beaks are subjected to aero- and hydro-dynamic forces associated with locomotion in a fluid environment. In general, the beak should be streamlined in order to minimize drag, however, conflicting functional demands likely challenge this assumption. We tested how avian beak morphologies have evolved in relation to their fluid mediums for both aerial species and species that function at the air-water interface. We examined the effects of beak morphology in hummingbird and toucan species by mounting 3D-models to a sting and measuring drag in a wind tunnel. We examined the effects of beak morphology on plunge performance by simulating dives with physical 3D-printed models of kingfisher beaks coupled with an accelerometer. From simulated dives of bill models, diving species have lower peak decelerations, and thus, enter the water more quickly, than terrestrial and mixed-foraging species (ANOVA $p=0.002$), and this result remains unaffected by phylogeny (phylogenetically corrected ANOVA $p=0.04$).

Terrestrial Walking in Fishes with Tetrapod-like Skeletons

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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 diagonal-couplets 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 is joined to the iliac process of 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 diagonal-couplet lateral-sequence gait was accomplished by rotation of the pectoral and pelvic girdles creating a standing wave of the axial body. These findings are significant because they represent the first example of behavioral and morphological adaptation in an extant fish that converges on the tetrapodal walking behavior and morphology.

Swimming Kinematics and Prey Processing in a Ram Suspension-feeding Fish, and Intraspecific Diversity in Trophic Morphologies in an Adaptive Radiation

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In many fish taxa, the kinematics of the trophic and locomotor systems are necessarily linked. For ram suspension-feeding fishes, effective foraging depends on the continuous flow of water through the buccal cavity, but it is not obvious how kinematic variables involved in undulatory swimming, namely yaw, heave, and stride frequency, are related to the functioning of the trophic system. We showed that the functioning of the filtration mechanism used by American paddlefish (Acipenseriformes: *Polyodon spathula*) is affected by both morphological and kinematic variables. Swimming kinematics play a role in concentrating food particles near the branchial arches and transporting them to the posterior of the buccal cavity, suggesting a potential role for behavioral modulation of the filtration mechanism via swimming kinematics. The relationship between morphology and swimming kinematics on the size selectivity of food particles remains unclear in paddlefish and other species, but this information could help describe population and evolutionary trends for both predator and prey species. One strategy to clarifying the effects of intraspecific variation in trophic structure and function is to conduct comparative studies using divergent populations. The threespine stickleback (Gasterosteiformes: *Gasterosteus aculeatus*) has extensive well-documented variation in trophic traits between populations, making it a good species for testing whether variation in trophic systems has ecological and evolutionary consequences. Stickleback have benthic or limnetic morphologies, in which individuals feed primarily on benthic macroinvertebrates or zooplankton, respectively, but it remains unclear whether there are morphologies associated with specific prey taxa or generalist or specialist feeding. Using 3D-geometric morphometrics, we are attempting to determine whether trophic lever morphologies are associated with prey taxa in parapatric pairs of stickleback populations on Vancouver Island.

3D-X-ray Particle Tracking Method: Inside a Fish's Mouth During Suction Feeding

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Suction-feeding fishes capture their prey by generating a high-velocity flow of water, entering the mouth and exiting at the back of the head. In spite of the prominent role of hydrodynamics to catch food successfully, difficult optical access to the buccal cavity makes it still poorly understood. We used the technique of 3D-X-ray particle tracking, optimized to quantify intra-oral flow dynamics in carp (*Cyprinus carpio*). Two synchronized and calibrated X-ray sources, associated with high-speed video cameras filmed the fish and its surrounding environment, seeded with radio-opaque particles. We specifically designed small, approximately neutrally buoyant, radio-opaque particles composed of 1.4 mm diameter polystyrene foam spheres with an insert of an X-ray absorbing metal marker. Two individuals of Carps were implanted with 0.35 mm diameter radio-opaque markers on the upper jaw, lower jaw, hyoid, suspensorium, branchial arches, opercula, skull and pectoral girdle. These implants allowed us to reconstruct the skeletal 3D-kinematics of the head, in order to unravel the relationships between the 3D-kinematics of the animal's cranial system and the associated intra-oral water during feeding.

Aquatic Foraging in Snakes: From Morphology to Behavior

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Despite their lack of limbs, snakes have successfully invaded all possible habitats. From burrowing to gliding or swimming, without mentioning moving in or above sand, snakes have developed specific adaptations to deal with the physical properties in all these different environments. Aquatically foraging snakes are particularly interesting, with more than 300 species invading water at various degrees; from species that never leave water, to species that are mostly terrestrial yet occasionally feed on fish. Snakes are primarily adapted to terrestrial conditions; thus to detect and capture a prey living in a dense and viscous fluid (such as water) has required additional adaptations. Underwater prey capture results in strong hydrodynamic constraints on the head of snakes, so they have converged toward a head shape that reduces these hydrodynamic forces. Some snakes use different behavioral strategies to capture their prey, to also circumvent hydrodynamic constraints. But before catching its prey, the predator must detect it, and the physical properties of water also affect the propagation of sensory cues in comparison with air. Moreover, other characteristics of water can also disrupt the propagation of some signals, such as turbidity and flow. How has the sensory system of snakes adapted to detect prey under water? Are these sensory abilities related to the shape of the brain? What is the relationship between brain, braincase and head shape in snakes? These are all questions we are currently addressing comparing the brain and braincase of several species of snakes using µCT-imaging of both iodine stained and unstained collection specimens. The sensory modalities are assessed by using behavioral experiments to isolate each sense and measure the response of the animal to a stimulus. Using this combined approach, we are able to draw the link between the properties of the environment, the sensory modalities, and the morphology of the head, brain and braincase of aquatic snakes.

Water Impact-Entry and Phenotypic Adaptability in Birds

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Birds present extreme morphological modifications in adaptation to flight. Concurrently, we find great structural and behavioral specializations for foraging. Diving birds live in the air and in the water, which requires morphological and physiological adaptations for dwelling in the two media. However, in plunge-diving behavior, the birds' structures have to absorb the impact forces during the air-water transition. Only a small group of birds has developed such foraging strategy as a behavioral trait, but two distant families are considered highly specialized: Sulidae (gannets and boobies) and Alcedinidae (kingfishers). To investigate the structures that may have gone through phenotypic adaptability to water impact-entry we used micro-Computed Tomography (µCT) and Geometric Morphometrics (GM) of the skull and cervical vertebrae. These structures endure high hydrodynamic forces externally and high compressive forces internally. GM analysis was used to investigate if specific structures or shapes are critical in the role of air-water transition. This may hint at a morphological convergence between evolutionarily distant groups that have similar plunge-diving behavior. Furthermore, we calculated the impact force related to ecological traits to understand the importance of environmental factors on the shape of the beak and of the skull. This should also reveal if there is a direct relationship between the environmental conditions and morphological traits that can be traced across the species.

Convergence and Constraint in Vertebrate Skull Evolution – Organizers: Anjali Goswami, Michelle Stocker

Cranial Morphological Evolution across Anura (Frogs)

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Anurans (frogs) are the most speciose, and most diverse, clade of Lissamphibia. Anuran crania are incredibly disparate, from streamlined aquatic skulls (e.g., *Pipa*) to wedge-shaped skulls of burrowing frogs (e.g., *Hemisus*), and this extreme morphological variation creates a significant challenge for quantifying cranial morphology across the clade. We use a high-dimensional data approach to capture the cranial morphology of 170 anurans, spanning the entire anuran clade and all major ecological niches. We place 82 landmarks and 480 sliding semilandmarks onto each skull, and semi-automatically apply ca. 500 surface semilandmarks across 19 cranial regions. We investigate phylogenetic, allometric and ecological influences on cranial morphology, as well as determining the disparity of each cranial region. Preliminary analyses of a subset of landmarks ($N = 58$) and sliding semilandmarks ($N = 387$) for 12 cranial regions were undertaken for 154 species. Allometry is a weak, but significant influence on cranial morphology ($R^2 = 0.12$, $p = 0.0001$), with larger crania appearing wider and more dorsoventrally compressed. Phylogeny was also a significant influence on cranial morphology ($K_{mult} = 0.64$, $p = 0.0001$). A phylogenetic MANOVA revealed that ecology (fossorial, aquatic, terrestrial) has an extremely small but significant correlation with cranial morphology ($R^2 = 0.04$, $p = 0.001$), suggesting some morphological convergence across anurans. Fossorial and aquatic species generally clustered separately in cranial morphospace, with fossorial species associated with dorsoventrally taller skulls and an expanded snout region. Of the 12 cranial regions, the squamosal was the most disparate, and the parasphenoid the least, with earlier ossifying bones generally less disparate. This study reveals an interplay of influences on anuran cranial morphology, and suggests cranial ossification timings may play a role in cranial disparity.

Constraint and Convergence in the Evolution of Beaks

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Several times in the history of the amniotes, the functional edge of the jaw margin has transformed from an array of mineralized teeth to an extended keratinous sheath — an integumentary beak or rhamphotheca. Hypotheses vary as to the selective pressures under which beaks have repeatedly appeared, and under which beak-bearing clades (including birds and turtles) have flourished. Here, we describe two cases of constraint and release of constraint that pertain to beak anatomy and function. First, we note that the beaks of birds and of turtles form as large patches of keratinized integument. We follow the development of head skin and the underlying dermal bones during the embryogenesis of several reptiles and find that archosaurs develop a continuous sheet of skin around the oral margin and rostrum. Evidence from extinct archosaurs suggests that at least some of their cranial integument was similarly continuous. Lepidosaurs, in contrast, have discrete scales that have been shown to derive from placodal precursors. Despite species diversity rivaling that of birds and morphological disparity far exceeding that of birds, lepidosaurs and stem lepidosaurs have never evolved beaks. Archosauromorphs, on the other hand, have repeatedly lost teeth and gained rhamphothecae. We suggest that the apparent ease of beak evolution in archosaurs and relatives owes in part to the configuration of their facial skin. Second, we note that beak disparity in birds is concentrated among the neognaths, most of which have a distinct, novel hinge between the mobile rostrum and the neurocranium. Using fossil evidence from the near-crown toothed avialan *Hesperornis*, which had a transitional avian beak, we suggest that the early form of avian facial kinesis constrained the anatomy of the beak and that the origin of the prokinetic hinge released it.

Ecological Influences on Cranial Morphology in Whales

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The order Cetacea is composed of two extant suborders, Odontoceti (toothed whales) and Mysticeti (baleen whales), which diverged ~39 Ma ago. Of ~90 extant cetaceans, >70 are odontocetes. Oligocene odontocetes rapidly evolved refined, high-frequency echolocation, shifted cranial bones further posteriorly and developed cranial asymmetry, while mysticetes evolved larger masses, and filter and suction feeding. However, to date, there has been little quantitative study of shape evolution spanning the full breadth of cetacean diversity. Here, 160 cetacean crania (64 extant, 96 fossil) were landmarked and analyzed in the 'geomorph' package in R. 66 landmarks and 63 sliding semi-landmark curves were placed on the left side and midline of the mysticete crania. 119 landmarks and 116 sliding semi-landmark curves were placed over the whole (right side, left side, and midline) of archaeocete and odontocete crania to capture natural asymmetry in the nares and the premaxilla. Landmarks were subjected to generalized Procrustes analysis, followed by a Principal Components Analysis. Centroid size was used to measure allometric effects, and ecological correlates of cranial shape were assessed with non-parametric MANOVAs. Most cranial variation (PC1 = 35.2%) reflects telescoping and a shift in the nares position. High positive values represent retrograde, odontocete telescoping and low values retrograde, mysticete telescoping. There is high variation in the length of the rostrum (PC2 = 25.6%) with dolicocephalic e.g., extant *Pontoporia blainvillei* and extinct *Xiphiacetus bossi*, and brachycephalic e.g., extant *Kogia sima* crania representing the extremes. Habitat does not significantly correlate with skull shape in this sample of extant species ($r^2 = 0.31$, $p = 0.14$), but diet does ($r^2 = 0.57$, $p = 0.001$). Assuming a similar ecomorphological relationship in extinct taxa, we can, therefore, hypothesize potential ecologies for our sampled fossil cetaceans based on cranial morphology.

Constrained in the Brain? Shedding Light on Avian Neuroanatomical Evolution with the Endocasts of Extinct Birds (Dinosauria: Avialae)

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The shape of the brain influences skull morphology in birds, and both traits are driven by phylogenetic and functional constraints. Studies on avian cranial and neuroanatomical evolution are strengthened by data on extinct birds, but complete, 3D-preserved vertebrate brains are not known from the fossil record, so brain endocasts often serve as proxies. Endocasts represent the external shape of the brain as impressed on the internal surface of the braincase and thus comprise an aspect of skull morphology in their own right. They have been shown to be faithful to the size and external morphology of the brains of birds, but little work has been done to quantify the relationship between avian brains and endocasts. Using a diverse sample of extant birds, we quantified the relationships between two vision-related brain structures—the hyperpallium and optic tectum—and their overlying endocast structures—the Wulst and optic lobe, respectively—which in both cases were strongly statistically significant. These analyses formed the basis of phylogenetic predictions of the optic tecta and hyperpallia of extinct birds based on their optic lobes and Wulsts, respectively. A phylogenetic ANCOVA approach indicated that, like their extant counterparts, none of the extinct birds studied had hypertrophied optic tecta relative to brain-rest volume. However, the moa stands out with an extremely reduced optic tectum, potentially indicating a release of constraint in this species on a trait whose expansion is considered to be key to avian brain evolution. Performing a phylogenetic ANCOVA on hyperpallium volume versus brain-rest volume indicated that none of the hyperpallia of the extinct birds sampled were appreciably different from extant birds sampled. Together, the results from these analyses represent case studies for a novel quantitative approach to incorporating extinct birds in studies of this aspect of skull morphology. NSF: DGE 1645419 to CME; IOS-1050154, IOS-1456503 to LMW.

Evolutionary Convergence and Constraints on the Skull Shape of Burrowing Wrasses

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The evolution of behavioral and ecological specialization can have marked effects of the tempo and mode of phenotypic evolution. Head-first burrowing has been shown to exert powerful selective pressures on the head and body shapes of many vertebrate and invertebrate taxa. In wrasses (Labridae: Percomorpha), burrowing behaviors have evolved multiple times independently, and are commonly used in foraging and predator avoidance behaviors. While recent studies have examined the kinematics and body shape morphology associated with this behavior, no study to-date has examined the macroevolutionary implications of burrowing on patterns of phenotypic diversification in this clade. Here, we use three-dimensional geometric morphometrics and phylogenetic comparative methods to study the evolution of neurocranium shape in fossorial wrasses and their relatives. We test for skull shape differences between burrowing and non-burrowing wrasses and evaluate hypotheses of shape convergence among the burrowing wrasses. We also quantify rates of skull shape evolution between burrowing and non-burrowing wrasses to test for whether burrowing constrains or accelerates rates of skull shape evolution in this clade. We hypothesize that burrowing wrasses will differ significantly in skull shape from their non-burrowing relatives and that they will exhibit a strong pattern of convergence towards similar skull shape morphologies. We also hypothesize that burrowing wrasses will exhibit reduced rates of skull shape evolution relative to non-burrowing wrasses due to the evolutionary constraints imposed by fossorial behavior.

Developmental Mechanisms Mediating Constraint and Evolvability of the Jaw

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Variation is necessary for morphological evolution, yet variation in development typically results in disease or death. How have developmental systems evolved to reduce variation while also supporting evolution? Robustness and canalization are mechanisms that buffer developmental variation, while evolvability structures variation. We propose that secondary organizers mediate tissue interactions that promote both robustness and evolvability. Organizers establish pattern and polarity in developing tissues, which constrain the direction of variation. However, polarity also contributes to modularity. Using examples predominantly in the mouse and chick systems, we show how organizers can simultaneously mediate robustness and evolvability of the jaw. Fgf8 is an important component of organizer activity in both the developing limbs and jaws. By modulating Fgf8 dosage in mouse development, we found that both jaw and limb development can buffer significant reductions in Fgf8 levels, but that jaw development is more sensitive to reductions in Fgf8 than is limb development. We hypothesize that limb development is more canalized than jaw development due, in part, to compensatory expression of other Fgfs. Fgf8 mutant mice also have directionally asymmetric jaw defects. This asymmetry is associated with abnormalities in jaw patterning (e.g, Dlx5 expression) in mutant embryos at E10.5 and defects in first pharyngeal pouch (PP1) morphology. Based on these and other data, we hypothesize that the jaw organizer is more susceptible to perturbation than the limb due to constraints imposed by developmental interactions between the jaw and heart. Finally, using Satb2 as an example, we highlight how organizers mediate evolvability through modularity of jaw elements.

Evolutionary Constraints On Bat Skull Morphology: Does Echolocation Matter?

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Flying mammals of the order Chiroptera underwent a dramatic evolutionary radiation that has led to disparate functional, behavioral and morphological adaptations. Multiple studies support a strong degree of association between bat skull morphology and functional traits such as feeding behavior. However, the influence of other factors (in particular echolocation) on bat skull form (i.e., size and shape) remains unknown. Echolocation adaptations are generally thought to be associated with soft tissue rather than bony structures, although there have been few investigations of this topic. We tested for associations between skull morphology and, respectively, feeding traits (diet, bite force and cranial muscles) and sensory traits (echolocation type and call characteristics) across ten bat families. We then accounted for the relative strength of these associations (feeding/morphological vs sensory/morphological traits). Bat skull size was not constrained by either diet or echolocation type. Nevertheless, diet and echolocation type explained significant proportions of skull shape variance. Bite force, muscle mass and echolocation characteristics strongly influenced skull size. However, when all species were included in the analyses, the major factors contributing to interspecific variation in skull shape were bite force and muscle mass alone. Echolocation characteristics were associated with shape within insectivorous bats, which showed a correlation between skull shape and frequency of maximum energy. Our results also suggest that feeding and echolocation may play a similarly important role in insectivorous bat skull evolution: the association between feeding traits and shape was of similar magnitude to the association between sensory traits and shape. Our findings provide new insights into the relationship between the skull and echolocation features and suggest that evolutionary constraints due to echolocation may differ between different groups within the Chiroptera.

Intrinsic and Extrinsic Constraints on Cranial Evolution within Cypriniformes (Actinopterygii: Ostariophysi)

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Breaking intrinsic developmental constraints can allow for the origin of morphological novelties that overcome functional constraints. Kinethmoid-mediated premaxillary protrusion within cypriniform fishes is one such novelty that breaks the morphological constraints seen in acanthomorph-type premaxillary protrusion. Within acanthomorphs significant protrusion requires remodeling of the neurocranium to facilitate sliding of a greatly elongated ascending process of the premaxilla, a constraint that is broken by the addition of a kinethmoid to the upper jaw linkage in cypriniforms. Epibranchial organs (EBO) improve filter feeding performance. Development of a complex EBO is constrained by the

availability of muscle progenitors. The most complex EBO is found in silver carp, where the same palatal organ that characterizes the trophic apparatus in all cypriniform fishes supplies this required resource. However, even this most complex EBO faces secondary extrinsic constraints associated with the mechanics of buccal pumping. Importantly, the impact that different cypriniform morphological novelties can have on the evolutionary and ecological history of a specific lineage varies. In the case of kinethmoid-mediated premaxillary protrusion this novelty is associated with ecological diversification; the novelty opens a great number of trophic niches via increased performance. This ecological diversification may have led to increased species diversity. In contrast, the most complex EBO appears in only two species, but the novelty has allowed for a massive expansion of trophic niche. Within the appropriate environmental context such an expanded trophic niche in an invasive species may lead to outcompeting native species. Here, we discuss some developmental constraints that promote diversification of species and function within Cypriniformes.

A Quantitative Framework for the Thylacine-Canid Comparison: Integrating Development, Morphology, Genomics and Evolutionary History

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Many large meat-eating marsupials roamed Australia over the past millions of years, but the Tasmanian tiger, or thylacine (*Thylacinus cynocephalus*), was the only one to survive into modern times. Here, I present some of the integrative techniques used to reconstruct the life, growth and death of this recently extinct predator and its extraordinary convergence with placental canids. By combining morphometric analyses with extinct genome assembly, we quantify for the first time phenotypic convergence between these distantly related lineages, and demonstrate that adaptive similarities in the skull are driven by non-coding regulatory evolution. Using newly assembled 3D-computed tomography models, we compare the ontogenetic trajectory of the thylacine skull to that of other mammals, to determine when during development they overcome their marsupial constraints to become more canid-like. Finally we contrast different hypotheses of cranial modularity across the postnatal growth period to test if different modules form at different time points, and weaken or strengthen during the animal's lifetime. Together these methods provide new insights into the thylacine's unique position among mammals, including its uncanny resemblance to wolves, its developmental dynamics, and its sister-group relationship to the insectivorous numbat (*Myrmecobius fasciatus*).

The Developmental Basis of Morphological Constraint in the Tetrapod Skull

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The field of evo-devo provides a conceptual framework that permits us to address theoretical questions about the origin and maintenance of morphological diversity over time, or lack thereof, from empirically-derived observations. The tetrapod skull, though highly diverse morphologically, has long been considered to be the product of deeply conserved evolutionary and developmental processes. Here, we review recent research wherein investigation into the mechanistic basis of the evolutionary development of the skull has shed light on instances of morphological constraint. First, experimental manipulation of *Hox* gene expression domains produced data that suggest the relatively anterior location of the skull-neck boundary in lissamphibians, relative to the condition seen in amniotes, may be the product of a homeotic shift in somite fate. Incorporation of fossil data suggests the shift took place in the lineage leading to lissamphibians, and that the amniote condition is plesiomorphic for Tetrapoda. As such, the occipital region of non-lissamphibian tetrapods represents one of the greatest examples of constraint in axial regionalization in tetrapods. We hypothesize this constraint is associated with the origin of an amniote-like complement of hyobranchial musculature derived from occipital somites at the base of Tetrapoda. Second, related experiments have revealed latent processes may constrain potential morphological evolution of the skull in the amphibian lineage. Disruption of the RA signaling pathway during development in axolotl phenocopies ancestral morphologies in the facial skeleton, rather than generating new ones. Together, data collected from this line of research is providing answers to questions such as what aspects of cranial morphology are evolutionarily negotiable (and which aren't?).

Genotype-Phenotype Mapping of Skull Development and Adaptation in Squamate Reptiles

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Skull bone diversification has played a major role in the adaptive radiation of vertebrates, and differences in facial morphology have significant ecological and clinical implications. However, the developmental mechanisms leading to different skull phenotypes are incompletely understood in vertebrates. In particular, squamates (snakes and lizards) are the second-most diverse group of tetrapods and show exceptional diversity in skull morphology, making them an ideal group for elucidating the mechanisms promoting phenotypic diversification. We performed a large-scale and integrative characterization of skull shape evolution in squamates, by covering all major lineages of lizards and snakes, using a geometric morphometric approach integrating developmental, ecological, and phylogenetic data. Strikingly, our data reveal major shape variations in both cranium and mandibular apparatus between major squamate groups, in particular between snakes and lizards, as well as significant cranial shape convergence among fossorial lizard and snake species. Additionally, analyses of morphological modularity and integration indicate the presence of evolutionary modules in the squamate cranium. Finally, our heterochrony analyses, based on quantification of ontogenetic trajectories in a unique dataset of embryonic squamate skulls, suggest that snakes have evolved novel craniofacial specializations through acceleration of ossification. This set of results demonstrates the importance of the relationships between skull shape, ecology, and development in snakes and lizards. Our current analyses involve the identification of the precise developmental mechanisms and signaling pathways underlying skull diversification within squamates, but also within vertebrates as a whole.

Can Ecology Explain Patterns of Morphological Integration Between Functionally Coupled Structures?

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A common feature of organismal evolution is that traits exhibit patterns of correlated evolution. This covariation or integration, is often attributed to interacting developmental pathways. However, integration could also arise if traits are subject to similar selective regimes. For example, the beak and palate of birds both function in feeding and thus their shapes may co-vary in response to selection on feeding performance. While not mutually exclusive, the potential importance of these mechanisms can be quantified by asking to what extent one mechanism can explain observed patterns of integration. Birds in the order Anseriformes (waterfowl) have evolved diverse feeding ecologies, including convergence of the more herbivorous “geese”. Quantifying integration using partial least squares (PLS), I find that waterfowl diets are closely associated with the shape of the beak (r-PLS1:0.80; P<0.001; N=40 spp) and palate (r-PLS1:0.77; P<0.001), which also show significant integration with each other (r-PLS1:0.70; P=0.003). In contrast, neurocranium shape is not significantly correlated with diet (P=0.90) nor the shape of the beak (P=0.50) or palate (P=0.85). These results are consistent with functional coupling of the beak and palate and feeding performance as a selective force on both. But can feeding ecology completely explain beak-palate integration? Using a new PLS residuals approach I find that whereas accounting for ecology significantly decreases beak-palate integration (Δr-PLS1=-0.08, -29% of the significant portion; P<0.001), the beak and palate are still significantly integrated after removing the portion of beak shape related to diet (r-PLS1=0.62; P=0.004). These results show that even ecological traits strongly associated with morphology cannot fully explain integration, suggesting more complete characterizations of organismal ecology, additional mechanisms, or both, are needed to fully account for patterns of morphological integration. Funded by NSF-1612230.

Convergent Evolution in Toothed Whale Cochleae

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Odontocetes (toothed whales) are the most species rich marine mammal lineage. The catalyst for their evolutionary success is echolocation - a form of biological sonar that uses high-frequency sound, produced in the forehead and ultimately detected by the cochlea. The ubiquity of echolocation in odontocetes across a wide range of physical and acoustic environments suggests that convergent evolution of cochlear shape is likely to have occurred. To test this, we used SURFACE; a method that fits Ornstein-Uhlenbeck (OU) models with stepwise AIC (Akaike Information Criterion) to identify convergent regimes on the odontocete phylogeny, and then tested whether convergence in these regimes was significantly greater than expected by chance. We identified three convergent regimes: (1) True’s (*Mesoplodon mirus*) and Cuvier’s (*Ziphius cavirostris*) beaked whales; (2) sperm whales (*Physeter macrocephalus*) and all other beaked whales sampled; and (3) pygmy (*Kogia breviceps*) and dwarf (*Kogia sima*) sperm whales and Dall’s porpoise (*Phocoenoides dalli*). Interestingly the ‘river dolphins’, a group notorious for their convergent morphologies and riverine ecologies, do not have convergent cochlear shapes. The first two regimes were significantly convergent, with habitat type and dive type significantly correlated with membership of the sperm whale + beaked whale regime. The extreme acoustic environment of the deep ocean likely constrains cochlear shape, causing the cochlear morphology of 40 sperm and beaked whales to converge.

Finding New Rules that Promote and Constrain the Diversification of Post-canine Teeth in Mammals: Insights from Noctilionoid Bats

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Teeth are ones of the most diverse organs in term of morphology and are a key organ for studying species and organ shape evolution in the context of adaptation. As a consequence, teeth have become an evo-devo model to study the rules governing the establishment of shape and the resulting intrinsic constraints that limit the repertoire of possible forms. Fundamental work has shown that the molar number and size are supposed to be established through a signaling cascade in rodents. However, the study of other groups has challenged this view and showed that this model cannot predict the patterning of premolars or the repertoire of shapes or teeth number of post-canine teeth observed across mammals. We established a new model for the patterning of the mammalian post-canine dentition using the hyperdiverse Noctilionoid bats as a reference group. We combined morphometric and quantitative data from 117 adult species exhibiting variations in tooth number and size. We showed that the number of post-canine teeth is related to the length of the jaw and that premolar and molar proportions are independent, suggesting distinct developmental mechanisms for their formation. To get insight into these underlying mechanisms, we analyzed the development of 12 different species across 8 developmental stages by μCT-scan, tested developmental markers and linked teeth formation to the growth rate of the jaw. Finally, we proposed a new Turing-based model based on these developmental results to explain the development of premolar and molar rows and predict the possible outcome and shapes that can evolve in this system. Our data reveal that the premolar and molar rows are established by two independent signaling mechanisms and that teeth number and size is linked to the local growth rate of the jaw, providing a testable framework for other mammal species. Our work also reveals the intrinsic constraints that both drive and limit teeth shape variation in relation with jaw/skull morphology.

Biomechanical Factors on the Evolution of Unique Cranial Modifications in Rabbits and Hares (Leporids): a Combined Effect of Locomotion and Mastication

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Mammals have evolved diverse craniofacial morphology to adapt to a wide range of ecological niches. The skull of modern leporid lagomorphs (rabbits and hares) is highly modified from other mammals as it is structurally specialized for providing intracranial movement, or cranial kinesis. Increasing evidence suggests that cranial kinesis, coupled with a hydraulic system in combination with massive external ears, functions as a shock-absorbing mechanism to dissipate kinetic energy during intense loads associated with locomotion. A pronounced ventral flexion of the facial region also strongly correlates with locomotor mode. The crania of leporids are also uniquely fenestrated, including the posterior cranial bones and the lateral portion of the maxilla. The posterior fenestrations have also been linked to locomotor mode, and overall it has been suggested that the highly fenestrated skulls reduce weight to increase speed. However, the functional (biomechanical) significance of the highly fenestrated rostrum has received considerably less attention. It is hypothesized that this is associated with the transmission of incisal occlusal forces away from the lateral part of the maxilla, and instead posteriorly along the superior and inferior struts, which may be linked to the prominent downward facial tilt. Early studies made comparisons between leporids and rodents. However, it is suggested here that macropods (wallabies and kangaroos) are a better comparison for functional analyses due to a number of similar features, including a large diastema and a long rostrum, yet lack the unique kinesis and fenestrations of leporids. Here, we present the first quantitative functional comparison between these superficially morphologically similar mammals using finite element analysis to get a new biomechanical perspective on leporid ecology, and leading to more investigations on the relationship between form and function in lagomorphs.

What Shapes Trait Covariation and How Does Trait Covariation Shape Phenotypic Divergence of Skulls in Toads and Lizards

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Interactions at different levels of organization are paramount for the adaptive evolution of vertebrate skulls. While trait interactions arising from developmental and functional processes at the individual level are expected to shape intrinsic constraints, the interaction between long-term evolutionary constraints and external selection may determine the directions of divergence at the macroevolutionary level. In this talk, I will discuss the relations among trait covariation and different types of natural selection (directional and stabilizing/correlational selection), and how the interplay between intrinsic and extrinsic factors impact the divergence of phenotypic trait means. Using the toad skull as a model, we tested whether functional interactions (i.e., within different anatomical subsystems of the skull) contribute more than developmental interactions (i.e., within different embryonic origins of skull bones) to trait correlations in adult species. We also quantified the influence of trait correlations and strength of directional selection on the evolutionary response of the toad species lineages. Using the lizard skull as a model, we tested whether multivariate stabilizing selection associated with functional performance (bite force) shapes mandible trait covariation. Although the effects of development cannot be completely disregarded, our results suggest that functional aspects of both the toad and lizard skulls are important to the evolution of trait covariation. However, extrinsic factors, such as strength of selection, interact with trait covariation to determine the pattern and magnitude of phenotypic divergence.

Novelty and Constraint: Convergent Evolution among Archosaurs and their Closest Relatives

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Cases of convergence provide iterative tests of disparity, selection, adaptation, and behavior across ranges of phylogenetic tree space. The resultant morphologies that arise through those extrinsic and intrinsic constraints can be observed in distantly-related taxa across large portions of geologic time. Because of the potentially subjective interpretations of convergent morphology and missing data in fossils, and the confounding effects on phylogenetic inferences, such observations must be made repeatable and testable. As new fossils are discovered, morphologies long thought to be unique are being shown to be repetitions of earlier examples. For example, non-avian dinosaurs had long been thought to have exceptionally distinct morphologies. However, new Triassic-aged reptile fossils and quantification of their morphologies are revealing earlier iterations of those classically dinosaurian body plans. Those Triassic archosaurs and their close relatives that flourished at the very beginning of the 'Age of Dinosaurs' are now known to have first displayed a remarkable range of body shapes that in some cases did not reappear in dinosaurs until over 80 million years later. It appears that ecology is the driving factor towards a certain morphology. Modern crocodylians have converged upon the morphology of Triassic phytosaurs; however, in both cases the acquisition of their distinctive morphological characters occurred subsequent to their transition to aquatic environments. This Triassic diversification and exploration of a disparate morphospace by archosaurs and their close relatives may have been a response to the ecological disruption of the end-Permian mass extinction that was followed by a period of ecosystem stabilization. Selective advantages associated with those disparate phenotypes in a recalibrated ecosystem then resulted in a strong and consistent influence on Bauplan evolution, laying the groundwork for dinosaurian success later in the Mesozoic.

Does the Diversity in Skull Morphology and Jaw Musculature Reflect the Functional Constraints Associated with Resource Use? Insights from Insular *Podarcis* Lizards

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Changes in the environment drive diversification in morphology as survival is intricately related to environmental features. Islands are strong selective environments since they provide only a limited amount and diversity of resources, thus increasing the intensity of intraspecific competition compared to mainland populations. Previous studies have highlighted that changes in diet are associated with changes in skull geometry and bite force in insular lizards. However, little is known about the functional consequences of skull shape differences related to access to food resources on islands. We here investigate whether insular lizards have converged on a similar morphology and muscle architecture in relation to diet and bite force. Maximal bite force was measured for each individual and food items were identified after stomach flushing. The heads of 140 individuals of two closely related species of *Podarcis* lizards from 16 islands across the Adriatic were CT-scanned. Three-dimensional surfaces of both skull and mandible were extracted and compared using 3D-geometric morphometrics. Jaw muscles were dissected and digested in nitric acid in order to calculate the mean fiber length and the physiological cross-sectional area. We tested whether changes in diet were correlated with bite force and muscle architecture, whether changes in bite force were associated with variation in skull shape, and whether skull shape variation co-varied with muscle architecture. We predict that higher bite forces will allow the inclusion of more plant matter and/or harder prey in the diet. Moreover, we predict changes in skull shape associated with higher bite forces. Finally, we predict that cranial shape co-varies with musculature as stronger muscles require robust bony insertion areas. The present study provides new insights into how insular environments select for different phenotypes.

The Brain as a Constraint on Craniofacial Evolution in Birds

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The skull is a remarkably complex, yet cohesive, structure shaped through myriad factors. Modern morphometric research has examined the effect of intrinsic (e.g., allometry, cranial integration, embryonic tissue origin) and extrinsic (environmental, functional) variables on avian skull evolution. Collectively, these studies have suggested that developmental mechanisms are a major driver of craniofacial evolution in birds while ecological factors account for proportionately small amounts of the total skull variation. Given these results, a largely neglected aspect of these analyses has been the potential constraint that other tissues enforce on skull morphology. Beyond its spatial adjacency to the skull, the brain has primacy in development and shares key developmental pathways with the formation of cranial bones. Therefore, the brain likely plays a critical role in dictating the course of skull evolution not only in birds but across vertebrates. Here, we combine high-dimensional geometric morphometric data of endocasts and skulls sampled across birds to assess the morphological integration between the brain and the skull. Comparative analyses indicate that skull and endocranial shapes are integrated to an extent, where the skull variation associated with endocranial shape spans the breadth of avian cranial morphology—from deep skulls with short beaks to gracile skulls with long beaks. Of the four major brain regions (cerebrum, optic lobe, cerebellum, medulla), the cerebrum was most integrated with the overall skull shape which agrees with the current molecular understanding of skull and brain development. Interestingly, we find that songbirds and species with elaborate cranial ornamentations deviate from the large-scale integration pattern, indicating elevated decoupling of brain and skull evolution in these taxa. Through synthesis of brain and skull shape data, this study provides an integrative approach to investigating the phenotypic interplay between brain and skull evolution.

How Developmental Bias can Shape Macroevolutionary Patterns: Earless Frogs as a Case Study

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This study combines physiological, morphological, developmental, and genomic techniques to understand how selection pressures (extrinsic factors) and developmental bias (intrinsic factors) produced surprising convergent middle ear loss. Most tetrapods, including frogs and toads (anurans), have evolved tympanic middle ears that amplify airborne sound. Anurans are known to locate and attract mates via acoustic communication, yet many anuran species lack tympanic middle ears. We found middle ear loss is common among anurans (at least 38 losses) and we find very little evidence that extrinsic factors related to environmental selection pressures can explain convergent tympanic middle ear loss. We further compared hearing among eared and earless species using auditory brainstem recordings (ABRs) and found negative hearing consequences associated with ear loss at high frequencies but similarity in hearing between eared and earless species below 1 kHz. Using microCT, we compared skull morphology between eared and earless species to reveal ear loss did not result from pleiotropic trade-offs with developmentally linked skull structures. Larger cell and genome sizes as well as prolonged middle ear development of earless species, point towards shifts in development rate (heterochrony) influencing middle ear lability in anurans. Using phylogenomic data for 55 species (36 eared, 19 earless) within the earless frog system, we found earless lineages exhibit relaxed purifying selection in putative middle ear coding sequences and we are now deciphering how demography, drift, and selection affect genomic evolution in earless lineages. We conclude that a combination of relaxed selection on the middle ear, lack of integration with other skull features, and changes in development rate have contributed to convergent loss of middle ear structures. Earless anurans provide a great case study for how intrinsic factors (developmental bias) can shape macroevolutionary patterns.

Ecology, Biomechanics and Evolutionary Constraints in Vertebrate Trait Diversification – Organizers: Brandon Kilbourne, Bárbara M.A. Costa, Daniela M. Rossoni

Changes in Skeletal Loading as a Mediator of Morphological Change across Evolutionary Transitions in Habitat

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The diversity of vertebrate structure and function is frequently related to the diversity of habitats in which species live. Within the musculoskeletal system, this relationship is often viewed through the lens of different physical forces imposed by different environments that can change the loads to which bones are exposed. Through the course of evolutionary transitions in habitat, changes in loading conditions might impose selection that could favor corresponding changes in skeletal morphology. For example, the limb bones of modern sprawling tetrapods are exposed to high torsional loads during walking on land. In this context, evolutionary changes in limb bone shape during the invasion of land by tetrapods, from a blocky to a tubular morphology, could be viewed as changes that improve resistance to torsion. As a counterpoint to transitions in which *increases* in particular loading regimes favor specific changes in skeletal morphology, the invasion of habitats in which loads *decrease* might allow skeletal structure to diversify. For example, recordings of limb bone strains from swimming turtles show greatly reduced torsion, compared to terrestrial walking. Such "biomechanical release" may have enabled the evolution of limb bone shapes beyond tubes suited to resist torsion, like the flat limbs observed in flapping lineages such as sea turtles. However, some shape changes in new habitats might evolve despite disadvantageous changes in loading. For example, the limbs of arboreal taxa are often longer than those of terrestrial relatives. Longer bones could be at greater risk of failure, but this risk is not reduced by loading changes: strain recordings from the femur of iguanas show higher, not lower, loads during climbing behavior. Thus, although loading may have mediated the evolution of bone shape during some transitions, tradeoffs with other aspects of function besides loading may also have shaped bone design in some environments.

Modularity and Evolutionary Constraints in Sigmodontine Rodents (Mammalia, Rodentia, Cricetidae)

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Studying modularity is fundamental to understand the evolution of complex features, given that the modular structure influences multivariate evolution. Here, we analyzed skull modularity patterns and constraints on a broad phylogenetic and a taxonomically structured sample of sigmodontine rodents, the mammal's clade with the greatest diversity and distribution in the Neotropics and adapted to a wide range of lifestyles. We used comparative methods and quantitative genetic approaches to investigate the covariance constraints and the presence of specific functional/developmental modules within-groups and between-groups in sigmodontine species along with their phylogeny. Our database includes 35 cranial measurements taken from 2,897 specimens representing 53 species for all tribes of the subfamily. We identified a significant association of within-species modularity patterns with the between-group divergence, with traits belonging to functional/developmental groups evolving in a correlated way among species more often than expected by chance. Specific traits (within bone measurements) of the face, including oral and nasal regions, are not only greater in terms of correlation within species but also evolve in a correlated way among species. Allometry seems to play a role in this result since those traits are the ones developing latter during ontogeny and contributing more to allometric size variation.

Ontogenetic Inertia Explains Neosuchian Giants: A Case Study of *Sarcosuchus imperator* (Archosauria: Suchia)

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Body size and body-size shifts broadly impact life-history and biomechanical performance parameters of all animals. These relationships emphasize the importance of accurate size estimates of fossilized individuals for understanding evolutionary dynamics. In this study, we estimate extinct neosuchian body mass using Bayesian phylogenetic prediction drawn from empirically measured body masses of 22 extant crocodylian species (total n = 76). We focus on the giant (9–12 m TL) *Sarcosuchus imperator*, a longirostrine Early Cretaceous neosuchian, and develop mass estimates for the taxon based on (1) strict phylogenetic placement within Neosuchia and (2) ecologically-informed nesting with longirostrine taxa. Contrasting body-size effects associated with evolutionary history *versus* ecomorphology demonstrates that *Sarcosuchus* was more massive than expected for its phylogenetic position by 25%. We hypothesize that this difference is the result of ontogenetic inertia working on the neosuchian precursors of *Sarcosuchus*. Our previous work examining 240-million years of suchian diversification has illustrated that over-performance in extant crocodylian bite force is the end-result of this phenomenon—namely, greater evolutionary rates towards higher performance were the result of developmental trends established as deep-time patterns, favoring access to larger food items earlier during ontogeny. In neosuchians, it appears that the decoupling of adult phenotypes from their ecological feeding niche is fundamentally the result of over-performance due to absolute bite-force gains. These gains are tightly correlated to body size, thus facilitating over-performance in especially gigantic taxa. Taken together, we propose that gigantism in *Sarcosuchus* resulted from heterochrony acting on the ontogenies of its direct precursors, which caused evolutionarily accelerated increases in bite force and, with them, the coincidental but desultory achievement of extreme body sizes.

Jaw Morphologies Provide Novel Insight on the Ecological Radiation of Early Therian Mammals

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The ecological radiation of therian mammals resulted in an incredible diversity of diets, locomotor modes, and body masses. However, there is considerable debate on the timing and dynamics of the radiation, particularly as it relates to the Cretaceous-Paleogene (K-Pg) mass extinction event 66 million years ago (Ma). This is due in part to difficulties in examining patterns of ecological diversity in deep time. One source of paleoecological data is jaw morphology, which is associated with feeding ecology. To examine the specific relationships between jaw dimensions and diet in modern therians (placentals and marsupials), I apply phylogenetic comparative methods to linear jaw measurements and quantitative dietary data for a taxonomically diverse sample. Results indicate that the distance between the jaw joint and the angular process (JAPr distance) is an especially powerful predictor of diet, increasing with greater herbivory and likely reflecting differences in jaw muscle sizes among dietary groups. I apply this finding to the fossil record by measuring the JAPr distance in over 250 species of cladotherians (therians and their closest relatives) from the Late Jurassic through Eocene (155–34 Ma). Fossil patterns and evolutionary modeling results suggest that therians were small insectivores for much of the Cretaceous and experienced a rapid increase in dietary diversity 10-15 million years prior to the K-Pg boundary, coinciding with the ecological diversification of flowering plants. In addition, the diversification of herbivorous mammals accelerated after both the K-Pg mass extinction event and the Paleocene-Eocene Thermal Maximum (56 Ma), possibly due to novel ecological opportunities that arose after these events. Thus, this study demonstrates a strong correlation between jaw morphology and diet, and offers new insight on early mammal evolution by suggesting a multistep ecological radiation.

The Role of Function in Morphological Diversification in Suites of Traits: Insights from Mustelid Mammals

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While limb morphological diversity is strongly linked to locomotor habit in mammals, this is largely known in terms of the lengths and diameters of bones. In contrast, there is less knowledge regarding how different locomotor habits are correlated with cross-sectional traits of the limb skeleton, such as cross-sectional area (CSA) and second moment of area (SMA) – measures of a bone's resistance to axial compression and bending, respectively. We sampled 28 species of Mustelidae, a functionally diverse carnivoran lineage, and tested for differences in CSA and SMA of the humerus, radius, and ulna among taxa specialized for climbing, digging, and swimming, in addition to taxa with a generalized locomotor habit. Given that the limbs of swimming and digging specialists function respectively in water and soil, we predicted that taxa with these locomotor habits should have the greatest values of cross-sectional traits due to the need to counteract buoyancy in aquatic environments and mechanical demands imposed by soil's density. Cross-sectional traits were calculated using μCT-scanning, and analyzed in 5% increments along the length of each bone. We identified significant differences in cross-sectional traits in the humerus, radius, and ulna. As predicted, swimming specialists had the greatest values of CSA and SMA, followed by digging specialists. Climbing specialists had the lowest trait values. Multi-rate Brownian motion and multi-optima Ornstein-Uhlenbeck models were the best-fitting trait evolution models for CSA and SMA. However, inspection of α-values revealed that many of the OU models did not differ from a Brownian motion model. As previous work has shown that the external dimensions of mustelid limb bones likely evolved adaptively, our results for cross-sectional traits suggest that functional specializations in a single organ (e.g., a limb) do not necessarily entail a single evolutionary process acting upon all of the organ's constituent traits.

Evolving in Isolation: Pleistocene Glaciation Resulted in the Speciation and Morphological Divergence of the North American Pine Marten, *Martes*

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Glacial cycles are thought be a driver of ecological niche shifts, allowing for novel niche formation and shifting existing niches. Many North American species are hypothesized to have undergone allopatric speciation due to glacial isolation during the late Pleistocene. *Martes americana* and *M. caurina* are examples of taxa thought to have diverged molecularly and morphologically during the Wisconsin glaciation (11.7 kya). The limb morphology of these species correlates with climate and biome, suggesting that their limb morphology evolved as an adaptation to selective pressures imposed by these unique Pleistocene habitats. However, such variation can also be achieved through non-adaptive processes, including genetic drift. Using 3D-geometric morphometrics to quantify shape and a Bayesian phylogeny constructed from cytochrome-b sequences of the same individuals, I tested the hypothesis that limb morphology of *M. americana* and *M. caurina* is an adaptation to climate and biome. I tested for evolutionary tempo and mode in the morphology of six limb elements. I found that phylogenetic signal was low in all elements and did not differ from what would be expected under a Brownian motion mode of evolution. Rates of evolution did not differ significantly among individuals from different biomes. Disparity is predicted to have been highest at approximately 180 kya, corresponding with the genetic diversification of both species. These results indicate that limb morphology of *M. americana* and *M. caurina* did not evolve under selection and instead likely arose through genetic drift. The variation seen in morphology in correlation with habitat and climate then results from differing evolutionary trajectories established during Pleistocene isolation. The ability of *Martes* to survive the final Pleistocene climatic fluctuations suggests that they are ecologically labile, which may be beneficial for the species when facing current climate change.

Biomechanical Relationships Shape Cranial and Locomotor Evolution in Labrid Fishes

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The influence of biomechanics on the tempo and mode of morphological evolution is unresolved, yet it is fundamental to organismal diversification. Across multiple four-bar linkage systems in animals, we discovered that rapid morphological evolution (tempo) is associated with mechanical sensitivity (strong correlation between a mechanical system's output and one or more of its components). Mechanical sensitivity is explained by size: the smallest link(s) are disproportionately affected by length changes and most strongly influence mechanical output. Rate of evolutionary change (tempo) is greatest in the smallest links and trait shifts across phylogeny (mode) occur exclusively via the influential, small links. Moreover, the strong mechanical relationships that guide the evolution of skull motion are correlated with macroevolutionary patterns of locomotor ability, indicating correlated patterns of diversification. Our findings illuminate the paradigms of many-to-one mapping, mechanical sensitivity, and constraints: tempo and mode are dominated by strong correlations that exemplify mechanical sensitivity, even in linkage systems known for exhibiting many-to-one mapping. Amidst myriad influences, mechanical sensitivity imparts distinct, predictable footprints on morphological diversity.

What to Do When There's no Phylogeny: Using Paleobiological Modeling to Trace Ecomorphological Trait Evolution in Deep Time

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Organismal performance shifts are often thought to convey ecological advantages that may be reflected in evolutionary patterns. Phylogenetic comparative methods are now commonly used to connect such trait-based performance proxies with macroevolutionary patterns. This ability to pair performance and ecomorphological trait data with well-resolved phylogenies enables diversification-related hypotheses to be tested in groups with little or no fossil record. Nonetheless, the fossil record remains the only direct evidence of historical diversification patterns, even as comprehensive fossil-inclusive phylogenies remain elusive. This study highlights the utility of occurrence-based methods for analyzing trait when phylogenies are unavailable, using selective brain cooling (SBC) as an ecophysiological model. SBC is an arterially-mediated physiology best-developed in artiodactyls (even-toed ungulates). By cooling the hypothalamus, SBC delays hydrologically-costly responses to heat stress (panting/sweating), providing significant reduction in evaporative water loss. Research on extant artiodactyls suggests that SBC is a key innovation that bolsters survivorship of climatic aridification. Although SBC performance has been intensely investigated and there is an extensive artiodactyl fossil record, there is no comprehensive extant/extinct phylogeny. Using osteological correlates for cranial arteries, I employ occurrence-based paleobiology modeling to trace SBC evolution through the Cenozoic. Results confirm SBC-related increases in speciation rate during warming and drying trends of the Late Eocene and across the Oligocene-Miocene transition. These results remain robust when accounting for other advantageous physiologies, such as rumination. Ultimately, this study highlights the utility of occurrence-based methods for modeling performance evolution, and also offers a unique opportunity to compare phylogenetic comparative methods with concrete patterns from the fossil record.

Turtles Traversing an Adaptive Landscape: Morpho-Functional Trade-offs of Divergent Locomotor Ecologies

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Locomotion in turtles is primarily driven by the limbs, and studies have shown that limb kinematics vary considerably across environments: marine turtles use a flapping gait during swimming; fresh water semi-aquatic turtles use a rowing gait; and terrestrial turtles use typical walking gaits. Further, turtles adapted to different environments also have different limb morphologies, though links between form, function, and ecology have not been quantitatively tested. Within the forelimb, the humerus has been shown to vary significantly with turtle ecology and has the potential to be functionally informative – it serves as the primary articulation point between the limb and the body and anchors the major muscle groups that drive locomotion. Here, we construct ecological adaptive landscapes of the turtle humerus to investigate functional trade-offs between divergent locomotor ecologies: marine, semiaquatic, and terrestrial. Humerus shape from 40 species of cryptodire turtles was quantified, and four functional traits were measured that represent strength, stride length, mechanical advantage, and hydrodynamics. Quantitative trait modeling was used to construct adaptive landscapes that optimize the functional traits for each of the three locomotor ecologies. Our data show that turtles living in different environments have statistically different humeral shapes. The optimum landscape for each ecology is defined by a unique combination of performance trade-offs, with turtle species clustering around their respective adaptive peak. Species adhere to pareto fronts between marine-semiaquatic and semiaquatic-terrestrial optima, but not between marine-terrestrial optima – potentially indicating a 'maladaptive zone'. Our study demonstrates the utility of adaptive landscapes in informing the link between form, function, and ecological adaptation, and suggests that the humerus can provide novel insights into the selective pressures driving ecomorphological evolution.

Exploring Body Shape Diversification across the Teleost Tree of Life (Actinopterygii, Teleostei)

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Teleost fishes exhibit a spectacular variety of body shapes spanning deep-bodied moonfish, elongate eels and needlefish, laterally compressed ribbonfish, dorso-ventrally flattened batfishes and globular pufferfishes. Biomechanical models can help us to understand how this diversity evolved, as they can link shape to performance, which in turn is linked to evolutionary fitness. However, attempts to comprehensively explore general patterns in the relationship between body shape, functional morphology and ecology across teleosts have been limited by data availability. We present a morphological dataset of eight functionally relevant size and shape variables, combining length, depth and width measurements on over 13,000 specimens from 6,151 species in the Smithsonian National Museum of Natural History collections. The resulting morphospace spans the phylogenetic diversity of teleosts and encompasses 90% of extant families. When analyzed in a phylogenetic framework, our data enable us to identify the primary axes of shape diversification across teleosts, to describe trends in shape diversity over time, and to detect potential ecological constraints on diversity. Our analyses indicate that once overall size is taken into account, elongation and lateral compression of the head, body and caudal region explain approximately 70% of the remaining variation. We are also beginning to test long-standing expectations for the relationship between shape and ecology. For example, our preliminary findings support the prediction that, due to increased maneuverability, laterally-compressed deep-bodied forms will evolve in complex habitats, as fishes living in reef environments have significantly deeper and less fusiform body forms compared to fishes living in other habitats. This research highlights the importance of generating large databases of functionally-relevant traits that span broad phylogenetic scales to investigate the factors that promote and constrain vertebrate trait diversification.

Diet Shift in Sub-Antarctic Mice: Morpho-Functional Response of the Jaw System

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By following human movements since the Neolithic, the house mouse was able to colonize most areas of the world, including inhospitable environments such as Sub-Antarctic islands. To sustain populations in these areas devoid of permanent human settlements, house mice switched their diet towards a more predatory behavior, compared to omnivorous-granivorous commensal mice. How jaw shape responded to this shift in functional requirements was investigated using a geometric morphometric approach coupled with biomechanical estimates. Jaw shape did not display convergent evolution in Sub-Antarctic populations because of the importance of the phylogenetic history and hence, of the source population which initially colonized each island. In contrast, biomechanical estimates provided evidence for convergent evolution among Sub-Antarctic mice. All populations were characterized by an increase of the mechanical advantage related to incisor biting, showing an increased performance for this function. This constitutes an adaption to catch prey more efficiently. In contrast, continental commensal mice, which mostly feed on grains hard to grind, display an increased performance for molar biting. A next step consisted of focusing on the incisor tooth itself. Sub-Antarctic mice display incisors with a sharper bevel, which appears as an efficient morphology for piercing prey. This suggests that adaptation of the jaw to incisor biting was complemented by an adaptive change of the incisor itself. 3D-imaging showed that this response was associated with a reduced pulp cavity, suggesting slower eruption counter-balancing a reduced abrasion on soft food material. A plastic adjustment of the dynamics of the ever-growing incisor may thus allow adaptive incisor sculpting, contributing to the success of mice in foraging diverse resources.

Comparative Quantitative Genetics and the Morphological Evolution of the New World Leaf-Nosed Bats (Mammalia: Chiroptera)

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Bats of the family Phyllostomidae represent the most noteworthy example of adaptive radiation in mammals, showing unique functional cranial morphology associated with feeding strategies. Such cranial diversity constitutes an excellent system for understanding how evolutionary processes shape the evolutionary potential of ecologically important traits. In a previous contribution, we demonstrated that natural selection was the key mechanism driving phyllostomid cranial diversification. Intense magnitudes of selection preceded colonization of new ecological niches and the appearance of novel feeding specializations. Here, we used comparative quantitative genetic approaches to identify cranial regions undergoing strong directional selection in transitions to most representative clades. Our database includes 35 cranial measurements taken from 2808 specimens and 57 species. We estimated the ancestral states for 35 traits using maximum-likelihood and then calculated the evolutionary response to selection for each trait as the difference vector between an extant species and its ancestor mean estimates. We reconstructed selection gradients along the phylogeny, representing the contribution of each trait to the relative fitness. Our results suggest that divergence of the clade comprising extant hematophagous bats was characterized by selection towards facial retraction and basicranium/cranial vault expansion. The reconstructed selection gradients along the branch leading to nectarivorous bats points to strong selection acting on facial projection, zygomatic length extension, and neurocranium retraction. The branch leading to obligate frugivores was associated with remarkably strong negative selection for shortening face traits and positive selection for neurocranium expansion. Selection pressure required to produce extant carnivores was positive for traits associated with the face and neurocranium, with evolutionary responses for these traits being all positive, indicating general size increase.

Evolution of Retinal Topography in Coral Reef Fishes

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Coral reef fish, one of the most speciose assemblage of vertebrates, display an enormous diversity in terms of habitat preferences, diel activity patterns, and trophic specializations. Such large ecological diversity is coupled with disparate requirements for vision, making coral reef fish a uniquely well-suited group to study evolutionary interactions between photic environments and the visual system. Physiology predicts specialized areas in the retina that may strongly reflect characteristics of the photic environment. One of the most prominent visual ecology hypotheses, the so-called 'terrain hypothesis', seeks to establish a link between the presence of a horizontally-oriented streak of high density of photoreceptors and retinal ganglion cells with viewing a well-defined horizon, such as sand flats associated with reefs. Retinal topography data on a single-species representative of a specific habitat type appear to corroborate the terrain hypothesis, but comprehensive phylogenetic comparative studies are lacking. New data from a large sample of coral reef fish, comprising mostly wrasses (labrids) and damselfishes (pomacentrids), paired with novel quantitative approaches reveal that phylogeny, and not ecology, may be the major axis of diversification in retinal topography. This result demonstrates the importance of well-designed phylogenetic comparative approaches for testing ecomorphological hypotheses, yet the analysis of retinal topography is difficult and time-consuming. New histological techniques and automated cell counting may pave the way towards such much needed large-scale studies.

VIRTMORPH – Using Virtual Reality to Visualize and Analyze Vertebrate Morphology – Organizers: Robert Cieri, Colleen G. Farmer

***Archaeopteryx holographica*: Bringing the Urvogel back to Life with Scientific Animation and VR/AR**

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Recent advances in virtual reality (VR) and augmented reality (AR) technologies are providing new opportunities for visualizing and analyzing morphology and motion in 3D. Here, a photorealistic digital *Archaeopteryx lithographica* skeleton was reconstructed using multiplanar X-ray microtomosynthesis and macrophotogrammetry of the Thermopolis specimen (WDC-CSG-100). To animate the skeleton, articular joint surfaces were analyzed and rigged with 3D-coordinate systems using Geomagic and Maya software. Next, *in vivo* locomotion datasets from extant archosaurs that phylogenetically bracket *Archaeopteryx* – alligator (*Alligator mississippiensis*) and chukar (*Alectoris chukar*) – were analyzed via marker-based X-ray Reconstruction of Moving Morphology. The resulting kinematic data was used to drive joints in the *Archaeopteryx* model using scientific motion transfer. To create low-poly anatomical assets necessary for real-time computer graphics, the high-resolution *Archaeopteryx* bone models were decimated, retopologized, and unwrapped with ZBrush, and the photogrammetry datasets were used to generate complementary texture atlases. The Unity game engine was utilized to develop custom VR/AR apps, which were deployed to various platforms including mobile devices and the Microsoft HoloLens. Such interactive and immersive content enables novel pedagogical approaches for engaging a wide variety of audiences, and for communicating complex 3D-data and concepts, such as flight stroke kinematics and anatomical evolution. Bringing digital dinosaurs "back to life" through next-generation visualization technologies provides the "gateway science" of paleontology with new avenues to foster interest in STEAM fields, and ultimately help inspire the next generation of vertebrate morphologists. This work was supported by a National Geographic Society grant and software donations from Capturing Reality (RealityCapture) and FEI (Avizo Fire) to Ryan Carney.

Breathing Life into Digital Anatomy Using Virtual Reality: Interactive Anatomy and Computational Fluid Dynamics (CFD) Simulations of Pulmonary Airflow in Monitor Lizards (Varanidae)

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Recent advances in virtual reality enable researchers to interact with fully-immersive, affordable, interactive digital environments and have revolutionized our study of pulmonary airflow patterns. Unidirectional pulmonary airflow, a condition where lung gases travel in the same direction through most of the airways throughout the respiratory cycle, has recently been shown to be present beyond Aves, including in crocodilians, green iguanas, and monitor lizards, and has raised new questions about the underlying fluid dynamical phenomena occurring in unidirectional lungs. Direct measurements of airflow can be difficult because lungs are complex, delicate organs and many portions of the respiratory system are inaccessible with conventional instruments. Computational fluid dynamics (CFD) modeling, which can be visualized in virtual reality, provides a new avenue to investigate how anatomical structure gives rise to fluid flow. To be accurate, the models must be based on anatomically faithful digital meshes. Virtual reality facilitates the creation of accurate meshes because it allows us to inspect these virtual structures' quality and accuracy before we run simulations. Virtual reality also improves our ability to communicate the results of fluid dynamics simulations in a more intuitive manner, because the viewer can take a 'particle's eye view' of the simulated flow regime. In this study, computed tomography scans were segmented into a detailed computational mesh, accurately representing the major and minor airways of monitor lizards, Varanidae. The surface of the computational meshes expanded and contracted to simulate lung motion during ventilation and provided the boundary conditions for flow. During both phases of ventilation in the model, air moves caudally through the intrapulmonary bronchus and cranially through the secondary bronchi, moving between secondary bronchi through intracameral perforations.

A Tesla Valve in a Turtle Lung: Using Virtual Reality to Understand and to Communicate Complex Structure-Function Relationships

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The complexity of behavior of fluids within byzantine solid structures, such as the conducting airways of the respiratory system of vertebrates, presents a challenge that scientists have only recently been able to tackle; thanks primarily to advances in software and hardware engineering. We have used these advances in the processing and analysis of radiological images, collected by either computed tomography or magnetic resonance imaging, to create mathematical models that faithfully represent pulmonary anatomy. These models allow us to analyze fluid flow, using the Navier-Stokes equation and open source computational fluid dynamics software (OpenFoam). Virtual Reality has proven an invaluable tool to both analyzing these results as well as communicating them effectively to non-specialists. Our investigations on patterns of airflow in the lungs of a semi-aquatic turtle, the red-eared slider, show that airflow patterns through this turtle lung are remarkably similar to the pattern of flow through a tesla valve. These surprising (and counter-intuitive) results are most powerfully communicated using Virtual Reality.

Where Does Footprint Morphology Come from? Developing Virtual Reality Visualizations for Exploring Dinosaur Track Formation

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Fossil tracks are purely sedimentary structures that preserve a substrate's flow around a moving foot. During the period of foot interaction, both the original surface and deeper layers are deformed. Fossil slabs can be exposed at bedding planes throughout this track volume. Variation in pedal anatomy, kinematics, and substrate properties are all known to influence track formation, but how do the features that make up footprint morphology arise? For extinct theropod dinosaurs, experiments with living birds offer valuable reference, yet substrate and foot opacity hinder direct observation of subsurface foot movement and sediment flow. We have developed Discrete Element Method (DEM) simulations based on guineafowl X-ray Reconstruction of Moving Morphology (XROMM) data and CT-scans of Early Jurassic fossil tracks. Foot motion data serve as inputs for dynamic DEM substrate simulations made up of millions of particles. DEM simulations of track formation are compared to the original fossil tracks, providing feedback for modifying the substrate parameters and foot motion. Splitting the substrate volume along "virtual bedding planes" exposes tracks as they emerge at any depth, elucidating how localized deformations associated with foot entry and exit generate specific features. To explore the dense volumes of 3D-data generated from these methods, we turned to an immersive virtual reality (VR) room, Brown's Yurt Ultimate Reality Theater (YURT). Our custom application creates interactive visualizations that allow us to synthesize substrate flow at the particle, particle cluster, surface, and volumetric scale. In the YURT, depth perception of the high-resolution particle volume frees up use of visual cues (e.g., colors, textures) to be used to display substrate flow patterns at any scale, while maintaining anatomical and sedimentological context—providing a dynamic perspective on the 3D-formation of dinosaur track morphology. Funded by US NSF.

Functional Morphology of the Reptile Heart

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The heart of non-crocodilian reptiles (snakes, lizards and turtles) has two atria that fill an incompletely divided cardiac ventricle with oxygen-poor and oxygen-rich blood from the right and left sides, respectively. The degree of admixture of the two blood streams is reduced by several septa within the ventricle that divide the heart into three chambers (cavum venosum, cavum arteriosum and cavum pulmonale). Using CT and MRI we have described how the atrioventricular valves play an important role in directing the inflows of blood streams during cardiac filling (diastole), while the horizontal septum and particularly the muscular ridge separates flows during cardiac contraction (systole). There are large differences in the size of the muscular ridge amongst species that correlate with their ability to shunt blood flows between the systemic and pulmonary circulations, and some taxonomic groups, such as pythons and varanid lizards, have particularly large septa that provides for pressure separation between the left and right sides of the ventricle. I will discuss our frustrations in trying to pinpoint the evolutionary drivers for this trait, and I will discuss the difficulties of assigning functional roles to the cardiac shunt pattern.

Evolution, Development, and Regulation of Ruminant Headgear – Organizers: Katherine Brakora, Gertrud Rößner, Andrew Lee

Disentangling Early Antler Diversity: Is There a Causal Link with Extrinsic (Climate-Related) Factors?

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Antlers are the only branched, bony appendages of apophyseal nature among mammalian headgear that can be regularly shed and rebuilt in an annual cycle. Annual cycles are controlled intrinsically by fluctuating hormone levels. At higher latitudes, this cycle is seasonally synchronized depending on extrinsic photoperiodicity, suggesting the influence of climate-related factors in their evolution. A single developmental and evolutionary origin has been assumed, and is considered a synapomorphy for Cervidae. Moreover, given their complexity and the physiological effort of the regeneration process, it has been argued that deciduous antlers could have been developed from previous non-deciduous antlers. Several types of branched frontal headgear (probably of apophyseal nature) were exhibited by early Miocene pecorans in the "Old World" and in North America. Differences in ontogenetical development, histological features, surface texture, and ramification mechanisms suggest that these appendages could be non-homologous, and thereby subject to independent evolution. In fact, they emerged at the same time as other headgear in several pecoran lineages, triggered by global climatic changes. As in modern antlers, four of these appendage types underwent spontaneous autotomy (or self-amputation). However, only three show evidence of complete regeneration. In these appendage types, a true coronet (indicative of regenerated antlers) is not developed, and there are differences in mineralization processes and histology, which suggest that their growth cycle was aperiodic. Antlers with true coronet and similar seasonal cycle were first recorded later, in middle Miocene sites of Eurasia. Although the meaning and origin of such innovative features is still not fully understood, it should be born in mind that these evolutionary changes were concomitant with the Middle Miocene Climatic Transition event, suggesting that the annual cycle was an evolutionary response to a new step in increased seasonality.

Headgear and Sexual Selection in the Fossil Record: Implications for Paleoecology

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Fossil vertebrates are often identified on the basis of diagnostic anatomical features of the skull that are shaped by environmental and dietary needs. Skeletal ornamentation that is under heavy sexual selection — such as headgear — provides an additional window onto the evolutionary history of a clade. Given different underlying selective pressures, headgear is expected to evolve faster (through random drift or female choice) and to be a more labile and sensitive indicator of population isolation than other parts of the skeleton, which are under intense anatomical and environmental constraints (e.g., cranial, dental, postcranial elements). For example, in the case of population divergence, changes in dental morphology are expected only if habitat divergence has also taken place. Changes in headgear, however, can arise rapidly following genetic divergence, even if environments and habitats remain constant. At any point in time then, headgear morphology should represent phylogeographic relationships at a finer scale than do other elements of the skeleton. This is the case in extant and fossil ruminants, in which headgear often varies significantly across the geographic and temporal range of a clade while the remainder of skeleton remains largely conserved or identical. The recognition of headgear as a rapid and sensitive marker of biotic isolation suggests that different components of the skeleton can be used to differentiate the contribution of different selective pressures on phenotype evolution. This requires a concerted study of variation and disparity in headgear, in the same way these are generally quantified in the remainder of the skeleton. Metric, geometric morphometric, and trait-based approaches are all possible. An example is given from the African late Miocene to Pleistocene bovid fossil record, in which the rates of morphological diversification in horns and teeth are decoupled.

Making Points: Past, Present, and Future Studies into the Origins of Ruminant Cranial Appendages

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Ruminant cranial appendages are a major feature of mammalian morphological diversity. These include four structurally distinct types of "headgear" in living ruminants (antlers, horns, ossicones, and pronghorns). Despite their familiarity, it is unknown if the different headgear types evolved in parallel or if they share deep homologies in their genetic and developmental architecture despite important anatomical differences. First, we summarize the main types of headgear and the living and fossil taxa that possess them. Then we review key discoveries in the 20th century that set the stage for current research, from Mendelian genetics and tissue transplantation experiments in domestic species to phylogenetic studies that produced diverse topologies and hypotheses of ruminant evolution. Many crucial questions remain in our understanding of headgear. What is the relationship between genotypes, molecular expression patterns, histogenesis, and phenotypes, especially in ossicones and pronghorns? How do these traits and processes vary between the sexes and across populations, species, and major clades? And how can we use a greater knowledge of development and variation in living species to most productively analyze and interpret the headgear of extinct species, and vice versa? Deeper, more integrative knowledge of headgear biology may suggest novel applications in biodiversity conservation and management, herd improvement, veterinary medicine, and models of human disease, and simultaneously help resolve ruminant phylogenetics, clarifying an important story in mammalian evolution. With greater collaboration by researchers across taxa, fields, and methods of study, we have the potential to gain powerful insights into one of the most recognizable and important groups of vertebrates.

Multiple Physiological Constraints Affect the Antler Growth, Morphology and Evolution

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Sexual selection has been widely accepted as the main force driving the evolution of animal weapons, including antlers, as suggested by both intra- and inter-specific studies. However, the genetic potential acquired during evolution is never reached in wild animals, but only under captivity with intensive care and nutrition. Thus, we have been trying to find evolutionary patterns in a sexual secondary trait grown under multiple constraints. Antlers have not reached their maximum potential development; they have not become the ‘perfect antler’. The most important constraints limiting antler growth are nutrition and biomechanics. Both have important effects on two commonly studied parameters: length and mass. However, even if these constraints are relatively well known, they have never been included in evolutionary analyses. First, a deer must deal with the resources available. Cervids are well known to suffer so called “cyclic physiological osteoporosis” through transfer of minerals (Ca and P) from the skeleton to the antler, but there is a limit in the degree of demineralization that an animal can afford without compromising survival. The intensity of this osteoporosis will thus be related to the amount of these minerals in the diet, which commonly are deficient worldwide. Body size is a key factor here: large means greater skeleton resources, but also lower feed intake (i.e., lower mineral supply). Subsequently, these resources must be allocated in the most effective way. A long but thin antler would be easy to break (biomechanically useless), while a short but thick one would be unnecessarily costly. Burr diameter (related to pedicle diameter and that to early growth; i.e., nutrition again) and the mechanical quality of the antler material will greatly determine the maximum length of an antler without compromising its main function as fighting tool. These factors need to be reviewed in order to bring some more light on the evolution of these amazing and incredibly costly structures.

Evolution of the Antilocapridae and Inferences about their Behavior from Headgear Morphology

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The endemic North American pronghorn (*Antilocapra americana*) are known for their speed and agility. Conservation of these animals is important because they are the only remaining species of the once-diverse family Antilocapridae. Understanding the evolutionary history of the pronghorn can aid in conservation efforts, and their headgear provides important insights into that history. The shapes of artiodactyl headgear play key roles in how they interact with their environment and each other and, consequently, can be used to predict behavior. For example, larger, recurved horns are typical of gregarious, large-bodied animals that fight for mates. Smaller spike-like horns are more characteristic of small-bodied, paired mates that live in closed environments. Here, we report a genus-level cladistic analysis of antilocaprids, testing prior hypotheses of their evolutionary history. We included post-cranial, cranial, and headgear characters, expanding on previous analyses that focused entirely on headgear. This phylogenetic analysis not only establishes ancestral headgear morphology but also allows inferences of the timing of behavioral changes. Previous workers had inferred through comparison to other families of artiodactyls that antilocaprids evolved from small-bodied monogamous pairs to large-bodied gregarious herds. However, our findings show separate, independent evolutionary trajectories within the clade. Preliminary analyses show *Cosoryx*, *Ramoceros*, and *Merycodus* diverging from other members of the subfamily Merycodontinae. This result differs from previous hypotheses that these small-bodied antilocaprids would be evolutionarily close as a tribe. Similarly, the large-bodied *Plioceros* groups with the derived *Antilocapra* and *Proantilocapra*, placing them sister to previously hypothesized merycodontines, which have been hypothesized to be a basal grade.

Development and Histology of Pedicles and Antlers in Deer (Mammalia: Cervidae)

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The cranial appendages of deer develop on the frontal bones and consist of permanent pedicles and deciduous antlers. Except for reindeer, antlers are grown only by males. Growth of pedicles and first antlers is caused by proliferation of areas of the frontal periosteum (antlerogenic periosteum, AP). The stem cells of the AP are committed to the formation of pedicles and first antlers, and autologous transplantation of AP causes ectopic pedicle and antler growth. Pedicle growth is triggered by rising testosterone levels and initially occurs by intramembranous ossification. In large species later pedicle growth involves endochondral ossification, while in smaller species it is completely intramembranous. Following first antler casting, antlers undergo periodic regeneration and loss linked to the annual reproductive cycle. Antlers form by endochondral and perichondral ossification, and growing antlers are covered by a specialized skin (velvet). The tips of forming antlers consist of chondrogenic mesenchymal growth zones with high proliferative activity, whose cells are derived from stem/progenitor cells of the pedicle periosteum. Antler cartilage consists of preferentially longitudinally oriented trabeculae around vascular compartments. Proximally, the cartilage undergoes mineralization and is replaced by woven bone. In the antler cortex, the intertrabecular spaces are filled by primary osteons. After cessation of antler growth, velvet shedding exposes the bare bony antlers. Due to the short lifespan of antlers, remnants of mineralized cartilage can be found in the woven bone scaffold, and secondary osteons are rare. In contrast, pedicles are heavily remodeled structures. Prior to antler casting, large osteoclastic resorption cavities form in the distal pedicles. Following antler casting, these cavities are filled with large, complex secondary osteons. This compaction gives the pedicle the strength to withstand the mechanical stress caused by antler use during the rut.

Paleohistology of Early Antlers and Implications for Fundamental Processes in the Antler Cycle

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The unique regenerative nature of antlers has always been interpreted as an evolutionary successive achievement of cyclic apoptosis, abscission, and regeneration in cervid artiodactyls (deer). It is the only example of complete organ regeneration in mammals. The physiology behind is complex and synchronized with behavioral and environmental specifics. Previous paleohistological evidence provided important insight in stem cervid antlers and allowed for a more differentiated view; however, it suffered from limitations in methods and material. We took advantage of a sample of more than 35 specimens of early and middle Miocene stem cervids, including the earliest known (≈ 20 to 19 Ma), to gather paleohistological data. In doing so, we used x-ray micro-computed tomography and petrographic thin-sections. These early antlers share the apophyseal, branched, and deciduous condition with those of crown cervids, but differ in morphotype by being generally smaller and simpler structured, lacking the longitudinal beam construction as well as burrs, and exhibiting a variety of branching patterns (dichotomous, trichotomous, multitomous). Our findings provide empirical data of growth patterns that demonstrate a cycle of apoptosis, abscission and regeneration and no longevity in stem cervid antlers, consistent with data from modern antlers. Accordingly, we conclude that primary processes and mechanisms of the modern antler cycle were not acquired in multiple steps during evolution, but were fundamental from the earliest record of antler evolution. The previous interpretation that proximal circular protuberances, burrs, are the categorical trait for the indication of ephemerality turned out to be mistaken. GER and XW received funding from the DFG (Projects RO 1197/11-1 and RO 1197/7-1).

Morphology and Evolution of Palaeomerycid (Mammalia, Ruminantia, Giraffomorpha) Headgear

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The Palaeomerycidae were strange Miocene Eurasian three-'horned' giraffomorph ruminants. The Giraffomorpha comprise pecorans with the strangest cranial appendages, and palaeomerycids were no exception. They sported both frontal (supraorbital) ossicones and a single forked occipital epiphyseal appendage. Ossicones, as those of giraffes and palaeomerycids, are apophyseal cranial appendages that fuse to the skull roof (frontals) after birth. They are almost identical in giraffes and palaeomerycids, and are diagnosed by the presence of both a distinctive suture line at the ossicone base, and a characteristic morphology of the inner surface of the ossicone base. On the other hand, the occipital appendage of palaeomerycids derives from a deep modification of the nuchal plane, and involves a relatively vertical growth of the supraoccipital area and a lateral expansion that results in the integration of areas belonging to the occipital crest. The nuchal plane and its muscular attachments are reorganized, with some of these areas of muscular insertion extending over the basal portion of the appendage. Thus, palaeomerycid necks were highly modified, with enhanced muscular packs related to the lateral and extension movements of the head. This is an outstanding example of a cranial appendage involved in deep anatomical and functional modifications related to the head-neck system. The presence of ossicones in two giraffomorph groups, palaeomerycids and giraffids, belonging to different clades within Giraffomorpha (Giraffoidea and Palaeomerycoidea), rises the hypothesis of a basal origin of ossicones that later produced the varied appendages of giraffomorphs. To test this we need: a) a deep histological study of the frontal appendages of prolibytheriids and climacoceratids; and b) to discover if *Propalaeoryx*, the African palaeomerycoid sister group of Eurasian palaeomerycids, was a horned pecoran, and if this was the case, what type of frontal appendages sported.

The Anatomy of the Giraffe Ossicone

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Except for a few studies by Ganey, Spinage, and Lancaster, the ossicones of *Giraffa camelopardalis* have not been studied in detail, which warranted this in-depth analysis. Developmentally, the earliest ossicone is a dermal pouch situated on top of the frontal bones. This pouch is laterally continuous with the dermal layers of the skull. In this respect, the ossicone closely resembles an embryonic placode. The overlying dermis is present throughout life and appears to decrease in overall thickness moving from the calvaria to the apex of the ossicone. Within the very young, the ossicone contains a central ossification surrounded by dermis. Under the base of the ossicone, numerous dermal fibers penetrate into the center of the element. As the animal matures, the core becomes completely ossified. New ossifications spread into the dermis. A secondary bone growth, termed the "epikouron", eventually covers the entirety of the posterior ossicones and passes onto the calvaria. All these ossifications begin as fibrocartilage. The epikouron forms the knob of the ossicones, while the true or ossicone proper is more pointed and entirely encased in epikouron. The nasal ossicone is similar in origin. In some specimens, there is epikouron underneath the nasal ossicone but not under the posterior pair. In coronal cross-section of the skull, the frontal sinus possesses a number of septa most of which are not organized in position. Two septa appear to be in specific locations: one at the sutures between the two frontal bones, and the other between the parietal and temporal bones bilaterally. We term these suture septa. The vasculature of the ossicone consists of only one superficial artery, providing blood to the ossicone proper. In comparison, there is little vasculature in the surrounding epikouron and dermis. We hypothesize that the reduced vasculature on the surface of the ossicones is an adaptation to avoid excessive bleeding due to their fighting style.

Contributed sessions

Reassessment of the Enigmatic Pterosaur *'Ornithocheirus' wiedenrothi* from the Lower Cretaceous of Northern Germany

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In stark contrast to the famously rich Jurassic fossil record, the documented occurrences of Cretaceous pterosaur remains from Germany are extremeley sparse. To date, only a few bones and footprint traces have been found in strata of Berriaisian–Hauterivian age. The most complete and best-preserved of these specimens is the holotype of '*Ornithocheirus*' *wiedenrothi* from the lowermost Hauterivian (Endemoceras amblygonium Zone) Stadthagen Formation of Engelbostel, near Hanover in Lower Saxony, northern Germany. This fragmentary skeleton comprises parts of the mandible, including a long symphyseal rostrum, some forelimb elements, and a section of a dorsal rib. The mandible displays several distinctive features, most notably, an anteriorly directed spur-like process at the tip of the mandibular symphysis, and an enlarged and anterodorsally inclined pair of teeth at the first tooth position in the jaw (these are also bordered by a prominent sulcus). When first described in 1990, *'O.' wiedenrothi* was assigned to *Ornithocheirus* based on similarities with *'Ornithocheirus' compressirostris*, which was then classified as the type species of the genus. However, *'O.' compressirostris* has since been referred to *Lonchodectes*, which resembles *'O.' wiedenrothi* in its lanceolate mandibular rostrum, and oval alveolar profile with raised alveolar ridges. *'Ornithocheirus' wiedenrothi* is not directly comparable with the likely monotypic *Ornithocheirus* sensu stricto as no equivalent mandibular elements have been recovered for the type species *O. simus*. Consequently, while we concur with lonchodectid affinity, we consider *'O.' wiedenrothi* to possibly represent a separate genus, and thus a novel addition to the Early Cretaceous pterosaur diversity of Europe.

The Relationship Between Eye and Upper Jaw Development in the Avian Embryo

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The embryos of birds and nonavian reptiles form exceptionally large eyes at early developmental stages. In the chicken embryo, the developing eyes span the sides of the face, take up approximately a quarter of the entire head, and directly abut the embryonic lateral nasal and maxillary processes. As development progresses, the maxillary processes grow anteromedially and fuse with the centrally positioned frontonasal mass in order to form an intact upper beak and nasal cavities. Due to the size and placement of the embryonic eyes, we suspected that they might play a role in pushing the maxillary processes forward in order to facilitate fusion of the upper beak. To test our hypothesis, we performed unilateral and bilateral ablation of the eye primordium in the chicken embryo and assessed downstream craniofacial development and patterning. If the eye does indeed perform a vital function in lip fusion, we would expect to see the formation of a cleft in the beaks of treated embryos. However, the beak remained unaffected, indicating functional independence between the developing eye and craniofacial prominence fusion. That said, we did observe minor changes in size, shape and position of the craniofacial prominences, later translating to effects on the developing skull.

Long Teeth, Long Life: Understanding the Effect of External Abrasives on Hypsodont Teeth and Defining the Duration of the Dietary Signal Created by Tooth Wear

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Maintaining healthy teeth is paramount to a healthy life. In herbivores, this means avoiding tooth wear. Dental wear is mainly caused by the ingestion of silica abrasives, which are either phytoliths (internal to plants), or external abrasives, such as dust and grit. High-crowned teeth are adapted to offset the effects of tooth wear, yet exactly how hypsodonty is affected by different forms of abrasives remains poorly understood. Analyzing tooth wear to reconstruct the dietary signal of the past is a common practice in paleontology, yet the rare experiments investigating how long these dietary signals take to form call the validity of these reconstructions into question. In a long-term feeding study, sheep (*Ovis aries*, n=46) were fed experimental diets containing high or low concentrations of external abrasives (silica dust) of three different sizes (7 diets in total, including a control). Tooth wear was measured using mesowear (crown shape and height) and absolute wear (crown and root volume) on *in vivo* CT-scans taken at the start, midpoint, and end of the experiment. Comparisons between diet groups showed hardly any significant differences after 18 months, irrespective of whether CT-scans, molds, or actual teeth were scored, though CT-scans produced the bluntest scores. When comparing mesowear scores between methods, CT-scans showed a higher correlation to the real teeth for crown height ($R2=0.93$ *vs* $R2=0.75$), while the molds showed a higher correlation to the teeth for cusp shape ($R2=0.64$ *vs* $R2=0.56$). When scoring crown height, CT-scans were more advantageous than dental molds. The expected wear gradient of "more wear on higher abrasive diets" appeared in visual representations of mesowear change over time, though orders of magnitude were extremely small. These results indicate dietary signal formation to be much more time-consuming than previously thought, in particular when assessing the influence of external abrasives on mesowear in ruminants.

Comparative Gonadal Ultrastructure in Cuban Frogs (Anura: Eleutherodactylidae) Revealed by Transmission Electron Microscopy

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Gonadal structure and cell types constitute an important tool for assigning reproductive status and are essential for understanding adaptations to different life styles. The Cuban anuran fauna comprises 58 species of *Eleutherodactylus*, approximately 98% of which are endemic. We studied a population of *E. atkinsi* on eastern Cuba and compared its gonadal ultrastructure with other direct-developing frogs (*E. goini*, *E. planirostris*, *E. riparius*, *E. varleyi* and *E. zugi*) from western Cuba. The general histological architecture of their gonads is very similar to other anurans. Ovaries are lobulated organs with a central cavity, covered by a transparent ovarian capsule and composed of germinative and follicular cells. Oocytes with moderate amount of yolk are surrounded by a single layer of flat follicular cells throughout folliculogenesis. Testes are paired ovoid organs, organized by a mass of seminiferous tubules, inside of which male sex cells are found in cysts and surrounded by a layer of fibrous connective tissue. We describe the ultrastructure of spermatogonia, spermatocytes I-II, spermatids and spermatozoa. Morphology of the spermatozoon head and tail exhibits interspecific differences and could be a useful tool in taxonomy.

Correlation between Morphology, Predator Escape Performance, and Material Properties of Vertebrae in the Yellow Perch *Perca flavescens* (Pisces: Perdidae)

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Many teleosts exhibit intraspecific variation that often correlates with different usage of habitat and resources. We evaluated the extent of intraspecific variation in the Yellow Perch, *Perca flavescens*, and established comparisons between two lakes (a mining-influenced lake *vs* a spring-fed lake) that differ considerably in ecological parameters (calcium bioavailability, pH and visibility). We examined their body morphology, kinematics and performance of predator escape response, and material properties of the vertebrae, in order to evaluate whether these traits indicate any correlation and intraspecific divergence. *Perca flavescens* from the mining-influenced lake (which has high calcium bioavailability, low pH, and low visibility) showed greater angular velocity and acceleration during predator escape response than the fish from the spring-fed lake (which has low calcium, high pH, and high visibility). These differences in predator escape kinematics and performance between the two *P. flavescens* populations appear to be correlated with their body morphology and material properties of the vertebrae. Compared to *P. flavescens* from the spring-fed lake, fish from the mining-influenced lake were shorter and deeper with a wider caudal peduncle, suggesting that these morphological traits contribute to their ability to quickly maneuver in the water column rather than the ability to cruise. The vertebrae in *P. flavescens* from the mining-influenced lake showed greater strength and Young's modulus than those in *P. flavescens* from the spring-fed lake, perhaps contributing to the greater recoilability of the vertebral column during predator escape response. In the context of predator-prey interactions, perhaps occurring differently due to ecological differences, body morphology and vertebral material properties change during growth in the way that these structural components of locomotor design in *P. flavescens* contribute to enhancing predator escape performance.

Overall Vertebra Bone Structure as Assessed by Anteroposterior Profile: an ImageJ-Based Approach

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Vertebrae play a key mechanical role in force transmission and weight bearing. But the overall bone structure (internal micro-anatomy) of individual vertebrae is poorly investigated. Many studies focus on the centrum (vertebral body) and the architecture of the trabeculae it contains. Indeed, it is assumed that the centrum has a major mechanical role in bearing most of the compressive loads withstood by the spine. But in the vertebrae of some taxa the centrum can be particularly reduced locally, presenting a simplified structure virtually devoid of trabeculae. A methodology to quantify the overall structure of vertebrae therefore has to be defined. Here, I propose a method that uses a CT-scan stack of transverse vertebral slices. It does not require the studied vertebra to be segmented out, which facilitates the use of articulated series. Using a custom ImageJ macro, an anteroposterior profile is built measuring desired parameters on each slice. Of particular interest is the global compactness, here the ratio between the area occupied by bone and the total sectional area. This requires to accurately select the latter area on each slice. This is not trivial when porosity connects the area corresponding to the exterior of the bone to large internal vacuity (e.g., the vertebral canal). To address this issue, the new macro offers the possibility to manually exclude slices for which the section is not complete. But this proved to be suboptimal for some specimens, and an additional row of slice exclusion should be applied based of the recognition of statistical "serial outliers" (this was be performed with a dedicated R script). The output of this procedure is compared to that of a simpler smoothing approach using local polynomial regression. As a test case, data was acquired for the middle lumbar vertebra in over 70 mammals of various body sizes and lifestyles. Example profiles will be presented, and the disparity of vertebral compactness across mammals will be discussed.

How Tool Morphology Influences Energy Transmission During High-Speed Puncture Events

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A viper injecting venom into its victim, a raptor grasping prey with its talons or a stingray stinging in self-defense are all examples of vertebrates performing high-speed puncture. While varying in materials, behavior, kinematics and scale, all three have the same fundamental goal: to use their puncturing tools to quickly and efficiently penetrate the integumentary tissues of their target. While a seemingly straightforward procedure, the actual energetics of puncture are complex.

When a puncture tool impacts a target at high speed, it has a set amount of energy available to create fracture in the target. However, not all of this energy can be used to create fracture; some of it may be lost via deformation of the target, imparting momentum to the target, or creating heat. The success or failure of a puncture attempt is dictated by how well organisms control this energy flow between them. One potential influence on energy flow is the shape of the puncturing tool itself. Previous work from our lab has shown that tool shape influences both fracture initiation and the energy required for full penetration in static systems. Here, we examine how tool shape influences impact dynamics in a high-speed puncture system combining ballistics experiments with Particle Tracking Velocimetry (PTV). Preliminary results show that the energy transfer between tool and target during puncture is scale dependent. Increased speed allows for increased puncture depth, but there is an upper limit partly controlled by the relative masses of the tool and target. PTV-analyses show that the curvature of the puncture tool alters the pattern of material deformation, creating pockets of high and low deformation within the targets during puncture, influencing how much energy is lost. Experimental analyses such as this will open the door for establishing a common framework for examining energy transfer dynamics between organismal systems across scale and phylogeny.

Anatomy of the Earliest Occurring Crown Squirrelfish (Teleostei: Holocentridae) from near the Cretaceous-Paleogene Boundary of New Jersey

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Squirrelfishes (Holocentridae) are marine, reef-dwelling, and primarily nocturnal fishes including approximately 90 living species. Although only modestly diverse, holocentrids occupy a critical phylogenetic position as a close outgroup to the hyperdiverse percomorphs. The earliest fossils associated with squirrelfishes are early Late Cretaceous (ca. 100-80 Ma) in age, deriving from deposits in the Middle East, Europe, and North and South America, and are loosely tethered to the holocentrid stem lineage. There is a gap between these taxa and the earliest well-known Cenozoic holocentrids, which are early Eocene in age (ca. 49 Ma) and clearly belong to the crown radiation. We used micro-computed tomography to examine three-dimensionally preserved holocentrid remains from near the Cretaceous-Paleogene boundary (66 Ma) of the Hornerstown Formation of New Jersey that punctuate this stratigraphic gap. The most significant specimen is a distorted but otherwise uncrushed and nearly complete skull. A posterior lateral expansion of the parasphenoid, imperforate ceratohyal, and strong notchings on the ventral border of the ceratohyal indicate that it is crownward of known Cretaceous forms. Presence of an edentulous dorsomedially-upturned process at the symphysis of the premaxillae, and an alveolar process of the premaxillae bearing an antero-lateral expansion overhanging the dentary are derived features suggesting placement as sister to Myripristinae within the crown group. This skeletal identification contrasts previous identifications of this fossil as a holocentrine on the basis of its generalized otoliths, although this may be consistent with placement deep on the myripristine stem. Past divergence-time estimates have placed the origin of the holocentrid crown in the lower Ypresian (ca. 53 Ma), but incorporations of the New Jersey taxon as a calibration shifts divergence into the Maastrichtian (ca. 70 Ma).

The Incus-Cranial Joint and Early Birth in Marsupials and Monotremes

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The mammalian jaw articulation, unlike that of non-mammal gnathostomes, forms between the squamosal and dentary bones. In mammals the ancestral jaw articulation is homologous to the malleus-incus joint of the definitive mammalian middle ear. Consequently, the mammalian middle ear initially develops physically attached to the mandible via Meckel's cartilage, only to be detached in later development allowing isolation of ear and jaw. Since both monotreme and marsupial mammals exhibit extreme altriciality and are born before the development of the mammal jaw joint, they must utilize the connection between the mandible and skull via the forming middle ear in the first period of postnatal life. In this study, we characterize the relationship between the malleus, incus and cranium prior to the formation of a functional squamosal-dentary joint in both marsupials and monotremes, as well as in placental mammals. We show that marsupials and monotremes have differing strategies for utilizing a functional cranial-mandibular connection before the development of the mammalian jaw joint. Fossil data suggest that the mammalian middle ear evolved independently on more than two occasions, including once in each extant mammalian group: monotremes, metatheria (marsupials) and eutheria (placentals), and our data presents further developmental evidence for this homoplasy.

Multivariate Genotype-Phenotype Mapping for Craniofacial Shape in the Diversity Outbred Population

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Studies of genetic association with complex traits seldom acknowledge the inherent covariation between genes in developmental pathways or processes. As a result, our inference from genome wide association studies typically relies on the effects of single mutations on the trait of interest. This study models craniofacial variation as combinations of genetic effects on the total shape of the craniofacial complex in the Diversity Outbred mouse sample. The Diversity Outbred (DO) mouse project aims to recapitulate natural genetic variation by randomly crossing 8 isogenic strains from the Collaborative Cross project across generations. Thus, every individual from the DO population is a mosaic of alleles from each of the 8 founder strains. Using a sample of 997 DO mice genotyped at ~48,000 markers, we show the regions of the genome most highly associated with craniofacial variation along with the relative contribution of each founder strain allele. We also use gene ontology to compare the effects of individual developmental pathways and processes in their association with craniofacial shape. Our objective is to better understand the extent to which the coordination of different developmental processes produces patterns of covariation in the face and skull.

Ontogeny of the Alligator mississippiensis Frontal

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As is the case in many apex predators, *Alligator mississippiensis* is known to undergo an ecological shift between juvenile and adult lifestyles that is predicated on an increase in body size and other ontogenetic shape changes. A deeper understanding of the ontogenetic shape changes can be obtained, in part, through a clearer understanding of the allometric changes in the individual elements of the cranium. In an attempt to work towards the goal of gaining insight into the nature of ontogenetic shape changes in *A. mississippiensis*, CT data obtained from five skulls of different ontogenetic stages were used to document changes in the ontogenetic shape in the frontal. Surface-based and landmark-based geometric morphometric analyses were performed on the digitally segmented frontals of the different ontogenetic stages of *A. mississippiensis.* Generalized Procrustes analysis and Generalized Procrustes surface analysis revealed the presence of a strong, significant positive correlation between the size and shape of the bone, with most of the ontogenetic variation occurring in the interocular and caudo-ventral regions. The analyses also revealed that although the shape of the dorso-rostral tip of the frontals is modified during ontogeny, at no point does it resemble the basal crocodyliform shape. This indicates that the previously reported taxonomically important shape of the dorsorostral tip is phylogenetically robust.

Investigation of Dental Evolution Using a Combined Analysis of Comparative Morphology and Molecular Evolution

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To understand what enabled mammalian radiations, it is critical to know the developmental and genetic basis of dental evolution. To understand the evolution and development of complex morphological characters, dental morphology is an interesting model. Traditional experimental studies using model organisms have revealed various developmental mechanisms. However, model organisms do not possess all characteristics that researchers focus on. Therefore, we suggest combined analysis of comparative morphology of museum specimens and molecular evolution, as well as the use of genetically modified mice. In the series of studies presented in this poster, we focus on evolution of the molar size ratio and molar shape (the trigonid and taronid ratio) in the mammalian order Carnivora. The molar size ratio is controlled by the developmental inhibitory cascade model. As previously reported, the molar size ratio and molar shape in carnivores correlate with the animals' diet. Therefore, determining the genetic basis of the evolution of the molar size ratio and molar shape elucidates the developmental basis of their dietary adaptation. The results of our analysis on genetically modified mice showed that bone morphogenetic protein 7 (BMP7), the signaling molecule, which may be involved in the inhibitory cascade, affects both the molar size ratio and the molar shape. Molecular evolutionary analysis of the dN/dS ratio revealed positive selection of BMP7 in the ancestor of ursids. Ursids possess a unique dental characteristic—the second lower molar is the largest among all lower molars. However, morphological analysis showed that the ursid molar still follows the trend observed in carnivores. The series of evidence suggested that BMP7 evolution imparts the unique characteristic to the ursid molar. In this poster, we intend to report on the analyses of comparative morphology and molecular evolution using a broader range of species.

Limb Muscle Architecture of the Smallest Terrestrial Mammal – the Etruscan Shrew (*Suncus etruscus*: Soricidae, Eulipothyphla)

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The Etruscan shrew (*Suncus etruscus*: Soricidae, Eulipothyphla) is the world's smallest terrestrial mammal, weighing merely 2-3 grams. Apart from being one of the smallest mammals, it is also relatively one of the fastest, which is reflected in its metabolism and likely in its limb muscle architectural properties. Force producing capacity of a muscle depends on the physiological cross-sectional area (PCSA), but also on a muscle's pennation. Potential for changes in muscle length depends on fascicle length. For a given volume, either PCSA or fascicle length can be optimized. Due to the differing scaling relationships of area (such as PCSA) and volume (which is reflected by muscle mass), the Etruscan shrew thus presents an intriguing study system to address the morpho-functional consequences of miniaturization. In this study, we aimed to establish a 3D-atlas of the fore- and hind limbs of the Etruscan shrew. Furthermore, we used diffusible iodine-based contrast-enhanced micro computed tomography (diceCT) scanning combined with a pattern recognition algorithm to resolve muscle fascicles (streamlines) and derive their spatial arrangement. By applying this technique, we will be able to gather information on important muscle architectural parameters, such as muscle volume, fascicle length, angle of pennation and PCSA. Preliminary data will be presented and discussed.

Body Temperatures and Life History in Mammals: Longitudinal Data from Armadillos

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Endothermic mammals and birds differ from most other organisms by virtue of their relatively high and constant body temperatures. Rather than decreasing their metabolic processes in cold environments, endotherms do the opposite in order to support this physiologically extravagant adaptive strategy. Nonetheless, some endotherms show substantial variation following daily and/or seasonal cycles. Life history events such as gestation are known to influence core body temperatures in certain species, a reasonable expectation given the demonstrable effects of temperature on (for example) developmental processes relevant to embryogenesis. Here, we present and interpret new data on core body temperatures recorded over several months from multiple, wild-caught individuals of the nine-banded armadillo (*Dasypus novemcinctus*). Individuals in our sample varied in terms of gestation (gravid *vs* nongravid) and enclosure (lab *vs* outdoor). Average body temperatures were very similar in our treatment groups, but gravid animals exhibited slightly less variation in body temperatures. While activity patterns of a given animal were reflected in its core temperatures, changes in ambient temperature resulting from seasonality, or the more constant thermal environment provided by indoor housing, did not appear to have major effects on variation in core body temperature. Our results are consistent with previous findings of high temperature fluctuations and periodic extremes in the armadillo, despite the apparent lack of torpor in this species.

Altering Hox Gene Expression Domains in Lissamphibians Produces New and Ancestral Morphologies

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While the fossil record alone reveals the pattern of morphological transformations throughout evolution, a more integrated approach is required to understand the underlying developmental processes that drove these transformations. Such approaches have improved our understanding of certain transformations (e.g., fin-to-limb) and their underlying developmental processes, whereas others, such as the evolution of the skull-neck boundary in tetrapods, remain poorly understood. Recent work synthesizing paleontological, phylogenetic, and developmental data reveals that the extant amphibian condition is the product of an anterior shift in the location of the skull-neck boundary relative to their fossil ancestors and other tetrapod lineages. Here, we aim to further understand the mechanistic basis of this transformation through the experimental manipulation of factors regulating the location of the skull-neck boundary in amphibians. The application of exogenous retinoic acid (RA) and an RA inhibitor to salamander (*Ambystoma mexicanum*) and frog (*Xenopus laevis*) embryos results in the translocation of the skull-neck boundary anteriorly and posteriorly, respectively. These experiments reveal a similar capacity in both salamanders and frogs to respond to changes in late-stage axial patterning. These experimental phenotypes are consistent with homeotic transformations of the skeleton leading to a change in the location of the skull-neck boundary. In salamanders, a posterior translocation of the skull-neck boundary results in a broader and more robust skull and vertebral elements in experimental animals compared to controls. Significantly, details of the resulting phenotypes in salamanders, from skeletal, muscular and nervous tissue perspectives, mimic variation observed in their closest fossil relatives. This suggests such homeotic transformations, and their underlying genetic basis, may have played a role in the evolution of the tetrapod skull.

3D-morphology of Pharyngeal Dentition of the Cyprinid Fish Genus *Capoeta* (Cyprinidae): Implications for Taxonomy and Phylogeny

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Capoeta is a herbivorous cyprinid fish genus, widely distributed in Western Asian water bodies. Recent species show a distinct biogeographic pattern with endemism to large fluvial drainage basins. For the first time, a detailed comprehensive study of the pharyngeal dentition of 10 *Capoeta* species has been provided. The morphological study of the pharyngeal dentition is based on the 3D-microtomography and follows the purpose to evaluate the potential taxonomic and phylogenetic signals of these elements. In the present study we propose a new methodology to categorize the studied pharyngeal teeth in 18 shape classes. The results of this study show that the detailed 3D-morphology of the pharyngeal teeth is a useful tool for identification of isolated teeth at the generic and/or specific level; in certain cases the tooth positon in the tooth rows can be identified. Besides this, the preliminary analysis shows that the morphology of the pharyngeal teeth provides a potential phylogenetic signal. Both these patterns are very important for the taxonomy of cyprinid fishes and especially can be applied to the fossil record.

Domestication and Cranial Shape Disparity in South American Camelids

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Phenotypic changes related to domestication concern a variety of systems including 1) cranial shape, 2) brain size, and 3) growth trajectories, as documented across vertebrate clades. Despite commonalities, a uniform pattern of domestication-driven changes in mammals is refuted by comparisons of growth in wild/domestic pairs. Morphological and developmental changes vary across both taxa and trait. South American camelids (Lamini) display the greatest magnitude of change between wild and domestic forms, second only to the wolf/dog pairing. Lamini are among the few species of domesticated animals from the Americas, as likely determined by biological and cultural factors. Here, we compare cranial shapes of the wild forms *Lama guanicoe* and *Vicugna vicugna*, and their domestic counterparts, *Lama glama* and *Vicugna pacos*. We analyzed 162 specimens using 62 3D-craniofacial landmarks. Multivariate analyses indicate significant cranial shape differences between the wild and domesticated llama. Shape changes between the wild/domestic *Vicugna*, where size is the main source of disparity, are less evident but further explored here. More importantly, both domesticated forms display changes in the same direction of PC space. Effected cranial changes were tested for modularity and compared to analogous studies of horses, pigs, and birds. Our phylogenetic study of South American camelids including fossils allows us to put the morphological changes associated with domestication in the context of the tempo and mode of evolution of the clade.

Understanding Locomotion on Snow: How Substrate Influences Trackway Characteristics of Svalbard Rock Ptarmigan

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Substrates have a profound effect on locomotion. Moving over snow will impact how animals move, due to the increased force or drag on the limbs required to move through the substrate, while also maintaining the extra stability needed due to limited traction on the surface. Here, we determine how the mechanical characteristics of snow (hardness, density and wettability) influence the trackways and therefore locomotor biomechanics of the Svalbard rock ptarmigan *Lagopus muta hyperborea*, a primarily terrestrial bird that lives on the Arctic islands of Svalbard. To investigate this, the track characteristics of the ptarmigan on the snow, in particular the depth of the track depression, were measured. Different snow properties affected the gait and speed selection of these animals. From this information, it was determined how the type of snow could impact the forces required for the ptarmigan to move through the substrate, having implications for their kinematics and the metabolic cost of transport.

Long Axis Rotation of the Frog Hip during Jumping – an XROMM Analysis of the Amazon Milk Frog

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Frogs display a varied repertoire of locomotor behaviors. Across the Anura clade, frogs are capable of jumping, swimming, running, digging and climbing. Frogs' three-dimensional posture and complex musculoskeletal anatomy are intrinsic in achieving this broad range of abilities. Flexion-extension and abduction-adduction kinematics are well characterized in frog jumping; long axis rotation (LAR) is less characterized, due to the technical challenges associated with measuring this plane of motion. Our previous modelling predicts that LAR during jumping may alter muscle mechanical advantage, or even change muscle function completely. To test this prediction, we studied the *in vivo* kinematics of the hip during jumping, in three adult specimens of the Amazon milk frog *Trachycephalus resinifictrix*. We used a marker-based XROMM technique, where the pelvis and femur were each surgically marked with three (non-linear) 1 mm tantalum beads. The relative rigid body motions of these segments were calculated. Our analysis of 15 jumping trials across these three individuals reveals that the femur internally rotates by 15° about its long axis during jumping. These kinematic data are combined with a musculoskeletal model of *Trachycephalus*, implemented in MuJoCo. This model is based upon anatomical data from contrast and non-contrast micro computed tomography of an additional individual. We calculate the muscle moment arm changes attributed to LAR at the hip, and speculate that this degree of freedom is an important moderator of muscle mechanical advantage.

Chewing Efficiency and Functional Occlusal Morphology of an Ontogenetic Series in the Chimpanzee (*Pan troglodytes*)

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The heterodont dentition is one of the key adaptations of mammals and one of the main reasons for their ecological success. Mastication is energy demanding and in order to be energy efficient in food breakdown it requires occlusal morphologies functionally adapted to the typical material properties of ingesta. Since mammalian permanent teeth cannot be replaced, wear induced morphological change needs to be functionally compensated. Here, we functionally analyze chimpanzee (*Pan troglodytes*) postcanine occlusal surfaces representing an ontogenetic series via experimental as well as virtual approaches. Topographic characteristics like Relief Index (RFI) and Orientation Patch Count Rotated (OPCR) were computed, and upper and lower dentitions cinematically occluded utilizing the software Occlusal Fingerprint Analyzer (OFA). Subsequently, we quantified the successive changes in contact areas during progressive wear. Moreover, to uncover a possible relationship between occlusal morphology and chewing efficiency, standardized test bodies were experimentally loaded between occluding tooth rows and force measurements were performed until the first break occurred. Finally, a dynamic Finite Element Analysis (FEA) was performed reproducing the experimental setting to provide virtual comparative data. We found that the molar occlusal morphology drastically changes during the lifespan. When wear progresses, functionality mediated by the unworn occlusal surface is successively replaced by secondary surface features, like shearing edges formed along the enamel-dentine junction (EDJ). These edges turned out to have an equivalent functionality to occlusal structures from earlier life phases. Both, force measurements and FEA, show that chewing efficiency decreases at first and starts to increase again, as soon as enamel ridges form. This pattern suggests structurally manifested adaptive mechanisms that can compensate for functionality loss due to wear.

Ecological Specialization and Elevated Ambient Temperature at the MCCO Underlie Modern Shark Species Richness and Distribution

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Lamniform sharks have an evolutionary history of almost 140-million-years. Previous diversity analyses have identified the Late Cretaceous as the peak diversity timeframe for the clade, but this was followed by widespread extinctions across the K-Pg boundary. Conversely, Cenozoic ecological restructuring favored the rise of carcharhiniforms, which constitute the most speciose shark radiation today. Although this major clade transition is well documented, the precise timing and drivers are poorly understood. Here, we therefore reconstruct the morphological succession of lamniforms and carcharhiniform sharks across the last 83-million-years, using a geometric morphometric dataset of 3400 fossil teeth. Our results show that the diversity of lamniform and carcharhiniform tooth morphologies was highest during the Late Cretaceous, but noticeably declined in disparity amongst lamniforms during the Mid-Miocene Climatic Optimum (MMCO, 17–14.75 Ma). In contrast, the dental disparity of coeval carcharhiniforms increased across this same interval with significant shifts in morphospace evident in both groups. Interestingly, super-predatory sharks, such as the famous *Carcharocles megalodon*, also appeared during this timeframe, which is a coincident event that we attribute to climate related oceanic productivity changes and a shift towards trophic specialization in response to the global diversification of baleen whales and larger ray-finned fishes. The co-occurrent success of carcharhiniforms is less easily determinable, but may have been a product of their generalist feeding strategies and corresponding ability to utilize intermittently available food resources at a time of environmental stress.

X-Ray Computed Tomography (XCT) in Life Sciences: Disrupting Its Limits by Technological Enhancements!

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Modern X-ray Computed Tomography (XCT) goes light years beyond regular two-dimensional X-ray technology to deliver accurate three-dimensional volume data of scanned objects. It has become one of the most important and powerful non-destructive testing methods both in any field of life science research and any industry branch - an achievement resulting from the continuous improvement of XCT-scanning techniques and reconstruction methods. This enables increased precision and resolution, the manufacturing of cheaper and more compact devices and finally innovative concepts allowing for highest user friendliness to simplify the execution of successful XCT-experiments with high quality results. Today's XCT-scanners have to be designed to achieve X-ray inspection results of extreme quality with respect to high spatial and contrast resolution, large scanning volumes or high speed scanning. E.g., on the one hand the XCT-technology is adapting to the predominant preparation methods for soft tissue samples, e.g., contrast enhancement by iodine (see "diceCT" = diffusible iodine-based contrast-enhanced CT), phosphotungstic acid (PTA) or lead diffusion. On the other hand there are challenges of very large or dense specimens, e.g., large parts of skeletons or heavily mineralized bones packed in compact stone blocks. In this presentation we will demonstrate how modern scanning techniques and technically enhanced XCT-scanners are able to disrupt the current experimental limitations in XCT-scanning, i.e., overcoming limited fields of view by using dual helical XCT-scanning or lack of contrast and spatial resolution by optimized geometries and component technology. In addition we will show how this well-established analytical technology will become accessible to a much broader user community by an increased user-friendliness.

Why Morphology Matters: A Reef Fish Perspective on the Links between Form and Function

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Morphological traits are an invaluable tool in all fields of evolution and ecology. However, their greatest value is when they can be causally linked to functions. Morphology per se is descriptive, while functional morphology implies operational usefulness. If something is functional it works; if it is non-functional it is either broken or potentially irrelevant. But how do we evaluate functionality? For functional morphology, performance-based links have been well established. Today, morphology is being embraced by a wider audience, especially ecologists, with an increasing interest in morphological traits as functional traits. I will discuss these functional linkages on coral reefs, a system that supports one of the most morphologically diverse vertebrate assemblages. In particular, I examine the meaning of the term 'function' and how morphology is related to the various 'functions' attributed to reef fishes. Remarkably, most 'functional' studies do not look at functions, and the widespread use of traits as indicators of function may be misleading. For many taxa, form-function links are assumed rather than demonstrated and the critical links to ecosystem functions are even less well understood. With the increased use and abuse of morphological traits, the value of empirically-established form-function relationships are now more valuable than ever.

Old Tools Open up a New World in Vertebrate Morphology: A Coral Reef Example

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When competing with You-tube, David Attenborough, and National Geographic, vertebrate anatomy classes are often playing catch-up with computer literate and technology savvy students, yet the direct contact with the natural world triggers the most valuable results: inspired new questions. At James Cook University, marine vertebrate morphology is a crucial component of core marine biology subjects. In order to identify the major biological challenges that aquatic existence imposes on marine organisms, and infer the structural and functional solutions developed to meet such challenges, we have used an integrated approach focusing on fishes. Students are introduced to fish anatomy in their 1st year general zoology classes, which is reinforced in a functional ecology course at the 2nd year, then applied in a specialist ichthyology course in their final, 3rd year. In these courses, the main teaching tool is the dissection of fresh material. Students are provided with whole fishes to dissect at 2nd year to answer the question: Does morphology inform us about the lifestyle and biology of fishes? At 3rd year, students are required to process and reconstruct a whole fish skull to explore the morphological basis for the diversity of feeding modes seen in coral reef fishes. In comparison to computer simulations and videos, we have found that a hands-on approach in the laboratory, followed by a week of behavioral observations on a reef, generates more enthusiasm and energy amongst students in the study of vertebrate morphology. Most importantly, it has triggered novel questions and opened up new research topics in marine ecology and paleontology. Enthused students have since undertaken morphology-based research projects at Masters and PhD levels, which have led to high-quality publications in key journals. Our experience confirms the dependability of 'old' tools in teaching vertebrate anatomy and the capacity of these hands-on experiences to inspire a new generation of morphologists.

Intra-specific Variation in Color Patterns, Morphology and Sexual Dimorphism in the Moroccan Spiny-tailed Lizard *Uromastyx nigriventris* (Sauria: Agamidae) along a Mediterranean-Saharan-Aridity Gradient

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Uromastyx nigriventris is a large-sized herbivorous agamid lizard species distributed from northeast-southwest Morocco to western Algeria, from the Mediterranean to the northern margin of the Sahara desert. The species exhibits intra- and inter-population variation in color patterns, but there is no apparent sexual dimorphism. However, it seems that head size and shape may differ between the two sexes. The present study aimed at analyzing: i) inter-population variation in body size and shape, and color patterns along a Mediterranean-to-Saharan aridity gradient in Morocco, and ii) checking the occurrence of an actual sexual dimorphism in head size and shape. We used traditional morphometry to analyze the morphological variation of lizards from four distant populations across the latitudinal aridity gradient. Adult individuals were sexed, weighed, photographed and measured for 2 meristic (number of tail whorls and number of scales around the 5th whorl) and 14 metric characters. There is a color polymorphism, but with no apparent sexual dimorphism, both within and between populations, with variation in proportions among four observed dorsal color patterns: yellow, green, orange, and red along with their combinations. Our results suggest sexual dimorphism for only four morphological variables analyzed: snout-vent length and tail length, and head width and ear-to-nostril distance. The four studied populations differed significantly in the two tail meristic characters and 10 body dimensions excluding head dimensions, except head depth. The observed differences seem to be related to local factors, such as climatic conditions, topography and substrate. Changes in skin color patterns might be related to both genetic and plant nutritional (e.g., carotenoids) determinants. The obtained results on sexual dimorphism are discussed in relation with breeding behavior, but information on mating system for this lizard is needed for better explaining the sexual dimorphism.

Postcranial Anatomy of a Gorgonopsian and its Implications for the Evolution of the Mammalian Sternum

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Gorgonopsians are one of the most iconic groups of non-mammalian synapsids and are common in middle–late Permian continental strata in southern Africa and Russia. Gorgonopsians are characterized by hypertrophied canine teeth and included the apex predators of the late Permian. Though gorgonopsian cranial anatomy is increasingly well-studied, comparable research on their postcranial anatomy has lagged. Here, we describe a new specimen of the namesake taxon *Gorgonops* (SAM-PK-K10591) from the Northern Cape Province of South Africa, revealing new insights into the gorgonopsian body plan and the diagnostic potential of gorgonopsian postcranial elements. Notably, this specimen provides novel information on the anatomy and evolution of a poorly understood component of the pectoral girdle of Gorgonopsia and Therapsida in general: the sternum. Plesiomorphically an undivided element, it often remains cartilaginous in 'reptilian-grade' amniotes and hence has a poor representation in the fossil record. By contrast, modern mammals usually possess an ossified, multipartite sternum consisting of the proximal manubrium and several sternebrae including the distal xiphoid process. An undivided but ossified sternum is known from several therapsid clades and is particularly well-represented in dicynodonts. The earliest documented multipartite, and therefore mammal-like, sternal complex previously reported belongs to the Middle Triassic cynodont *Diademodon tetragonus*. SAM-PK-K10591 shows an earlier occurrence of a multipartite sternum in a gorgonopsian, pulling the origins of this characteristic mammalian trait deep within theriodont therapsids in the Permian. It furthermore underlines the robust and agile design of the gorgonopsian Bauplan, well-adapted for handling large prey.

Mandibular Shape Disparity and Convergence in Ichthyosaurs and Toothed Cetaceans

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Ever since they first made the transition to life on land around 350 million years ago more than 30 lineages of tetrapods have reinvaded the water independently, filling important roles in aquatic ecosystems. The constraints that arose from living in water rather than air have forced the evolution of similar morphologies within these groups, making them among the most iconic examples of evolutionary convergence. In particular, modern toothed cetaceans are often compared to the ichthyosaurs, a diverse clade of extinct marine

reptiles which also evolved a 'fish-shaped' body plan with tail propelled locomotion. Both are groups of raptorial marine tetrapods with long evolutionary histories and good fossil records, yet surprisingly their ecological convergences and the macroevolutionary pathways behind them are poorly understood and lack a thorough, quantitative framework. The goal of this project is to investigate convergences of ichthyosaur and cetacean skulls on similar morphologies and ecological functions. Here, we present results of a preliminary analysis focusing on the shape of the mandible from a sample of archaeocete and odontocete cetaceans and parvipelvian ichthyosaurs. Landmarks and semi-landmarks were placed onto photographs of specimens or 3D-models made with an Artec Eva handheld scanner. The resulting coordinates were subjected to a principal components analysis in R to show mandibular shape disparity, with preserved stomach contents and tooth shape data used to correlate this morphological variation with possible ecological functions. Up-to-date phylogenies can be superimposed to show convergences and trajectories of evolutionary change in the two groups through time. Using these ordination techniques adaptive landscapes can be created to reveal which areas of morphospace ("peaks") are colonized more frequently. These results will form part of the first detailed quantitative analysis of ecomorphological convergence in ichthyosaurs and cetaceans.

Is the Lateral Semicircular Canal a Reliable Proxy to Infer Head Posture?

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The orientation of the lateral semicircular canal of the bony labyrinth is habitually used to infer head posture of modern and extinct animals (mammals, birds, archosaurs and early "reptiles"). It is believed to be influenced by ecology, diet and behavior (browsers and semi-aquatic species would hold their head higher than grazers and head-butting species). By placing the plane of the lateral semicircular canal parallel to the horizontal, the 'spontaneous', 'neutral' position of the head would be revealed. Though widespread in the literature, this assumption has not been tested on a large sample size in mammals, while it has been challenged in archosaurs and humans. Using direct field observations of living animals and CT-scanning on almost 200 dry skulls representing some 130 modern species, the aim of this project is to investigate the orientation of the plane of the lateral semicircular canal and its reliability for the reconstruction of neutral head posture in modern mammals. Preliminary results indicate that LSC orientation might be governed by factors other than head posture alone. This would question a century of assumed linear relationship between the two metrics. A possible effect of body mass has been detected since small taxa seem to hold their head more horizontal than larger ones. A phylogenetic effect is not ruled out. This study was conducted with the financial support of the DST-NRF Center of Excellence in Palaeosciences, the Palaeontological Scientific Trust (PAST) and the Claude Leon Foundation.

Similar Appearance but a Different Behavior – a Behavioral Study of Leaping in Four Species of Callitrichidae

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The tamarins and marmosets (Callitrichidae; Primates) are a species-rich radiation within the New World primates. Apart from fur coloration, especially external appearance of tamarins is very conserved and suggests a similar behavior of all species. Nevertheless, ecological differences and differences in locomotor behavior have been previously documented in tamarins. To further explore this system, we are interested in fine-grained ecological differences between species related to locomotion. To pinpoint these, we have documented and evaluated data of four tamarin species in terms of substrate use and relevant biomechanical and morpho-functional parameters (such as leaping distance and durations of sub-phases of the leaping motion) in two behavioral studies. These were conducted in a natural habitat in Amazonian Peru and in a naturalistic setting in a zoo in France. We found significant differences in the leaping behavior of the species, based on which we can now expect to find differences in their morphology. While *Saguinus midas* mostly avoided vertical leaps, *Leontocebus nigrifrons* preferred vertical leaps. *Saguinus imperator* and *Saguinus mystax*, on the other hand, appeared to be generalists with no clearly preferred leaping behavior. Morphological differences in muscle architecture, bone shape, and bone internal structure reflecting these differences can be expected and will be traced down in ongoing analyses. This study thus aims to integrate field work with the study of morphology in order to identify potential adaptations.

Postnatal Dental Morphogenesis of Lagomorphs Point out Potential Developmental Heterochronies as Evolutionary Processes

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Cheek teeth have changed considerably during lagomorph evolution, from rooted to unrooted evergrowing teeth, with an increase in crown height and modifications of the occlusal morphology. The adult upper cheek teeth of extant lagomorphs are characterized by the presence of two lophs separated by a lingual enamel fold. We observed that juveniles and adults have different dental morphologies. In order to characterize changes in the occlusal surface morphology related to age, we studied its variability in different species of lagomorphs from birth to adulthood. Using X-ray microtomography, we extrapolated the occlusal surface at different wear stages by making virtual sections of 3D-tooth reconstructions. We demonstrate that leporid upper cheek teeth have a crescent valley when the tooth is unworn, which disappears by wear a few weeks after birth. This loss is associated with an increase of the re-entrant fold invagination. The fold is initially smooth in juveniles and can become increasingly crenulated with age. Using an irradiation protocol in rabbit teeth, we were able to modify the crenulation shape. We propose that modifications of the proliferation rate at the basis of the tooth may explain how the tooth shape can change continuously over the life of the animals. Furthermore, the chronology of the morphological modifications occurring during dental development corresponds step by step to what is observed between basal and derived species of lagomorphs. This observation leads us to hypothesize a peramorphic dental evolution of lagomorphs that follows the ancestral character states during ontogeny.

Molecular Limb Evolution in the House Gecko *Hemidactylus* (Gekkota, Squamata)

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The tetrapod limb shows a variety of phenotypes coupled to ecological specialization. At times, such adaptive demands can involve digit reduction. Especially among squamates, the degree of reduction of phalanges and digits varies among species, to the extent of entire limb loss in snakes, amphisbaenians, and dibamids. Information on developmental mechanisms underlying digit and phalanx reduction is scarce, apart from the little that is known about expression alterations in, e.g., *shh*, *ptch1*, *hoxd11*, *d12* and *d13* in selected reptilian and mammalian species. In manus and pes of *Hemidactylus*, a member of the clade Gekkota, which is sister to most other squamates, several phalangeal elements are highly reduced. These disc-like phalanges are likely related to adhesive toepads and associated ecological constraints, but also hypothesized to be eventually lost. The aim of this study is to elucidate pathways of fundamental gene networks in this species. Preliminary results include a morphologically conserved AER, and *fgf8* expression canonical to other tetrapods. The restricted and early terminated expression of *shh* compares to what is seen in another squamate, *Hemiergis quadrilineata*, which has two digits, as opposed to extended expression in five-digited *Hemiergis initialis*. *hoxd13* is not expressed in digits I and V at the handplate stage in the house gecko, which stands in contrast to what is seen in the limbs of other tetrapods, except for the axolotl. The expression pattern seen in the latter and the house gecko potentially suggests that *hoxd13* is evolutionarily more variable than previously assumed. Moreover, it shows additional strong expression bands located in the prospective regions of developing disc-like phalanges. Results from these ongoing analyses contribute both to our understanding of molecular limb evolution in tetrapods and the generation of the various ecophenotypes in squamates.

A Comparative Context for Zebra Finch Vocal Repertoire Ontogeny

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Vocal repertoire elements emerge at diverse points in life history: Túngara frog calling behavior does not develop until sexual maturity, yet humans converse within their first few years. Call repertoire acquisition has been studied in birds, but in limited taxa and rarely comparatively. This is partly due to lack of data—for much of the avian tree, we know little about when vocal behaviors emerge relative to changes in parent-offspring interactions, visual signaling of sexual maturity, sexual behavior, and neurological growth stages. Zebra Finch, a model organism, is an exception to this trend: patterns of brain development, vocal learning, parental care, mate choice have all been investigated. Here, we reassess what is known about the timing of Zebra Finch vocal repertoire acquisition relative to an array of other life history events and compare these data to Red Junglefowl, a non-learning taxon whose vocal and behavioral ontogeny has also been well characterized. We then draw comparisons to sparser data from other learning and non-learning avian taxa. We find that call repertoire development varies significantly across birds with altricial taxa tending to vocalize later in life and with greater functional diversity than precocial ones. However, total call repertoire size across development may be greater in non-song learning taxa regardless of developmental strategy. We hope that this study will spur future work integrating repertoire development and life history in diverse taxa, a program that could yield new insights about the evolutionary origins of learned and innate vocalization across vertebrates.

Upper Molar Proportions in Placental Mammals: Is there an Allometric Rule Accompanying the Inhibitory Cascade Model of Molar Development?

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Molars constitute a highly integrated unit of the dentition and show many features such as cusps and crests being serially repeated at successive loci. Their integration is not limited to their occlusal shape, as a strong linear relationship appears to explain their proportions within the molar row. Since its discovery in mice, the Inhibitory Cascade model of lower molar development has been investigated in many groups, but often at a rather limited phylogenetic scale or using a restricted sampling of an otherwise much wider diversity. The pertinence of such model remains also largely unexplored for the upper dentition. Here, we analyze for the first time the proportions of upper molars in a large sample of placental mammals (312 specimens belonging to both extant and extinct species) representing most of the group's dental diversity. Areas of M1, M2 and M3 (M1a, M2a, M3a) were calculated for each specimen based on photographs of molar rows oriented parallel to the occlusal surface and measured with ImageJ. A Principal Component Analysis including the ratios

M2a/M1a, M3a/M1a and the logarithm of the sum M1a+M2a+M3a revealed that all three variables are highly covarying (80% of the variance explained by PC1, with correlation coefficients r between the three variables and PC1 higher than 0.8). Our findings suggest that large-sized taxa (here measured by the absolute size of the molar row) have relatively larger posterior molars in comparison to small-sized taxa within placentals. This relationship is further tested within a phylogenetic generalized least square analysis. These results are reminiscent of a recently evidenced allometric trend for the genus *Homo* and may provide a further explanatory mechanism for several aspects observed within mammalian dental evolution such as the sequences of molar loss. The implications of an allometric rule on molar proportions is also discussed for its potential impact on character covariation among successive molars.

Adventures in Scaling and Remodeled Morphology: The Case of the Ocean Sunfish

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Mola mola (Ocean Sunfish; Tetraodontiformes: Molidae) are recognizable by their distinct morphological characteristics, including large lobate dorsal and anal fins which fuse to form a clavus in place of a non-existent caudal fin. Adult mola lack axial musculature, but by synchronous flapping of the dorsal and anal fins they are able to dive to depths of 600 meters and cruise at a speed of 3.2 km/h. Larval mola more closely resemble sister species of pufferfish, but early in ontogeny undergo rapid morphological changes. Previous work examined some of the skeletal changes during mola ontogeny using cleared and stained specimens, with particular focus on the formation of the clavus, but no studies to date have evaluated the myological changes that occur as a result of the body shape and skeletal transformations that take place. Using computed microtomography (microCT) scanning, we were able to produce high-resolution three-dimensional skeletons of three stages of mola fry and an adult mola for ontogenetic comparison. Phosphotungstic acid (PTA) staining and re-scanning of mola fry generated images of soft tissue morphology, allowing comparisons of muscle volume, position, and fiber angle through ontogeny with measurements from dissections of adult mola. Herein we discuss the functional implications of drastic morphological modeling and changes in body size during ontogeny on the locomotor performance of *Mola mola*.

Slips, Trips, and Computer Chips: the Promises and Pitfalls of Dynamic Optimization of Locomotion Simulations

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Computational models can offer unique insights into musculoskeletal function. For instance, simulations based on models can provide information on aspects not easily measurable from experiments alone. However, simulations that track experimental data are limited to what was measured *in vivo*, which may not represent natural conditions or an organism's maximum capabilities. In contrast, *in silico* predictive simulations can explore musculoskeletal function under any range of conditions, enabling investigation of 'what if' questions. Under the assumption that a given behavior maximizes some performance objective, dynamic optimization can be used to generate simulations of behaviors *de novo*, including maximal performance behaviors. Here, we explore the ability of two dynamic optimization approaches – shooting and direct collocation – to generate various maximum performance simulations in the fastest terrestrial biped, the ostrich. In shooting, the model's initial states and control history (e.g., muscle excitations) are optimized. However, this approach is computationally expensive (sometimes requiring supercomputers) as it involves forward numerical integration of highly nonlinear system dynamic equations, which furthermore can make the problem very sensitive to the initial conditions. In direct collocation, the system dynamic equations are approximated by Lagrange polynomials over short time intervals, obviating the need for forward integration, and the states and controls throughout the entire behavior are optimized simultaneously. By avoiding forward integration, the optimization problem can be solved orders of magnitudes more quickly, e.g., our 18 degree-of-freedom ostrich model could be solved on a single laptop core in <10 minutes. We present comparisons between the two approaches for simulations of walking, running and jumping, demonstrating that direct collocation offers a powerful, accessible framework for simulating locomotor biomechanics in vertebrates.

Skeletochronological Analysis of the Long-Lived European Blind Cave Salamander, *Proteus anguinus*

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The purpose of this study was to perform a skeletochronological analysis in the European blind cave salamander *Proteus anguinus*, a long-lived species that lives in a stable cave environment. Skeletochronology utilizes lines of arrested growth (LAGs) in stained, histological cross sections of long bones. Because bone growth is a genetically based, cyclical, circannual phenomenon, and also reflects seasonal alternations, the number of LAGs should be correlated with the age of individual specimens. Analysis of LAGs was done on the decalcified long bones of the limbs of fixed archived *P. anguinus* specimens (N = 32) of known age (8-40 years) that were hatched and raised under controlled conditions in the cave laboratory of the CNRS Station d'Ecologie Expérimentale in

Moulis, France. All investigated specimens exhibited visible LAGs, although in most cases these were difficult to discern. In specimens under the age of 15, the number of LAGs coincided with the actual age of the animals (± 2 years). In older individuals, the number of clearly visible LAGs was significantly lower than their age (the correlation coefficient was low and there was no significant linear dependence; $p > 0.005$). But if we take into account all visible LAGs (distinct and less visible), a moderate positive linear correlation was present between the number of LAGs and the age (R^2 0.61, $p < 0.0001$). The poorly visible LAGs probably reflect the constant biotic and abiotic conditions of the cave environment, as well as the specific structure and growth dynamics of the pseudo-lamellar bone. We think that the visible LAGs in the long bones of *Proteus* probably represent an intrinsic (i.e., genetically assimilated) mode or cycle of bone growth retained from surface ancestors that were exposed to seasonally changing environmental conditions.

Rates of Evolution in the Skeleton of Extant Birds (Neornithes)

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Extant birds (Neornithes) are one of the most diverse adaptive radiations of vertebrates, with large phenotypic disparity and numerous skeletal adaptations for locomotion, posture and feeding. A major question in vertebrate evolution is how rates and mode of evolution gave rise to phenotypic disparity, specifically whether it evolved early in the clade, gradually over time, or more recently. To investigate, we measured rates of evolution in 100 neornithine genera for 12 bones representing the cranium, mandible, pectoral and pelvic girdles, forelimb and hindlimb, using 3D-models from CT-scans, geometric morphometric analysis, and phylogenetic comparative methods. Many bones, especially in the skull and forelimb, show high rates of phenotypic evolution during deep divergences that occurred in the late Cretaceous and Paleocene. This supports the general hypothesis of an early burst, especially in cranial and forelimb structure. However, specific patterns vary among elements, and include later bursts in some groups of some elements. The skull, mandible, and scapula have the highest overall rates of evolution, with high initial rates followed by lower rates in the Eocene, and increases in the Oligocene. In the synsacrum, high initial rates are followed by lower rates in the Eocene, and higher rates in the Miocene. The humerus, ulna and radius share high initial rates followed by lower rates in the Eocene, and higher rates in the Oligocene and Miocene. Some bones deviate from this overall pattern. The coracoid has intermediate rates throughout, and the carpometacarpus, femur, tibiotarsus and tarsometatarsus all have lower overall rates, with only weakly elevated initial rates. Shared patterns of evolution are linked to an extent by shared functional roles, with strong early divergences in dietary adaptations for the skull and mandible, and locomotion in the humerus, ulna and radius. Patterns in the hindlimb, scapula and carpometacarpus require further exploration.

Fight of the Century: Functional Redundancy *vs* Ecosystem Resilience

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In the face of current biotic crisis, one possible conservation strategy is to maximize functional diversity with the hope that biotas hold more chances during future environmental disturbances. Under this rationale, assessing the resilience of functional-diverse systems during past events of ecological disturbance can help to enlighten the effectiveness of such conservation strategies in preserving species richness over evolutionary-relevant timescales. We do so by investigating the trends in functional morphology of Iberian macromammals during the last 20 Ma. Our dataset includes functional information for 386 species grouped in 102 functional entities (i.e., unique combinations of functional traits). We estimate changes in functional disparity, functional redundancy and functional vulnerability, and compared these trends with speciation and extinction dynamics over the analysis interval. Functional redundancy peaks were followed by accelerating extinction and a marked species loss, typically extirpating species with the same functional ecology. The resulting system shows low functional redundancy, and eventually would rebound its resilience by gaining species with already-existing ecological roles. In terms of functional entities, the recovery after episodes of functional depletion were followed by a stasis or slow recovery. In particular, we observe periods of sustained positive and moderate diversification rates, fueled by a progressive increase in functional entities and broadening of the multivariate functional space (a pattern observed between 14 to 9, and 6 to 1 Ma). After the extinction event around 9 Ma, the system underwent an increase in functional disparity and richness at the expense of increasing its functional vulnerability (many ecological roles played by just one species), which enhanced the biotic collapse of the Iberian faunas during the Messinian Salinity Crisis. Functional redundancy does not ensure ecosystem resilience over evolutionary time scales.

Might the Postcranial Skeleton Significantly Contribute to Eusuchian Phylogeny?

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It is commonly thought that the crocodyliform skeleton is morphologically conservative throughout its evolutionary history. Thus, postcranial anatomy is usually neglected in many works, and taxonomic descriptions of fossil specimens are usually based exclusively on skulls. Likewise, morphological phylogenetic datasets are strongly biased towards the cranial anatomy, whereas the postcranial skeleton only represents 12.9 – 22.5% of the scored characters. Although eusuchians are mainly restricted to semiaquatic habits, cursorial forms and differences in locomotor patterns have been identified amongst crocodylians, and some studies noted significant morphological differences under the apparent phenotypic conservation of the skeleton. So it is expected that postcranial bones may contribute with their own phylogenetic signal. The effects of the postcranial information in the phylogeny are here tested for the family Allodaposuchidae. This clade is mainly known from some fossil skulls (Late Cretaceous of Europe) and considered basal eusuchians, but few specimens have associated postcranial remains. A set of three consecutive analyses was performed: a first included all species with cranial and postcranial characters; a second, for which all postcranial information was removed for this clade; and a last one added the postcranial information from those specimens with associated skeletal remains, but excluded them as single OTUs. The results show that the basal position is only recovered when the analyses are completely based on cranial characters, whereas the phylogenetic emplacement of allodaposuchids shifts from basal Eusuchia to Crocodylia when postcranial characters are considered, regardless of the addition of new taxa. This suggests that postcranial elements might hide more phylogenetic signal than commonly thought, and phylogenetic hypotheses might change when the postcranium is included in the dataset. Funded by Xunta de Galicia (grant ED481B 2017/027).

Patterns of Vertebral Column Segmentation of the Catfish Genus *Gladioglanis* Ferraris & Mago-Leccia, 1989 (Heptapteridae, Siluriformes)

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Variation in the number of vertebrae within the Neotropical catfish family Heptapteridae is particularly striking, ranging from 35 to 60. Concerning this aspect, the genus *Gladioglanis* is notably interesting because it contains very short-bodied species, such as a new form from the Tapajós River having only 36-37 vertebrae, up to very elongated species, such as a new form from the Madeira River that has 55 vertebrae. *Gladioglanis* is nested within an intermediate zone of the family phylogeny. In order to understand the evolution of the vertebral column segmentation and its implications, comparisons were carried out with the following monophyletic groups of Heptapteridae: 1) the basal clade *Brachyrhamdia* + *Pimelodella*, 2) the *Heptapterus* + new genus clade, and 3) the genus *Phenacorhamdia*, being the two latter positioned as apical lineages of the family. Meristic characters, features related to position of the unpaired fins and morphometric attributes were used as markers to discriminate putative differences. In a first analysis, it is noticed that in the basal clade and *Gladioglanis* all variation occurs in the postdorsal region of the vertebral column, and the size of the adipose and anal fins is totally correlated with segmentation (elongation or shortening) of the vertebral column. Not coincidentally, these are lineages in which the dorsal fin is primitively attached to the back of the head. Moreover, in the apical lineages, which exhibit a dorsal fin unconnected to the head, elongation of the adipose and anal fins occurs largely independently of the segmentation of the vertebral column. This study highlights the need to recognize co-dependent attributes in order to avoid mistaken homology statements, unwanted inflation of cladistic information that can generate spurious topologies, and erroneous interpretations on character evolution. Funding: CAPES, CNPq, FAPESP, FINEP.

Vertebral Morphometry in *Felis catus* in relation to Sex and Skull Shape

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In many vertebrate species, sex and other body characters such as skull shape are related to bone morphology of the whole body. However, in domestic cat (*Felis catus*) such an association is not well established. This study aimed to investigate relationships between vertebrae (cervical=7, thoracic=13 and lumbar=7) morphometrics, sex, and skull shape type in the domestic cat. A total of 70 dry bone samples of cat (*Felis catus*) were evaluated in this study. Bone having pathogenic lesions, or incomplete samples, were excluded. Morphometric measurements were obtained twice using digital vernier calipers, with an interval of one month between the measurements. Variables such as angles were established by digital photography and image software analysis. Statistical analysis was performed using Student Independent samples T-test and logistic regression in R studio. For skull shape estimation, the highest training data accuracy rate was up to 88.89% in C3, followed by L1 (85.41%) and L6 (84.21%), respectively. The lowest accuracy rate (65.78%) was observed in T2 and T13. For sex estimation, the highest training data accuracy rate was up to 80.95% in C3. The lowest accuracy (63.63%) was C1. However, there were 7 bones (T4, T6, T8-11 and T13) that could not be used to establish a prediction equation, as there was no statistical difference between sexes. In conclusion, the data support our hypothesis that sex and skull shape in cat are related to vertebral morphometrics. Moreover, vertebral morphometrics are related more to skull shape than to sex. The C3 showed to be a key vertebral bone for predicting skull shape and sex in the cat.

Skull Allometry and Sexual Dimorphism in *Laticauda colubrina* (Serpentes: Elapidae)

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Sexual dimorphism in size and shape is widespread among squamate reptiles. However, allometric trajectories underlying such differences remain largely unstudied in several lineages. The sea krait *Laticauda colubrina* exhibits a very clear sexual dimorphism in body size, with females being the larger sex. Also, females are reported to have relatively longer and wider heads. Moreover, both sexes differ in their feeding habits. Males tend to prey in shallow water on eels of the family Muraenidae, whereas females prey in deeper water on Congeridae eels. In order to analyze sexual dimorphism in skull size and shape, I measured 61 (27 males and 34 females) cleared and dried skulls. All measurements (29 distances) were log-transformed and subsequently analyzed using Principal Component Analysis (PCA), and the slopes of each of the measurements were regressed (Reduced Major Axis Regression) against the skull length. The slopes were compared between the sexes using ANCOVA. PCA revealed statistically significant differences in the skull shape between the sexes. Further analysis showed that structures associated with feeding performance, i.e., jaws, palatine, pterygoid bones and suspensory elements, scale with positive allometry with skull length in both sexes. Moreover, slopes for these distances differ between sexes (they usually grow faster in females). This is because bigger snakes usually can eat relatively larger prey items. Relative elongation of structures related to gape size (jaws, quadrates and supratemporals) and enhancing prey handling (maxilla and dentaries) may be a morphological response to increasing the prey size and to a dietary shift from muraenid to conger eels in female snakes.

Role of Thyroid Hormones in the Skeletal Development of the African Catfish (Teleostei; Clariidae) *Clarias gariepinus*

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Thyroid hormones (TH) are shown to play a critical role in the skeletal remodeling of fish undergoing metamorphic transformation (e.g., flatfish). In contrast, the role of TH in skeletal development in fish without a pronounced metamorphosis remains rather poorly studied. To evaluate TH participation in fish skeletal development, timing and sequence of appearance of skeletal elements were compared in the developing African catfish (*Clarias gariepinus*), reared under different TH levels. For this aim, development of the cartilage and bone elements of skull, axial skeleton, Weberian apparatus, paired and unpaired fins was described from specimens ranging from newly hatched larvae to juveniles and reared in normal conditions and under artificially induced TH deficiency (110 and 75 specimens, respectively). Changes in the TH-level influence the timing, rate, and sequence of skeletal elements' appearance. In the hypothyroid larvae skull and postcranial skeleton, the differentiation was retarded and prolonged if compared with normal development. The results obtained indicate TH involvement in the mediation of catfish skeletal development and suggest TH-dependence to account for the concentration of skeletal differentiations within a rather narrow ontogenetic interval. The African catfish *C. gariepinus*, as a species with a high commercial fisheries value, is rather well studied. Data summarized from the different studies provide evidence that many developmental events in the digestive, sensory, respiratory, and other systems are accumulated within this ontogenetic interval. Such coordinated changes suggest TH to be a global signal inducing these transformations. However, to prove this, further studies are needed to elucidate a mediating role of TH in the development of different systems alongside those studied here. This work was partially supported by the Russian Foundation for Basic Research, project no. 18-34-0010318.

A Morphological and Histological Investigation of Imperfect Fin Regeneration

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Within the last decades regeneration became an intensive research subject. However, the capacity of living mammals to regenerate is very limited. Among tetrapods, salamanders show unparalleled capacities of tissue regeneration that include replacement of body parts, such as limbs, in a seemingly perfect fashion. Outside of tetrapods, lungfish show regenerative abilities that are comparable to those of salamanders. Outside of Sarcopterygii, fin regeneration was also observed for some actinopterygiians. While great progress has been made in understanding the cellular mechanisms of regeneration on a molecular level, rather few studies have addressed details of the gross morphological and histological features of regenerated body appendages beyond the blastema forming phases. Likewise, very little is known about how fin regeneration may compare to salamander limb regeneration. Further studies with a broad taxonomic sampling including non-model taxa are necessary to untangle similarities and differences between regenerating taxa. Here, we provide a morphological and histological investigation of regenerated fins of lungfish and gar. Data from histological serial sections, 3D-reconstructions, and x-ray microtomography scans of all lungfish families, as well as of the spotted gar, were analyzed to assess capacity, quality and anomalies of fin regeneration. An abundance of anomalies resulting from imperfect regeneration in fins were visible by exterior and interior observations in all species studied. Therein, abnormalities seem to occur frequently in wild fin regeneration, and include fusion of elements, distal branching and more or less skeletal elements. Compared to salamander, this indicates that anomalies are a common phenomenon of appendage regeneration in both Sarcopterygii and Actinopterygii. The similarity of patterns in regeneration anomalies supports the hypothesis that regenerative capacities have an even more ancient origin than previously thought.

Never Enough Monkey Business: Integrative Approach to Callitrichidae's (Mammalia: Primates) Locomotor Evolution

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Callitrichidae are highly arboreal, small-sized South American monkeys. This diversified family (43 species, 23 subspecies) shows clear differences of locomotor behavior between closely-related species that form mixed species groups. Some species are specializing in horizontal branch leaping while others are vertical clinging and leaping specialists. In this context the question of the adaptation to one of these locomotor modes arose. To investigate this question, we opted for a broadly integrative approach – from behavioral level down to the micro-structural level. First, we quantified habitat utilization with a focus on leaping behavior *in natura* and in a zoo with naturalistic enclosures. Currently, locomotor kinematics and reaction forces are measured during leaps both for horizontal small diameter (terminal branch-like) and for larger vertical (trunk-like) supports. These will provide us with a comprehensive and comparative understanding of the Callitrichidae locomotor behaviors and the associated performances, all in a naturally relevant context. A second line of investigation will focus on the locomotor apparatus itself to identify the morphological correlates linked with the observed behaviors. We realized a series of µCT-scans of museum specimens' long bones. A morphometric study will determine the form changes associated with the locomotor specialization. Bone inner structure will be investigated through cross sectional properties alongside the trabecular structure of the epiphyses. Finally, cadavers will be obtained from zoos, iodine-stained, and µCT-scanned to perform digital dissection to study muscle architectural properties such as physiological cross-sectional area, fiber length and pennation angles. This highly integrative approach will give an in-depth understanding of the locomotor evolution of this group, providing elements to evaluate the potential impact of man driven rain forest modifications on theses monkey populations.

Patterns of Shape Integration of Weberian Vertebral Centra and Associated Bones in Piranhas and Pacus (Serrasalmidae)

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Otophysan fishes possess modifications of the anterior vertebrae (v1-v4) and associated elements as part of a Weberian apparatus morphology. The Weberian apparatus involves a chain of ligaments and ossicles associated with v1-v3 that transduce sound pressure induced vibrations of the swim bladder to fluid motion in the ear, which provides indirect sensitivity to sound pressure. Morphology of these vertebrae may be influenced by selection pressures for different functional roles of these bones: linking the cranium to the rest of the vertebral column, supporting the Weberian ossicles, suspending the swim bladder (os suspensorium), and protecting the anterior spinal cord. We examined these features in the otophysan family Serrasalmidae (piranhas and pacus) to test the hypothesis that morphological variation of this region may be associated with integration of these elements. We used 3D-landmark based geometric morphometrics to characterize anterior vertebrae shapes of 20 serrasalmid species. Data were obtained from µCT-scans of 54 specimens. We measured morphological covariation among v1-v4 (v4 plus additional fused skeletal elements: os suspensorium, supraneural, and neural arch of v3), and the Weberian ossicles and cranium (characterized in previous studies). Shape integration among serrasalmids was observed between all vertebrae except v1-v2. However, after accounting for phylogenetic history, shape integration was only evident between v1-v4 and v2-v3. Some vertebra shapes covaried with overall neurocranium shape, otic neurocranium shape, or both. Many vertebra shapes also covaried with Weberian ossicle shape. However, after accounting for phylogenetic history, different covariation patterns were observed among vertebrae and these features. These initial results indicate that variation of Weberian apparatus morphology among serrasalmids is associated with shape covariation of individual elements and some of this covariation does not parallel phylogenetic history.

Biomechanics of the Mandible in Canids: the Functional Consequences of the Variability in Mandible Shape and Jaw Muscle Architecture in Dogs and Red Foxes

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The dog is the morphologically most variable species, as a result of its high phenotypic plasticity and the drastic artificial selection that humans have been practicing since the domestication of the wolf. The diversity of morphotypes is particularly well-illustrated in the head, where the bony reliefs are mainly shaped by the muscles of the masticatory apparatus connecting the skull and the mandible. However, no study to date has explored the functional impact of this variability and high intentional selection. Here, we compare two canid species, one domestic (*Canis familiaris*) and the other commensal (*Vulpes vulpes*). For the red fox, anthropogenic selection pressures are unintentional and are more closely linked to a modification of the ecological niche and of the available resources with respect to human activity. Fifty dogs of various breeds and 50 red fox jaws were dissected to study their jaw muscle (temporal, masseter and pterygoid) architecture and to develop a biomechanical model validated by *in vivo* data. Mandible shape was quantified using geometric morphometrics and the co-variation between muscle architecture, bite force, and mandible shape is explored using 2BPLS approaches. Applying these approaches to archaeological material will make it possible to follow the morphological and functional evolution of these canids over time, depending on their proximity and the nature of their relationship with humans.

Quantifying Shape Complexity in the Carnivoran Baculum

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Genitals are some of the fastest evolving and morphologically complex structures within a given organism. Quantifying their shape complexity is therefore of considerable interest to evolutionary biologists. The baculum (*os penis*) is a mineralized bone within the glans penis of most modern mammals, and is remarkable for its extreme divergence in size, shape and complexity amongst closely-related species. Despite captivating morphologists for over a century, interspecific variation in the baculum shape and its shape complexity has not been rigorously quantified yet. For the first time, we calculate 3D-shape complexity of the carnivoran baculum (n=73) using a novel alpha shapes metric. Specimens were subject to micro-computed tomography and their 'alpha complexity' calculated in MATLAB. Alpha complexities were compared to pre-existing metrics of shape complexity, such as fractal dimension and Dirichlet Normalised Energy (DNE). Bacula were successfully isolated along family-level lines on the basis of alpha complexity. In contrast, the assumptions of fractal analysis were invalidated when applied to bacula. Whilst DNE captures complexity at the level of surface rugosity, alpha complexity is particularly sensitive to features possessing macro-scale concavities such as grooves, fossae and hook-like distal projections. A strong phylogenetic signal characterized alpha complexity in bacula. Ursids and pinnipeds possess bacula with low shape complexity, whilst cats, herpestids and musteloid mustelids seem more complex. Baculum length was positively correlated to normalized testes mass (a common proxy for post-copulatory sexual selection), yet alpha complexity was not. Baculum complexity is related to social system however; socially monogamous carnivores possess more complex bacula than group-living species. Application of new shape analysis tools such as alpha shapes facilitates further testing of functional hypotheses for the role of the baculum.

Effectiveness of Caribou Antlers as Ecological Indicators

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Rangifer tarandus (Woodland Caribou) are of both ecologic and socioeconomic importance to the North. However, given pronounced Arctic climate change, many major Caribou populations in Canada are in decline, including half of the Yukon populations. This study aims to determine whether *Rangifer tarandus* antlers can be used as effective ecological indicators in comparison to other hard tissues such as bone and teeth using stable isotopes of oxygen, carbon, and nitrogen. Variation in the rate and timing of tissue development should create different stable isotopic profiles for each tissue. Antlers are unique in that they grow over a protracted period of time and, for caribou, are present in both males and females. Antlers should therefore reflect the isotopic composition of food and water taken in during the spring and summer of a single year, providing a high-resolution record of ecological conditions. Bones and teeth form and are mineralized over longer periods of time and therefore reflect averages of diet and water intake over months to years. Five males and five females will be chosen from the Canadian Museum of Nature's collection based on geographic location, sex, maturity, and collection date. 10 mg of samples will be taken from the jaw bone, enamel from the third molar, and antler. Three samples will be collected from each antler, one at the base, middle, and tip. We will follow the standard procedures for pretreatment for collagen extraction. We predict that stable N, O, and C ratios will differ among the three tissues. Antler samples will also differ vertically along the antler. This study will help provide a better understanding of the utility of stable isotopic analysis of antler tissues for understanding the ecology of Canadian Caribou. Moving forward, antlers, which are commonly preserved in Pleistocene sediments, can be used to address the ecological changes that characterized their survival through the extinction of 88% of North America's megafauna.

Functional Morphology and Kinematics of the Humboldt Penguin (*Spheniscus humboldti*) Flipper

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Several lineages of birds have independently evolved underwater wing-propelled diving (WPD). Among them, penguins (Spheniscidae) are highly specialized for aquatic locomotion and have entirely lost the ability for aerial flight, using their hydrofoil-shaped wings for underwater propulsion. In this work, we investigated the functional morphology of the flipper musculature via gross dissection and swimming kinematics of the Humboldt penguin (*Spheniscus humboldti*) using marker-less 3D-photogrammetry to capture surface geometries during WPD. This novel approach was chosen as it has the advantage of being self-calibrating based on the separation of the cameras and will work automatically with unmarked animals. Swimming Humboldt penguins were filmed at Chester Zoo using four synchronized video cameras to generate 3D-reconstructions of a range of diving modes and velocities. By analyzing the acceleration of the penguin bodies during underwater flight we measured values for whole-body drag and lift coefficients that are comparable to those of different species of penguins. Similarly, thrust is generated over the whole wing-stroke cycle in contrast to flying birds. Our study presents the first quantitative analysis of flipper myology and swimming kinematics of *S. humboldti* in 3D for a variety of diving styles, allowing us to link the underlying biomechanics of the penguin flipper with locomotion performance. Our results will enable us to create advanced computational fluid dynamics simulations of swimming penguins to explore the detailed physics behind their adept maneuvers.

Decoupling of Disparity and Rates in Evolutionary Radiations: Paleozoic Herbivorous Tetrapods Show Increased Dental Diversity but Reduced Rates of Character Change

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The origin of herbivory in tetrapods was a crucial event in the establishment of terrestrial vertebrate ecosystems. By allowing access to the vast resource represented by plants, it led to considerable changes in patterns of trophic interactions on land. By the end of the Permian, herbivory had evolved at least eight times independently. These early radiations represent ideal case studies of a core macroevolutionary theory, the adaptive radiation: increased rates of morphological diversification when evolutionary lineages exploit ecological opportunities or underexploited resources, leading to increased morphological diversity. We analyze the macroevolutionary effects of the origins of amniote herbivory by examining patterns of dental disparity, rates of evolution, and patterns of character saturation among early amniotes. Our study spans from the Carboniferous origin of amniotes until the Early Triassic, incorporating a matrix of discrete dental characters and a supertree of 440 taxa time-scaled using the fossilized-birth-death process. Herbivores had similar rates of dental evolution to those of carnivores, even during their evolutionary origins in the Carboniferous and earliest Permian. Middle–late Permian herbivores have notably lower rates of dental evolution. Nevertheless, herbivores have consistently higher disparity than carnivores (excluding Triassic marine taxa). This results from apparently greater constraints on dental evolution in carnivores, indicated by more rapid exhaustion of morphological character states in carnivores than in herbivores. We suggest that the origin of herbivory may be characterized as an ecological release resulting in highly disparate dental tools among groups. Although herbivores have explored an expanded trait space, this exploration did not occur significantly faster than that of carnivores. These analyses highlight the importance of herbivory in driving eco-morphological diversification in terrestrial ecosystems.

Learning to Breathe: Ventilation Mechanics in Archosaurs and Evolutionary Robotics

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Archosaurs – including birds, crocodilians, dinosaurs and pterosaurs - are a highly successful clade of tetrapod vertebrates. Throughout their history they have evolved a range of diverse respiratory and metabolic strategies, and so they provide an excellent opportunity to study the functional evolution of the respiratory system. However, reconstructing the evolution of breathing requires integration of anatomical, kinematic and physiological data. Here, we use computer simulations to combine these multiple data units into multi-body dynamics musculoskeletal models. Such models use evolutionary robotics optimization approaches to estimate muscle activation patterns and predict ventilatory movements. They also calculate changes in volume and pressure in the respiratory system and – for the first time in a simulation study – the energetic cost of breathing. First, we constructed a model of a wild turkey (*Meleagris gallopavo*), based on data from CT-scans and dissections, together with literature surveys. The predicted muscle activations and skeletal kinematics output by the model were validated with *in vivo* data from electromyography and XROMM (X-ray reconstruction of moving morphology). Estimates for cost of ventilation from our simulation data were broadly in-line with the limited experimental information that exists. Subsequently, we modified the initial model to reflect morphologies seen in the fossil record of early birds (e.g., by removing the sternal keel). This approach allowed testing how evolutionary transformations of the ribcage and sternum associated with flight have affected breathing mechanics. A keeled sternum increased the cost of breathing, but other features, such as uncinate processes, lowered it and acted as compensatory mechanisms. In the future, we intend to extend this approach to other extant birds, as well as to non-avian dinosaurs and other fossil archosaurs.

Evolutionary Morphology of Osteoderms in Squamates

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Osteoderms - bony elements embedded in the dermal layer of the skin - constitute an intriguing component of the tetrapod integumentary skeleton. The expression of osteoderms, albeit a common occurrence in extinct lineages, is remarkably rare among modern taxa and restricted to crocodiles, turtles, lizards, armadillos and a dozen species of frogs. Much of our current knowledge on osteoderm form and function is therefore based entirely on fossil evidence, with few studies using extant taxa to unravel the structurally and functionally enigmatic nature of these bony elements. Squamates provide a unique opportunity to address some of these issues given the vast amount of interspecific variation in osteoderm morphology. In this study, we use high-resolution x-ray microtomography to provide more insight into the evolutionary morphology of osteoderms in squamates, focusing particularly on two of the most variable clades: cordyline and anguimorph lizards. Detailed information on the structural organization and microarchitecture (e.g., vascularization), as well as the mineral composition (i.e., presence of the enamel-like tissue, osteodermine), allows us to make predictions on the evolution of osteoderms in squamates. More specifically, we address how progressive evolutionary development might have shaped the current diversity of osteoderms in squamates. CB is funded by the FWO-Flanders (projects 12V0518N & 1514119N).

A Well Preserved Symmoriiform (Chondrichthyes) Cranium from the Fayetteville Shale of Arkansas, USA (Upper Mississippian, Middle Chesterian)

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Fossilized cartilage is rare, but three-dimensionally preserved cartilage is even scarcer. The Fayetteville Shale of northwestern Arkansas (USA) has yielded numerous well-preserved fossil chondrichthyans over the last several decades, due to a depositional environment that preferentially preserves cartilage instead of bone or shell. One such fossil is a three-dimensional, mostly complete cranium of a symmoriiform chondrichthyan, revealed by computed tomography (CT) scanning. This cranium is preserved alongside fragmentary branchial elements, putative mandibular fragments, and what appear to be head denticles. The endocast can also be reconstructed from the CT-scan, including three-dimensionally preserved skeletal labyrinths of the inner ears. The inner ear has a clear crus commune, and there is no chondrified median capsular wall, so the labyrinth is confluent with the cranial cavity (as is the case in *Cobelodus* and most early chondrichthyans). The morphology of this ear is interesting in light of current discussions regarding the relationship between holocephalans and symmoriiforms (holocephalans do not have the same specializations for low-frequency sound detection that are present in the inner ears of elasmobranchs, such as a separate posterior semicircular canal). This specimen adds another symmoriiform to the diversity described from the Fayetteville Shale assemblage, in addition to *Ozarcus* and *Cobelodus*.

The Early Evolution of Vestibular Morphology in Archosauria

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During the first stages of the Triassic (ca. 245 Ma), Archosauria diverged into two major lineages, that including crocodilians and the one that includes birds. Compared to their disparate living members, earlier members of these lineages shared many traits, but nevertheless span a wide range of ecologies and document important shifts in locomotor style, from primitive sprawling to crocodilian-like semi-erect and bird-like erect limb orientations, and to flight in pterosaurs. To chronicle the divergence of these groups, we focused on the labyrinth given that the living members of these lineages have highly disparate anatomies. The bony labyrinth, within the braincase, is part of sensory systems associated with balance coordination and gaze stabilization during locomotion. Hence, its morphology potentially provides a wealth of ecological information for extinct taxa. We compiled a dataset of reconstructed 3D-models of the endosseous labyrinths of 27 extinct archosauromorphs (Early Triassic – Early Cretaceous; 252 – 112 Ma) accessed via microcomputed tomography of the braincase. Variation was analyzed by applying geometric morphometrics methods to 3D-virtual models. The results of a principal component analysis show small overlap between the morphospace associated to labyrinth morphology of Triassic pseudosuchians (crocodile-line) and avemetatarsalians (bird-line). These data suggest that differences in labyrinth morphology between the lineages were already present at their divergence, and the separation was maintained through time. Overall, avemetatarsalians have generally higher than wider labyrinths, matching the proportions of the occipital region of their skull. On the other hand, pseudosuchians generally have labyrinths with an inverse relation between height and width, also mostly matching the architecture of their skull. The differences in labyrinth morphology seem thus related to skull structure of the animals rather than to aspects of their ecology.

The Early Evolution of the Tympanic Hearing in Sauria: Do Different Osteological Correlates Indicate Independent Origins in Lepidosauromorpha and Archosauromorpha?

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The current view on the evolution of the tympanic hearing in Amniota recognizes at least two independent origins, one in Synapsida and one in Diapsida. Recent studies have also suggested that it appeared independently in the two major lineages within Sauria, Lepidosauromorpha (the 'lizard-snakes-tuatara line') and Archosauromorpha (the 'crocodile-bird line'). To assess this hypothesis, we employed maximum-likelihood estimates across alternative phylogenetic scenarios for Sauria, including extinct taxa, in order to infer the ancestral condition for the group, i.e., presence/absence of a tympanic membrane. The analysis of different topologies evaluates the impact of ambiguous position of a series of early taxa. Presence of a tympanic membrane in extinct taxa was inferred based on the presence of two reliable osteological correlates, the periotic fossa for archosauromorphs and the tympanic crest for lepidosauromorphs. The likelihood that the presence of a tympanic membrane corresponds to the ancestral condition of Sauria varied between 0.58 to 0.94 among the phylogenetic scenarios tested. Nevertheless, if the tympanic hearing has indeed a single origin within Sauria, differences in the morphology of the osteological correlates of the membrane observed between lepidosauromorphs and archosauromorphs might indicate that variances in the otic region accumulated rapidly, still during the early stages of the evolutionary history of each lineage. For instance, earliest lepidosauromorphs such as *Sophineta cracoviensis* (c. 250 Ma) already exhibit a tympanic crest, whereas the periotic fossa is also seen in the earliest archosauromorphs, such as *Howesia browni* (c. 246 Ma). However, a putative homology between the tympanic crest of lepidosauromorphs and the periotic fossa of archosauromorphs has not been established, and thus represents a key aspect to elucidate the early evolution of the tympanic hearing in Sauria.

Ecomorphological Approach to Study Limb Bone Adaptations

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Locomotion type and ecological pattern determine limb bone shape which adapts to the prevailing loads. The aim of our study was to investigate this correlation. We studied 22 mammalian species from different orders (Monotremata, Didelphimorphia, Diprotodontia, Insectivora, Carnivora, Artiodactyla, Primates, Rodentia, Lagomorpha). Species were divided into nominal groups according to systematic and ecological principles: running (7 ungulates, 1 lagomorph, 1 marsupial), swimming (2 rodents), carnivorous (4 species), primates (2 species), and non-defined (1 monotreme, 1 marsupial, 2 insectivores, 1 rodent). Ten linear and cross-sectional geometric parameters of the stylopodium bones were obtained. Principal component analysis was applied. All absolute bone parameters corresponded to PC1 (especially cortical area). Cross-sectional index and ratio of second moments of area corresponded to PC2. Some specialized well-diving swimmers (beaver), less derived forms (echidna, opossums), and some larger ungulates have maximal positive distortion of the sectional ratios (thus, they are relatively increased). A relative decrease of sectional ratios was shown for some primates (more terrestrial species), some rodents (digging marmots) and most of the specialized runners (including lagomorphs, kangaroo), so the diaphyses of all of them are more thin-walled and rounded. On the other hand, absolute parameters in ungulates tend to increase. As an exception, lagomorph and kangaroo humeral ratios tend to increase according to different locomotor roles of their fore- and hind-limbs. Also, carnivorous species have different ratio distributions of the humerus and femur. Their femoral ratios resemble each other more closely between species, so they are more monotypic. Humeral ratios indicate the relative diaphyseal thinness and roundness for bears and the opposite for cats. Thus ecomorphological bone adaptations may be shown by the variation of section ratios relative to all the other parameters.

Evolution of Fore limb Size and Shape in Nonavian Theropod Dinosaurs

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Nonavian theropod dinosaurs represent a taxonomically large and ecologically and morphologically diverse clade of bipedal tetrapods in which the fore limb did not have a primary locomotory role. This apparent lack of constraint has resulted in negative allometric scaling of the forelimb being invoked as the primary driving force behind the variation of fore limb size within the clade, particularly when considering fore limb reduction of tyrannosaurs and elongation of the fore limb along the avian lineage. This study used geometric morphometrics, phylogenetic regressions, and stepwise Ornstein-Uhlenbeck modeling to investigate large-scale trends in fore limb size and shape evolution across the clade. We found no single allometric trend that characterizes fore limb size among nonavian theropods. Additionally, the size of individual fore limb elements does not show a simple correlation with their shape. Smaller fore limb elements occupy an almost exclusively gracile morphospace, whereas larger elements show much broader variation in morphology from very gracile to very robust. Abelisauridae, Tyrannosauridae, and Alvarezsauridae all exhibit convergence in relative forelimb length for extreme fore limb reduction, but stem members of these lineages are characterized by fore limb ratios that fall within the basal regime as classified by the model. So-called "short-armed" dromaeosaurid species were not identified as converging on either of these reduced fore limb ratios, but instead are consistent with the regime that characterizes the stem of Maniraptora. Although derived dromaeosaurids and troodontids both exhibit lengthening forelimb ratios, these regimes were not identified as convergent and troodontids possess a higher optimum value. Taken together, these studies indicate that fore limb evolution in nonavian theropods was complex and that biomechanical, developmental, or functional constraints were important in influencing fore limb proportions in most members of this clade.

3D-Cranial Morphospace and Modularity in Extant Crocodylia: a Preliminary Study

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Modern day crocodiles, which include ghavials (Gavialidae), alligators and caimans (Alligatoridae), and true crocodiles (Crocodylidae), are the only descendants of the diverse Crocodylomorpha, which exist since the Late Triassic. During their long evolutionary history, crocodylomorphs radiated into terrestrial, freshwater, and marine environments on multiple occasions, each time adapting to the constraints enforced by these different environmental conditions. These fossil crocodylomorphs therefore also display a great morphological diversity. In contrast to that, extant crocodylians, which count only 27 species, are not as diverse. Tools such as geometric morphometrics and concepts such as modularity and integration provide a way to investigate how cranial shape evolved through time. The present work focuses on recent Crocodylia and explores their 3D-cranial morphospace, as this has never been approached for the complete group. Patterns of modularity and integration are also investigated. This study is preliminary to the examination of the morphological evolution, namely the disparity, modularity and integration patterns of the cranium in the entire clade Crocodylomorpha.

Stags of the Sea? Comparisons of Territoriality and Cranial Weapon Morphology in the Fish Subfamily Oligocottinae (Pisces: Cottoidea)

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Many vertebrate groups have weaponized their skulls, and mammalian horns have attracted the lion's share of attention from evolutionary biologists. Though some cranial weaponry aids defense, intraspecific combat appears to drive the evolution of these structures in most terrestrial cases, such as in Cervidae or Bovidae. Equally impressive weaponry adorns aquatic vertebrates, such as the sculpins in superfamily Cottoidea. The skulls of these diverse fishes bear antler-like preopercular spines of remarkable variation, and the males of many species defend nesting sites during the breeding season. Does the intensity of territoriality predict the extent of skull weaponization? We tested for differences in spine shape and sexual dimorphism among guarding and non-guarding species in the sculpin subfamily Oligocottinae, by quantifying spine shape with 3D-geometric morphometric techniques applied to reconstructions from microCT-scans of males and females of each species. Multivariate analysis of variance (MANOVA) tested for sexual dimorphism of spine shape and compared the degree of dimorphism for guarding *vs* non-guarding species. In addition, we compared the mean shape of spines of guarding and non-guarding species using phylogenetic MANOVA. Nest-guarding species show greater sexual dimorphism in spine shape, with males possessing more robust spines that project further from the head of the fish. This suggests that males in nest-guarding species use their preopercular spines for additional or different purposes than do conspecific females. We conclude that, as in many terrestrial vertebrates, the need to establish and defend territories promotes the evolution and augmentation of cranial weapons beneath the waves.

Ecomorphology of Papuan Microhylid Frogs: Performance, Hindlimb Musculature, and MicroCT

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The microhylid frogs of New Guinea and its satellite islands form a large monophyletic clade of over 300 species with tremendous ecological and morphological diversity. These frogs have long been hypothesized to be part of an adaptive radiation with specializations suggested for burrowing, terrestrial, semi-aquatic, arboreal, and scansorial lifestyles. We conducted a comparative phylogenetic analysis of ecology, morphology, and performance in 24 species based on field-collected data. Here, we present a comparative analysis of skeletal features using microCT and a detailed morphological analysis for a jumping and swimming specialist to understand their design features. We characterized the hind limb musculature including the major extensors and flexors at the hip, knee, and ankle joints and modeled hind limb forces. Analysis of skeletal morphology using microCT revealed that while characteristics of the femur are highly conserved, there is clear variation in the length and shape of the tibiofibula and pelvis. We interpret these results in relation to specializations for jumping and swimming locomotor modes. We gratefully acknowledge funding support from NSF IOB-1145733.

Origins of Craniofacial Diversity in New World Leaf-Nosed Bats at the Developmental, Cellular and Genetic level

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The New World Leaf-Nosed bats perform ecologically important functions associated with diverse craniofacial morphology. In this study, we quantify how craniofacial morphology is changed during development within a species and how it is changed during evolution between species. Shape data is obtained by imaging the head with micro-computed tomography and geometric morphometrics. We then quantify and compare cranial neural crest cell (cNCC) dynamics and spatiotemporal gene expression during midfacial morphogenesis between species. A key signaling pathway related to cNCC dynamics, bone morphogenetic protein (BMP), correlated with altered cartilage growth. Changes in BMP protein level in bat facial variation were functionally evaluated with tissue-specific conditional mouse lines. Specifically, bat gene expression was experimentally replicated in the mouse embryo cNCC and the subsequent phenotype mimicked species patterns. The results provide a platform for a focused comparative study on the genetic processes that generate biological diversity.

Morphology of the Gonoduct of the Viviparous Teleost *Heterandria formosa* (Actinopterygii: Poeciliidae)

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Female teleosts do not have oviducts because Müllerian ducts do not develop, consequently, the caudal zone of the ovary, called gonoduct, connects to the exterior. Then, the structure of the ovary is formed by two zones: germinal and gonoduct. In the germinal zone oogenesis occurs and, in viviparous species, also the gestation takes place. The gonoduct lacks germinal cells and separates the germinal zone from the exterior. The goal of this study is to describe the morphology of the gonoduct in the fish *Heterandria formosa*. The structure of the gonoduct, from the exterior to the germinal zone includes three regions: 1) a wide region with large and thick folds, like a cervix; 2) a narrow region with short folds where abundant spermatozoa are seen with the heads towards the epithelial cells; 3) a short region with the lumen more open, communicating to the germinal zone of the ovary. The three regions contain abundant macrophages, lymphocytes, eosinophils and melanocytes in the lumen; some of these cells form melano-macrophage centers, contain abundant blood vessels and secretory activity. These structural elements of the gonoduct indicate its main functions: protecting the germinal zone, where embryos may be in gestation, from the exterior, and the relationship with the reception of spermatozoa during insemination and their storage, providing a good condition for their preservation.

Morphological Adaptations of *Scincus scincus* and *Eumeces schneideri* (Lepidosauria, Scincidae) to Sandy Terrestrial Substrates

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Sandy deserts cover a large part of our planet. Numerous species have colonized these ecological niches by living in or under sandy substrates. A large number of morphological adaptations have appeared to sustain life and locomotion in or under the surface of sandy substrates. Organisms living under the sand face two major constraints caused by this material, the abrasion and the low oxygen level. Among those species are the Scincidae (Lepidosauria) *Scincus scincus* and *Eumeces schneideri*. These two psammophilic species have been investigated by histological and immunohistochemical techniques, and also by scanning electron microscopy. Results allowed us to describe two major systems of these organisms: the integument and the muscular system. For the first one, three parameters were considered, the pattern of scale surface, the thickness of the integument and the cellular turnover of the epidermal cells. For the second one, the surface and the proportion between the fast glycolytic, the intermediate oxidative glycolytic and the slow oxidative muscle fibers were determined. Briefly, data suggest that the pattern of *S. scincus* scales was smoother, the integument was thinner, and the proliferating epidermal level was lower, when all of these parameters were compared to *E. schneideri*. The total surface of intermediate fibers was larger for *S. scincus* and smaller for slow fibers, compared to *E. schneideri*. The cross sectional areas of intermediate and slow fibers were smaller for *S. scincus*. More detailed analysis splitting the data between ventral and dorsal fibers on the one hand, and between body and tail fibers on the other hand, highlighted the fact that the cross sectional area of ventral slow fibers was smaller for *S. scincus* and that *E. schneideri* had more slow fibres at the tail level. These results are discussed according to the multiple selective pressures encountered by both psammophilic species living in the sandy dunes of hot deserts.

Skeletal Distribution of Medullary Bone in Neornithes - Implications for the Identification of Reproductive Tissues in Extinct Avemetatarsalia

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To date, the skeletal distribution of medullary bone (MB), a sex-specific tissue formed by female birds during lay, has been poorly documented in wild birds. Studies investigating MB structure, composition, and metabolism, have focused almost exclusively on long limb bones, spurring the common misconception that its deposition is concentrated within these skeletal elements. The present work i) constitutes the first comprehensive investigation of MB skeletal distribution across Neornithes, using micro-computed tomography and histochemical data, ii) revisits previous hypotheses pertaining to MB distribution patterns, and iii) provides new criteria for identifying purported MB-like tissues in extinct Avemetatarsalia. We document that the skeletal distribution of MB varies interspecifically, but does not differ between captive and wild-caught individuals. We find MB is a systemic tissue that can be deposited within virtually all skeletal regions, including cranial elements, and note that it is uniformly present in the proximal tibiotarsus of all studied specimens. Moreover, our results confirm previous hypotheses that skeletal distribution of MB is directly related to the distribution of red bone marrow, and inversely correlated to the combined skeletal distributions of pneumaticity and yellow bone marrow. The extent of skeletal distribution of pneumaticity is linked to the body size and lifestyle habits of bird species. Hence we find that small-bodied and diving birds possess widespread deposition of MB, whereas MB distribution is highly restricted in large-bodied or efficient flyers. The proposed homology of the pulmonary system between living birds and some non-avian dinosaurs permits us to derive a series of location-based predictions that can be used to critically evaluate purported MB-like tissues in fossil specimens.

Do Female Penguins Deposit Medullary Bone?

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Medullary bone (MB) is an ephemeral tissue, unique to female birds and used as a reservoir of calcium to form the eggshell. Until recently, its phylogenetic extent across Neornithes was largely unknown. New studies revealed that MB is relatively widespread among modern birds, yet it is still unclear whether it is ubiquitously used by female birds to produce the mineralized eggshell. MB has not yet been unambiguously reported in Spheniscidae, which are of particular interest to assess this question. The dense microstructure of penguin bones does not leave many voids for the deposition of MB. Moreover, the clutch size of all penguins is small (1-2 eggs) and species laying two eggs have relatively long laying intervals. Their momentary calcium requirement to form the eggshell is thus probably lower than in most other birds. Finally, adult penguins often exhibit cortices formed of a dense Haversian system, testifying of high bone remodeling and mineral homeostasis. From these observations, we hypothesize that female penguins could resort in part or exclusively to the calcium contained in their thick bone cortices, without having to form large amounts of MB during egg-laying (H1). Our study investigates the bone histochemistry of penguin females that died during the egg-laying cycle, in order to test H1, assess whether different penguin species resort to different sources of calcium (MB *vs* cortical bone) to form the eggshell, and improve our understanding of MB phylogenetic distribution in Neornithes. Preliminary results support H1. *Pygoscelis adaliae* UAM 10951 died with an unshelled egg in its oviduct. Micro-computed tomography (μCT) shows extensive resorption cavities throughout the hindlimb cortices, yet no signs of MB deposition. Histochemical analyses and μCT data reveal that *Spheniscus magellanicus* KU 81495 has resorption cavities in the deep cortex and only trace amounts of MB-like tissue in the marrow cavity of its femur and tibiotarsus.

Ribs All the Way Down: 3D-Rib Kinematics during Lung Ventilation in *Boa constrictor* (Reptilia: Serpentes), Comparison with Three Non-Serpentine Squamates, and Implications for Evolutionary Convergence

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Similar to other squamates, snakes use motion of their ribs to ventilate their lungs. Each rib can rotate about three axes: a dorsoventral axis (bucket handle), a craniocaudal axis (caliper), and a mediolateral axis (pump handle). However, while most squamates ventilate with vertebral and sternal ribs, snakes lack sternal ribs and use only unipartite vertebral ribs. This study aimed to quantify rib rotations of *Boa constrictor* during ventilation and compare their kinematics and muscular morphology to three previously studied squamates, *Iguana iguana*, *Varanus exanthematicus*, and *Salvator merianae*. We implanted radio-opaque markers into the ribs and vertebrae of three *B. constrictor*, and measured rib rotations during ventilation with marker-based XROMM. We found that *B. constrictor* use primarily bucket handle rotations, moderate caliper rotations, and substantial pump handle rotations, with bucket and pump consistently opposite in polarity. These patterns were almost identical to *V. exanthematicus* and opposite to those of *I. iguana* and *S. merianae*. We compared relative contribution of each axis to overall rib rotation with linear mixed effects modeling, and found no significant difference between *B. constrictor* and *V. exanthematicus*, but significant differences between *B. constrictor* and the two other species. Interestingly, *V. exanthematicus* is the only non-serpentine species to actively ventilate with unipartite floating ribs, ribs anatomically similar to *B. constrictor*. Moreover, *B. constrictor* and *V. exanthematicus* have convergently evolved costal muscles that run anteriorly from each rib to either an anterior vertebra or muscle bundle. Combined with recent phylogenies, our findings suggest that these morphologies and kinematic patterns evolved convergently, and that similar musculature may enable similar motions of floating ribs in both species.

Temporal and Biogeographic Patterns of Morphological Disparity in an Ancient Lineage of Teleost Fishes (Teleostei: Osteoglossomorpha)

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Osteoglossomorphs (commonly known as bonytongues) are one of the earliest diverging lineages of crown teleost fishes, dating back to at least the Middle–Late Jurassic. Although containing relatively few species and restricted to freshwater environments, they display a stunning variety of body forms, from the knife-shaped notopterids and the eel-like aba to the gigantic arapaima. There are more known extinct osteoglossomorph genera than living ones, and well-preserved fossils reveal patterns of body shape diversity over 150 million years. Shape data for over 100 extant and fossil osteoglossomorphs was analyzed in a geometric morphometric framework to characterize how morphological diversity within this group changed through time and how it is partitioned geographically and taxonomically. Most of the observed morphological variation pertains to the relative length and position of anal and dorsal fins and, to a lesser extent, to body depth and elongation. Despite the high taxonomic diversity of Cretaceous osteoglossomorphs from East Asia and North America (around 30 genera known), these occupy a small portion of the morphospace compared to modern taxa. Two extant subclades strikingly depart from Cretaceous fossil forms and other extant taxa: the African and Indo-Malayan Notopteridae, characterized by an extremely long anal fin and short (or absent) dorsal fin; and the African Mormyroidea, including the disparate elephantfishes and the aba. Remarkably, early Paleogene fossil osteoglossomorphs that diversified in marine environments are within the range of body shape morphologies defined by freshwater taxa and occupy a relatively small portion of the morphospace, despite displaying a broad variety of cranial adaptations presumably related to different feeding ecologies. This study highlights how an integrative approach merging paleontological and neontologic data can help illuminate spatio-temporal patterns of morphological disparity in a long-lived vertebrate clade.

Phylogenetic Implications of Evolutionary Transformations in the Appendicular Skeleton of the Highly Diverse Superorder Elopomorpha

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The superorder Elopomorpha is a highly diverse group of fishes that constitutes one of the main living lineages of Teleostei and comprises the orders Elopiformes, Albuliformes, Notacanthiformes, Anguilliformes and Saccopharyngiformes, encompassing 25 families and about 1040 species. This taxon is currently recognized as monophyletic, having as its most notorious synapomorphy the presence of a leptocephalus larva. Elopomorphs have considerable variation in body shape and several aspects of their biology. The Elopiformes, which occupy a basal position within the Elopomorpha, retain many primitive teleost features and a somewhat conserved body morphology, including that of the appendicular skeleton. For instance, members of this group retain the dermal pectoral girdle connected to the back of the skull, a mesocoracoid on the chondral pectoral girdle, postcleithra and posttemporal bones on the dermal pectoral girdle and fully formed pelvic girdle and fins. The Notacanthiformes have a relatively elongate body and retain pelvic girdle and fins, but lack some elements of the pectoral skeleton, such as mesocoracoid and postcleithra. The true eels (Anguilliformes) and the Saccopharyngiformes are further derived, having a long, cylindrical body lacking pelvic fins and, in some species, additional supporting elements of the pectoral skeleton. The reductions of the pectoral skeleton range from loss of the ossifications of the scapulocoracoid cartilage (e.g., scapula, coracoid) and proximal and distal radials, to complete loss of all supporting skeletal elements of the pectoral fins, including eventually the pectoral-fin rays. This wide morphological body variation in Elopomorpha turns this group an ideal model to study variations in the appendicular skeleton. Accordingly, evolutionary transformations in the appendicular skeleton along the phylogeny of elopomorphs are portrayed based on 152 species analyzed, encompassing 22 families.

Connecting the Embryo: Anatomical Network Analysis of the Skeletal Development of the Altricial Monk Parakeet (Aves: Psittaciformes)

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We used for the first time the powerful quantitative tool AnNA to provide new insights on the sequence of bone to bone connection, loss, and fusion events leading to the adult skeletal organization during the development of a bird. Connections (physical junctions) of the bones (nodes) of the skeleton of 36 specimens of the altricial monk parakeet *Myiopsitta monuchus* were documented through the ontogenetic trajectory, from embryonic stage 34 to adult. Besides node and whole-network parameters, we also assessed changes in modularity and complexity during ontogeny. Results showed that: (1) during development, 31 of a total of 163 bones lose independence due to fusions (reduction of nodes), the majority in the skull between day 22 after hatching (AH) and adult, (2) 12% of the total connections (338 in adult) are present prior to hatching (of some bones of the skull, mandible and metatarsals), (3) the largest increase in connections is between days 15 and 18 AH, (4) the skull connects with the column at day six AH, (5) vertebral connections do not follow a distinguished pattern, (6) girdles connect to the column AH, (7) the pelvic girdle connects with the column earlier than the pectoral girdle, and (8) pelvic girdle and hind limb connections begin and ends before those of the pectoral girdle and the forelimbs. These connectivity patterns match well with the known skeletogenesis process in this species. Particularly, connections of the girdles could be linked to the altriciality due to requirements for active movement in the use of the hind limbs inside the nest, but not the need to use forelimbs to fly until much later. DRG funded by grant BFU2015-70927-R. CPT funded by grant PICT2330.

Optical Properties, Ecological Differences, and Virtual Ophthalmoscopy: Morphometry of Optical Parameters in Diapsids and a Case Study in Restoring Visual Fields in Terror Birds (Aves: Phorusrhacidae)

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Visual fields provide inroads to quantitatively study selection pressures at the intersection of anatomy, ecology, and optics. The visual fields and optical properties of living vertebrates are commonly studied using ophthalmoscopy, which cannot be applied to extinct species. A literature search was performed to collate optical data—radius of curvature, refractive index, and visual fields—across diapsids, supplemented by new data collected from diceCT, spiceCT, and other microCT-datasets of an additional 30 diapsids. Significant correlations were recovered between radii of curvature and orbit and scleral-ring dimensions, as well as between the orientations of optic axis and orbit—thus, these bony metrics constitute osteological correlates for the quantitative optical traits. An intriguing case-study for reconstructing the visual abilities of an extinct species is *Llallawavis scagliai*, an exceptionally well-preserved phorusrhacid that preserves scleral rings and exemplifies the uniquely narrow bill morphology typical of phorusrhacids. Here, we present estimates of eye size and shape for *L. scagliai*, and we make quantitative predictions of the optical properties and performance of its visual system. Phylogenetically-informed regression equations for eyeball and lens dimensions for *L. scagliai* were calculated, and an eyeball was virtually modeled and optically tested using Virtual Ophthalmoscopy (VO), our recently-validated modeling technique for estimating visual properties of extinct species. When its eyes were converged, *L. scagliai* would have had a binocular field of view between 18° and 38° wide. In addition, the tip of the bird's bill would have fallen squarely within this binocular field, consistent with an animal that was using its beak to acquire food, a key perceptual challenge for birds. Funding: NSF IOS-1050154, 1456503 to LMW; Jurassic Foundation grant to DGC.

The Osteological Data of the Neck Region in Dibamids, with a Comment on the First Possible Fossil Record of this Clade

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The atlas-axis complex plays an important role in locomotion of limbless, fossorial squamates. We present a study of the atlas-axis complex in selected members of the peculiar and enigmatic clade Dibamidae, a family of poorly-known fossorial squamates that are distributed in tropical or subtropical climates. The clade contains only two taxa - *Dibamus* and *Anelytropsis*, with a disjunct, trans-Pacific distribution. Members of the genus *Dibamus* occur in tropical Southeast Asia, whereas *Anelytropsis* is distributed in northeastern Mexico. The atlas-axis complex of members of this clade is characterized by several important features, such as the complete absence of the first intercentrum or the appearance of the first free cervical rib on the axis. Moreover, our study shows morphological differences of this skeletal bridge in *Anelytropsis* relative to those of *Dibamus*. With respect to the taxonomy and phylogenetic topology of the Dibamidae within Squamata, a huge conflict exists between phylogenetic trees obtained from morphology-based and molecule-based analyses. The morphology of the atlas-axis complex is therefore compared with several potential sister clades - dibamids share several features with limbless Gekkota, Scincoidea or Amphisbaenia. However, some of these characters may be the result of a limbless, burrowing ecology and thus could represent homoplastic characters. The atlas-axis in dibamids shares most character states with fossorial skinks. This conclusion is consistent with the results of most morphological observations rather than supporting molecular tree topologies. According to molecular analyses, dibamids are an early-diverging group within the Squamata, sister to all other clades either alone or with Gekkota. The stem clade is estimated to have originated in the Mesozoic, but their fossil record was completely unknown. We here present the material of the first potential dibamid from the early Oligocene of Mongolia.

Teeth in Axolotl Arise from a Common Odontogenic Primordium at the Ectoderm-Endoderm Border

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Teeth of extant vertebrates embryonically arise from a zone of odontogenic competence. This zone becomes progressively compartmentalized to give rise to individual tooth germs and, eventually, to a patterned dentition. We analyzed initiation and establishment of dentition in the Mexican axolotl, where teeth are assembled into several tooth fields constituting outer and inner dental arcades. By studying expression patterns of several odontogenic genes, we show that establishment of axolotl tooth fields and their subsequent arrangement into dental arcades occur via splitting of the initially compact zone of odontogenic competence into discrete tooth-competent regions. The pattern of addition of tooth germs varies among the individual tooth fields and seems to be determined by the shape of the respective tooth-competent region and the position of the initiator tooth. These characteristics then define, whether teeth will be assembled into a single row or into a tooth patch. Interestingly, our fate-mapping analysis shows that positions of initiator-teeth correlate with presence of ectoderm-endoderm border in the mouth in case of three out of five tooth fields. This correlation suggests that the ectoderm-endoderm border may have a role in the factual initiation of the axolotl dentition.

The Barb Itself: A Review on an Highly Plastic Weapon, the Causal Barb in Stingrays

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In animals, mechanical defenses can take various shapes, from the protective plates of the armadillo, the venomous spurs of the male platypus, and the quills of the porcupine. Stingrays choose an aggressive way to defend themselves with a whip-like motion of the tail, which drive a serrated spine, named barb, into predators. Barbs are highly-modified dermal denticles that vary considerably in shape from the tip to the base, and also in terms of serrations shape and number. We used microCT-scanning to visualize fine-scale barb morphology across 98 species of stingrays, representing around 30% of total taxon diversity, including freshwater potamotrygonids (*Potamotrygon*, *Plesiotrygon*), tropical dasyatid whiprays (*Dasyatis*, *Neotrygon*, *Fluvitrygon*), mollusk-crushing myliobatids (*Myliobatis*, *Rhinoptera*), New and Old World round rays (*Urotrygonidae*, *Urotrygon*, *Urobatis*, *Urolophidae*), and butterfly rays (*Gymnura*). We then examined the evolution and morphological disparity of barb shape across a time-calibrated molecular phylogeny for all stingrays. We found that barb shape is highly variable, in particular the serrated length of the barb, length of the barb base, and overall number of serrations. Variability is also evident in barb cross-sectional shape, which varies from a flattened blade (*Urotrygon aspidura*) to a more complex, T-shaped bayonet (*Rhinoptera bonasus*). We found no overt morphological distinctions between the barbs of marine *vs* freshwater taxa. Instead, we identified more nuanced differences between taxa inhabiting pelagic, reef, deep riverine, and coastal habitats. We discuss these results using barb morphology as a taxonomic character, which is especially relevant given their prevalence in chondrichthyan fossil beds, and the ecological significance of the barb as a defensive structure.

Mechanisms of Development and Intraspecific Variations of Dental Morphology in Rodents

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In vertebrates, the dental morphology is set up during development and is further modified only by injuries or wear. Intraspecific variations of the dentition can thus reflect modifications to standard odontogenesis and provide information about the developmental mechanisms and constraints. Because they broaden the spectrum of developmentally possible shapes, these variations can challenge computational developmental models. Here, intraspecific variations in incisors of *Zapus princeps* and in molars of *Praomys jacksoni*, *Lemniscomys belieri*, and *Lemniscomy striatus* have been studied. *Zapus princeps* incisors have been found to be variable in the number of enamel grooves. The other studied species have variations in the number and arrangement of cusps in the occlusal surface of their molars. These variations are used to test the robustness of developmental mechanism hypotheses at the basis of current computational models of dental morphogenesis. These models are based on parameters such as the balance between activators and inhibitors, the presence of inhibitory fields around developing cusps and the directional resistance to growth. A morphometric study of the occlusal surface in *P. jacksoni*, *L. belieri*, and *L. striatus* suggests that the observed variations in accessory cusps are consistent with the existence of a specific inter-cusp below which the development of additional cusps is inhibited. In addition to these indications on the developmental control of the final tooth shape, the comparison of some morphological variants with the classical morphologies of other rodent species can also be viewed as an illustration of the evolution of morphological features.

Developmental Relationships between Teeth and Jawbones in Stem Gnathostomes and Stem Osteichthyans Revealed by 3D-Histology: Insight into the Evolution of Tooth Replacement and Tooth Organization

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Osteichthyan dentitions are characterized by cyclic tooth replacement and linear tooth rows. The acquisition of these characters can be explained by an intimate relationship between the growth of jawbone and the initiation of teeth, supported by substantial evidence from synchrotron microtomography that reveals the 3D-pattern of successor teeth, vascular canals, growth-arrested and resorption surfaces. The growing bone provides space for new teeth to attach and the

succession of larger teeth maintains the number of teeth as the animal grows. In non-shedding dentitions, whether the spiral addition of acanthodian tooth whorls, the anterior addition of ischnacanthid dentigerous jawbones, or the radial addition of arthrodire gnathal plates, the sequential addition of teeth is synchronized with the appositional growth of bone. The most ancestral teeth of the most basal stem gnathostome *Radotina* and *Kosoraspis* already display the lingual addition of tooth rows shared by the gnathostome crown group. When *in situ* resorption evolved in osteichthyans, the first-generation teeth of the stem osteichthyan *Lophosteus* are shed semi-basally forming deeply overlapping tooth rows. As the bone growth slows down at later developmental stages, the succeeding teeth overlap the preceding ones entirely, causing the preceding teeth to be shed basally and replaced *in situ*. Therefore, tooth replacement may have emerged via a tooth initiation rate higher than the bone growth rate. When a lingual shelf is formed on the marginal jawbones of crown osteichthyans, the lingual growth of bone is restricted, and new tooth rows cannot be added lingually to the previous rows, only apically. The replacement of the marginal linear tooth row of the basal actinopterygian *Moythomasia* is actually a vertical piling of alternate tooth rows by semi-basal resorption. Thus a single linear tooth row may have transformed from a lingual-labial compressed version of transverse tooth files.

More than Just Size: How Does Shape Contribute to Morphological Variation between Crania of Aurochs (*Bos primigenius*) and Domestic Cattle (*Bos taurus*)?

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The aurochs (*Bos primigenius*) has long been recognized as the extinct ancestor of the domestic cattle (*Bos taurus*), but the extent to which these two species differ from one another remains unclear, with some researchers simply regarding aurochs as large cows. This study is the first to use geometric morphometric (GM) methods to quantify cranial morphology in aurochs and cows to evaluate shape variation between them and to determine the degree to which this is an effect of size change. Crania of over 140 British specimens were modeled with photogrammetry to create 3D-digital surfaces. Three landmark sets of different sizes were then recorded to enable use of fragmentary remains. In the complete landmark set aurochs were clearly separated from cows on the second principal component. For the reduced landmark sets aurochs and cows separated on the first principal component. In analyses using shape only, cows were discretely separated from aurochs, with aurochs crania being relatively longer and narrower than those of domestic cattle. However, when adding size, it was apparent this played a major role, contributing a large proportion of the total variance on the first principal component. Notably, the isolated population of Chillingham cattle was found to be morphologically distinct from both aurochs and other domesticates. Sexual dimorphism was also strongly expressed in both the shape and size of skulls. Much of the variation was observed to occur in the posterior part of the cranium around the horns, which may be due to the anatomical architecture required to support the large horns seen in aurochs. Selective breeding for increasing docility via a reduction in horn and body size may therefore be the most significant trait of human cattle husbandry. The morphological distinctiveness of Chillingham cattle, which have been unmanaged by humans for over 400 years, indicates the fast rate at which anatomical variation can occur in small and isolated populations.

Creodonts and Carnivorans of the Calf Creek Local Fauna (Late Eocene, Chadronian) from the Cypress Hills Formation Occupied Different Dietary Niches

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Modern North American carnivorous mammals are members of a single clade, the Carnivora. This was not always the case however; in the first half of the Cenozoic, carnivorans coexisted with another meat-eating clade called the Creodonta. Creodonta is an extinct, polyphyletic group containing two clades, the Hyaenodontida and Oxyaenida. Creodonts emerged around the same time as Carnivora (Paleocene; ~60 Ma) but were extirpated from North America during the late Eocene and extinct globally by the Miocene. Determining the factors leading to the creodont extinction may therefore provide insight into the ecological conditions that led to the emergence of modern mammal assemblages. In this study, we employ a community ecology approach to determine the degree of dietary niche overlap between carnivorans and creodonts from a single late Eocene fauna (the Calf Creek LF; Chadronian North American Land Mammal Age) in southwestern Saskatchewan. To determine the degree of niche overlap between the two groups, we used Orientation Patch Count and Dirichlet's Normal Surface Energy to quantify differences in carnassial tooth shape. We also included body mass estimates for all species of carnivoran and creodont in the Calf Creek LF. We show that, although the Calf Creek LF carnivorans and creodonts share some similarities in tooth shape, which suggests similarities in dietary preference, differences in body mass indicate that they would feed on different types of prey. Prey focus mass calculations indicate that even the smallest creodont present at Calf Creek likely would have hunted prey that were on average twice as large as that of the largest carnivoran. We suggest that, although competition may have decreased creodont diversity earlier in the Eocene, their extirpation from North America was driven by factors unrelated to niche overlap with carnivorans.

Breathing as Bilateral Walking: Similar Rib Motions during Walking and Breathing in Two Species of Lizards

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In the evolutionary history of vertebrates, ribs functioned as part of the locomotor system long before they became part of the respiratory system. It is clear that the transformation of ribs from pure locomotor to dual respiratory-locomotor structures occurred at the base of Amniota, but data and even theories about this evolutionary innovation are lacking. How did ribs become mobile and develop the musculature for expanding the thorax and drawing air down into the lungs (i.e., aspiration breathing)? We set out simply to measure whether and how the ribs move relative to the vertebrae during locomotion in savannah monitor lizards (*Varanus exanthematicus*) and Argentine black and white tegus (*Salvator merianae*) and were surprised to discover that locomotor rib motions are similar to those we measured previously during lung ventilation in the same individual lizards. Ribs rotate cranially around the costovertebral joints during forelimb support phase and backward during swing phase, corresponding to inspiration and expiration, respectively. These kinematics are due to locomotion and not ventilation because selected contralateral ribs in varanids show the opposite pattern of bucket and pump motion, so both sides of the rib cage are not moving forward simultaneously as would occur during inspiration. These are the only locomotor rib kinematics measured to date and suggest that aspiration breathing may have arisen from modified axial locomotor motions. In addition, because the ribs move cranially on the same side of the body that rib-articulating hypaxial muscles are contracting and pulling caudally on the ribs to cause lateral bending, these rib motions may increase the magnitude of lateral bending and locomotion. Our results therefore suggest an early locomotor selective pressure on rib design that may have set the stage for the evolution of aspiration breathing in amniotes.

Skull Blood Supply Allowed Physiological Adaptations to Land Transition during the Devonian

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Although the move of tetrapods onto land led to drastic physiological changes (while facing desiccation, gravity and air-breathing) during the Late Devonian period (400-360 million years ago), it nevertheless conducted to their successful radiation worldwide. Understanding this evolutionary event has long been a topic of main focus for the research community of paleontologists. However, despite this large interest, lifestyles of stem-tetrapods are still debated. Here, we investigate certain physiological adaptations required for the move of tetrapods onto land, such as thermoregulation, acidosis buffering and cutaneous respiration. Due to the lack of soft-tissue preservation (including skin dermis) in fossils, only speculative hypotheses could be advanced so far. Based on state-of-the-art imaging technologies, we aim to compensate for this lack of knowledge by providing a model based on the quantification of vertebrate cranial vascularization. We imaged skull bones of a large range of stem and crown tetrapods (50 species) at the beamline ID19 of the European Synchrotron Radiation Facility (France). Our observations reveal that the number of blood vessels significantly increases in living animals performing some or all of the following physiological functions: 1) heat transfers when basking; 2) acidosis buffering; and 3) cutaneous respiration. This strongly supports the idea that fluid transportation through blood vessels in the dermal bone of the skull plays a major role in these physiological functions. Although the implication degree of each function is not easy to determine, preliminary results nevertheless exhibit an obvious shift of blood supply prior to the fish-to-tetrapod transition. We therefore conclude that this anatomical trait probably facilitated the above mentioned ecophysiological adaptations during the water-to-land transition in the Devonian period.

Phylogenetic Signal and Linear Model for High-Dimensional Multivariate Comparative Data: a case study with the MANOVA

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Phylogenetic linear models (e.g., regressions, ANOVA, or ANCOVA) provide a statistically rigorous framework for comparative studies of phenotypic traits across taxa. However, the development of their multivariate counterparts is still lagging behind because of the computational challenges encountered with multidimensional datasets. In particular, when the number of traits p approaches or exceeds the number of taxa n, the conventional likelihood-based statistical machinery is limited, and we have to rely on alternative methods that are approximate and restricted to the Brownian motion model of trait evolution. Here, we developed more flexible multivariate analogues to the phylogenetic linear models (e.g., multivariate regressions, MANOVA, MANCOVA) to deal with the high-dimensionality of modern high-throughput phenotypic and morphological comparative datasets. We used intensive simulations based on the MANOVA procedure to assess the performance of the proposed approaches to various levels of phylogenetic signal, correlations between the traits, and distributions of phenotypic changes in the multivariate space. We show that the proposed approaches outperform conventional ones when p approach n, and current alternatives when $p>n$. We further show that current available approaches for dealing with high-dimensional datasets - such as geometric morphometrics - lack the power to detect differences in multivariate datasets and can have high type I error rates under some circumstances. Finally, we provide an empirical illustration of our phylogenetic MANOVA on a geometric-morphometric dataset describing the mandible morphology in phyllostomid bats along with data on their diet preferences. Overall our results show significant differences between ecological groups while accounting for the mild phylogenetic signal of these ecomorphological data. We provide some guidance on the use of multivariate statistics for comparative analysis and discuss some recent concerns about the use of phylogenetic comparative methods.

In vivo X-Ray Imaging of Mammalian Reproductive Biomechanics

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The mechanical behavior of an individual's genitals directly impacts upon their fitness. If reproductive structures cannot function mechanically, this can affect sperm transfer or receipt and fecundity. The biomechanics underlying the physical act of mammal copula is almost entirely unknown, due to the inherent 'hidden' nature of the process. Here, we present the first attempt to quantify the 3D-kinematics of non-human mammal genitalia during copulation. We capture the motion of the pelvic girdle and baculum (penis bone) of the ferret, *Mustela pitorius furo*, using a live biplanar x-ray imaging system, X-Ray Reconstruction of Moving Morphology (XROMM). Ferrets were chosen due to their relatively large, well-defined baculum, predictable breeding season and well-established husbandry practices. By taking this novel approach, we aim to advance our understanding of the role of the carnivore baculum beyond the traditional methodological paradigm of inferring function from skeletal form. Ferret pairs were mated inside a customized Perspex enclosure. XROMM was used to visualize and measure the 3D-kinematics of the baculum relative to the male and female pelvis. Biplanar x-ray videos (25 Hz) were captured at short intervals throughout the extended phase of copulation and synchronized with two standard light videos collected continuously. Pilot data suggests the movement of the male baculum is readily discernible from biplanar footage. The motion of the baculum appears more tightly coupled to the male pelvis than female, suggesting movement of the penis bone within the vaginal tract. During periods of mate-guarding, the baculum remains quiescent relative to the female. A better understanding of the *in vivo* kinematics of ferret genitalia will help resolve the longstanding debate regarding the biomechanical function of the carnivoran baculum, and the specific mechanics adopted by both sexes to encourage ovulation/fertilization.

Snake Fangs Vary in Shape and Sharpness with Diet

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Venomous snakes are among the world's most effective predators, largely due to their unique feeding style, where toxic venom is used to immobilize, kill, and finally dissolve the prey as part of their digestive process. Crucial to this venom delivery system are the fangs, specialized teeth that are used to penetrate the skin of prey before administering a dose of venom. Tools are a good analogy for teeth, where variation in the overall shape of a tool will change its effectiveness in penetrating certain types of materials. Therefore, we hypothesize that the type of prey targeted in the wild likely influences the shape and sharpness of fangs. We used a combination of microCT-scanning, 3D-computer modeling and geometric morphometrics (3DGM) to examine and compare the sharpness and shape of fangs within venomous snakes. In order to compare these shape and sharpness measurements with snake diets, we used four diet categories based on the hardness of their known prey targets, ranging from soft-bodied prey to scaly and hard-shelled prey. Our results show variation in both sharpness as well as 3D-shape among the venomous snakes. In the latter, the main differences are in fang robustness and fang curvature. When the 3DGM data are plotted against the diet categories, there is a clear relationship between fang robustness and food hardness. More robust fangs are found in snakes that specialize on hard-shelled prey while snakes that feed primarily on mammals have more slender fangs. The increase in robustness in relation to food hardness might be an adaptation to resist breakage. Knowing the relationship between fang shape and dietary preference can be of importance in both ecology and conservation, since it will help to interpret the feeding range of lesser-known snakes. These results aid in demonstrating how fangs work, and provide insight into why snakes are such successful predators in ecosystems around the world.

Heterochrony, Heterotopy, and the Origin of Otocephalan Epibranchial Organs

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While heterochronic mechanisms affecting morphological change are commonly studied, relatively few studies have investigated the role of heterotopy during morphological divergence. Heterochronic shifts, changes in developmental timing, or heterotopic shifts, changes in the spatial arrangement of developmental tissues, can both result in morphological innovation. A trophic adaptation in certain filter-feeding and detritivorous fishes is the epibranchial organ. Epibranchial organs are paired food-aggregating structures, ranging in architecture from simple slits on the posterior pharyngeal roof to complex spiraling structures. Morphological divergence is often due to differential incorporation of additional trophic structures such as gill rakers and in Cypriniformes, the palatal organ. Despite this morphological diversity and broad phylogenetic distribution, little is known about the evolutionary development of epibranchial organs. Here, we investigate the origin of the epibranchial organs by comparing ontogeny within three different species. *Anchoa mitchilli* (Engraulidae) represents the more basal condition of a simple epibranchial organ, *Brevoortia tyrannus* (Clupeidae) has a more complex epibranchial organ, and *Hypophthalmichthys molitrix* (Cyprinidae) represents the most complex epibranchial organ yet described as it incorporates all branchial arches as well as the palatal organ. All epibranchial organs seemingly develop from an initial epithelial involution that is subsequently surrounded by muscle dorsal to the fourth and fifth pharyngeal arches. There were distinct heterochronic and heterotopic shifts during epibranchial organ development including differences in ossification and growth rates of the supporting hypertrophied branchial arches. Heterochronic shifts within the pharyngeal cavity supported the growth of larger epibranchial organs while a heterotopic shift supported the development of a more complex epibranchial organ.

Predicting Loading from Tooth Shape - Are you Prepared for Anything?

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Teeth tell a story of the interaction between predator and prey, shaped by a compromise between function and load. If the teeth in a jaw look the 'same' we call them homodont; and if there is distinct regional specialization in size or shape they are heterodont. Implying that homodont teeth act the same while there is regionalization of function associated with heterodonty. Conical teeth are a simple shape with a putatively simple job - puncture. Nevertheless there is wide variation in size and placement of conical teeth. We show that teeth that look alike don't always act alike — morphologically heterodont teeth are functionally homodont. Furthermore the arrangement of large and small conical teeth affects the load teeth can transmit to prey. Load not only affects position but the directionality and predictability of load should affect tooth orientation. Consider a tooth that can be hit from any angle: a circular right cone resist all potential loads equally well. But teeth are rarely right circular cones. A more predictable load, usually in the antero-posterior direction for example, should favor a right elliptical cone. Any bias in loading so that more comes from the posterior than anterior direction should result in an elliptical cone with an acute angle of inclination. We created a model that measures the strength of various conical teeth as load is applied equally in any direction. We identify trends in loading that drive the shape, position, and placement of conical teeth. We suggest that measurements of how shape affects stress distribution in response to loading gives us a fuller picture of the evolution of conically shaped teeth.

Structural Changes in Collagen Fiber Orientation Within the Forelimb Bones of Long-Lived Big Brown Bats (*Eptesicus fuscus*, Mammalia: Vespertilionidae) Relative to Mice (C57BL/6)

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Insectivorous bats offer a novel perspective in aging research compared to typical model taxa as they live at least 3 times longer than terrestrial mammals of an equivalent body size. Bone is a dynamic tissue that is mechanosensitive and reorganizes collagens and minerals within its extracellular matrix to match principal strains. No studies have quantified age-related changes in the orientation of the bone matrix across the lifespan of long-lived bats. This study uses quantitative polarized light microscopy (qPLM) to test two hypotheses. First, we expect that volant bats display a different pattern of bone tissue organization compared to terrestrial mice, due to increased torsional strain generated during flight. Second, we expect that bats and mice share similar strategies for age-related changes in bone organization. This study compared the matrix of the humerus, radius and metacarpals within big brown bats (*Eptesicus fuscus*) to the humerus and radius of C57BL/6 mice. Results showed bats retain a larger endocortical region (10-25%) of bone cross-section compared to mice (0.5-3.5%), even with age, suggesting that they are unique (Hyp. 1) and display a different aging strategy compared to mice (Hyp. 2). Within this endocortical region, bats displayed overlapping lamellae with more helical collagen fiber orientation with age. Within the cortex of both taxa, collagens were oriented more longitudinally compared to that of the endocortical region and few age-related changes were seen. Among bats, 56% of variation within cortices was explained by a proximodistal gradient in bones along forelimb, and only 6% of variation was explained by age, suggesting there are few age-related changes seen in bat bones along their lifespan. Results therefore suggest that bats differ from mice in the large size and helical organization of the endocortical region that is retained throughout their lifespan, and that bats uniquely display a proximodistal gradient in matrix structure.

Support for the Developmental Hourglass Model: Is there a Phylotypic Stage in Mammals?

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Embryonic development is a continuum characterized by shifts in cell behavior, growth, and proliferation. These temporally dynamic changes ultimately lead to the differentiation of tissues and organs that comprise the organism. Consequently, alterations of such developmental processes are expected to give rise to morphological differences among species. This phenomenon was formalized by Karl von Baer in the first half of the 19th century, as he proposed an "early conservation" theoretical model suggesting that developmental variation underlying morphological diversity is more likely to emerge later in embryogenesis. More recently, his theoretical framework was expanded via the "hourglass" or "spinning top" theoretical patterns. Although these models have been recently evaluated within the context of gene expression, they have not been tested using external morphological characters that span all stages of embryonic development in vertebrates, as originally intended by von Baer and other embryologists. By comparing the timing of emergence for over 77 embryological characters in 75 mammal species, we provide support for a developmental "hourglass" model. Contrary to previous findings in mammals, our results indicate that variation does indeed decrease towards the middle stages of the development, congruent with the existence of a phylotypic stage. We discuss the implications of these empirical findings to clarifying current theory on the variational properties of vertebrate animals.

Building a Catalogue of the Ear Region for Ruminants

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The ear region has long been recognized as a source of invaluable ecological and phylogenetic data. Its use in both neontology and paleontology dates back to the 19th century. Recent technological advances, such as CT-scanning, have dramatically increased the interest in the ear region. Investigations have focused on understanding the deep time relationships and evolution of vertebrates, potential biological innovations related to the senses of hearing and balance as well as the constraints on the evolution of morphological features of the skull. Despite all this, only recent works, such as that of O'Leary (2010, Bull. Am. Mus. Nat. Hist. 335:1–206), have contributed to our broader knowledge of the petrosal bone through the description of characters and their states in a larger collection of living and fossil mammals, especially artiodactyls. In the past two decades, the wealth of published digital data on the bony labyrinth embedded inside the petrosal bone has contributed to our understanding of the relationships and ecology of fossil mammals but only a few studies, such as that of Ekdale (2013, PLoS ONE 8, e66624), have described the morphology of this structure in detail, and indeed only at high taxonomic levels. Here, we describe the combined use of surface and CT-data to build a large catalogue of the morphology of the petrosal bone and bony labyrinth in ruminants that includes more than a third of their extant diversity and samples all tribes. Both classical metrical and 3D-geometric morphometrics approaches, as well as ontogenetic data, add information to the variability and growth of the ear region. They eventually help describe new characters with phylogenetic relevance.

The Road to a Phylogenomically-Based Bioinspired Robotic Model Approach to Address the Evolution of Terrestrial Locomotion

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The evolution of the pelvic girdle as a weight-bearing structure was critical to terrestrial tetrapod diversification. Using a convergent fish model, we are studying the evolution of anatomical structures that support the vertebrate body against gravity and will investigate how adjustment of muscular control can produce a tetrapodal walking gait via a range of skeletal morphologies. The blind cave loach, *Cryptotora thamicola* (Cypriniformes: Balitoridae), walks and climbs waterfalls with a salamander-like gait and evolved a robust pelvic girdle that shares morphological features associated with terrestrial vertebrates. Other species of balitorid loaches possess varying degrees of this convergent morphology providing an opportunity to further understand the mechanism underlying a major event in the history of life: how fishes are, and were, able to transition to a terrestrial lifestyle. We will examine the phylogenomic relationships, morphology, biomechanics, and walking performance from an evolutionary perspective among balitorid loaches. Using our experimental biomechanical data, we will develop a validated bioinspired robotic model to take a modular approach to examining the effect of pelvic morphology on walking performance in extant and extinct fishes and tetrapods. Funded by the National Science Foundation Rules of Life initiative, this research will inform our understanding of mechanisms underlying the convergent evolution of morphological innovation. The broader impacts of this project will promote teaching, training, and learning by offering new educational opportunities and access to research equipment to high school students in a diverse and underprivileged community and by bringing a diverse population of undergraduates to do foreign fieldwork and work on all aspects of this project.

Variation in Snake Fang Puncture Efficiency

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The fangs of venomous snakes have an unambiguous function: the delivery of venom to a target. However, while the mechanism of venom delivery is a shared ancestral trait, there is a fair amount of morphological variation in the fangs across lineages. Viperids, elapids, and some atractaspids represent independent derived instances of the front-fanged condition, with either enclosed, non-fused tubular fangs, or enclosed, fused tubular fangs on a reduced, mobile maxilla. This is in contrast with the rear-fanged condition, with grooved fangs on the caudal end of the maxilla. The position of the venom orifice, whether a distinct hole or groove, should indicate the functional penetration depth that must be achieved for successful envenomation. However, the properties of snake venom have been shown to allow it to be drawn into the body through a puncture wound, potentially enabling envenomation even if only the distal edge of the venom orifice penetrates the target. Given the variation in both morphology and functional penetration depth, there is the outstanding question of how much this variation influences puncture efficiency between snakes from different lineages. Here, we ask two main questions: 1) how does the morphology of the venom orifice vary between lineages; and 2) does the work required to achieve functional depth vary between snake lineages with different fang morphologies? Our results show that the basic functional puncture depth, from the tip of the fang to the proximal edge of the venom orifice, scales with fang length for viperids and elapids. However, the size of the venom orifice varies between lineages, meaning that the minimum functional puncture depth scales differently. While work to initiate fracture depends on fang tip morphology, work to puncture is related to the functional penetration depth and varies with both size and the morphology of the venom orifice.

Origin of Suckling in Therian Mammals

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The tensor veli palatini (tvp) muscles, and the pterygoid hamuli that support a soft palate between them, play an essential role in suckling. The first appearance of these features indicates when suckling may have first occurred. Mammalian suckling requires two oral seals: an anterior seal formed by the tongue wrapping the teat and pushing it against the hard palate; and a posterior seal between the tongue and soft palate. At the beginning of a suckling cycle, with both seals intact, the tongue between them is depressed and the resulting negative pressure draws milk from the nipple into the oral cavity. We studied serial sections of *Monodelphis* and *Ornithorhynchus* and CT-scans of non-mammalian cynodonts, ictidosaurs, mammaliaforms, marsupials and monotremes. We conclude that in the first mammals, the tvp arose from a remnant of the reptilian posterior pterygoideus; and stress generated by the tvp on the precursor cells of the pterygopalatine bosses led to the formation of secondary cartilages that later ossified and fused with the bosses to form hamuli.

The Chameleon (Family Chamaeleonidae) Axial Skeleton in an Evolutionary and Ecological Context

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Morphological variation can be driven by adaptation to different environments and to different functional uses or by the phylogenetic history of the species. Chameleons (family Chamaeleonidae) are extremely diverse with over 200 taxa in twelve genera specializing to occupy disparate ecological environments and spanning a wide range of body sizes, anatomical specializations and behavioral adaptations. The number of presacral (cervical, thoracic and lumbar) and caudal vertebrae, as well as the number of sternal and parasternal ribs, is extremely variable in chameleons and may vary based on the ecology of individual species or based on their phylogenetic lineage. In fact, chameleons are known to have 14-23 presacral vertebrae and 17-62 caudal vertebrae, with species possessing fewer than 19 presacral vertebrae having among the lowest known among all squamates. This variation, however, is based on the examination of a limited number of taxa and has not been put into a proper phylogenetic or ecological (e.g., more arboreal *vs* terrestrial species) context. We quantified the rib and vertebral numbers from microCT-scans of 234 chameleon specimens, representing 74% of all described chameleon species and all genera. We then tested whether this variation correlates most closely with ecological characteristics or phylogenetic relationships within the family. Our data reveal previously undocumented variation in vertebral and rib counts within all specimens of particular chameleon lineages, suggesting a strong phylogenetic signal to certain axial elements. We also found, however, that more terrestrial lineages (i.e., *Brookesia*, *Palleon*, *Rhampholeon* and *Rieppeleon*) have lower counts of certain axial elements than more arboreal lineages, suggesting that ecology drives some variation as well. These results provide insight into the morphological evolution of the axial skeleton in chameleons and of the axial skeleton across disparate ecological environments.

Paleohistological Inferences of Resting Metabolic Rates in Notosuchia (Crocodylomorpha, Pseudosuchia)

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Notosuchia is a clade of terrestrial and semiaquatic Crocodylomorpha including herbivorous, omnivorous and carnivorous taxa. They appeared in the Middle Jurassic and disappeared in the Miocene, about 11 million years ago. We inferred the resting metabolic rates of several taxa (*Araripesuchus* sp., *Armadillosuchus arrudai*, *Baurusuchus* sp., *Iberosuchus macrodon*, *Mariliasuchus amarali*, *Stratiotosuchus maxhechti*) using quantitative bone histology. The bone histological features quantified were: primary osteon density, orientation of vascular canals (proportion of circular, oblique, radial and longitudinal canals) and osteocyte lacunae density, size and shape. Paleobiological inferences were performed using histological data and resting metabolic rate values quantified in a sample of 13 species of extant tetrapods including two birds, one crocodile, three testudines, four lepidosaurs, two mammals and one lissamphibian. First we tested whether the histological variables explain significant fractions of the variation of the resting metabolic rates in extant taxa using Phylogenetic Generalized Least Squares Regressions (PGLS). Second we inferred resting metabolic rates of Notosuchia using Phylogenetic Eigenvector Maps (PEM). This method takes into account the phylogeny and one explanatory (histological) variable. An Akaike Information Criteria (AIC) is used to find the best model (phylogeny + one histological variable) explaining the variation of the response variable (resting metabolic rate). Third, we analyzed the evolution of resting metabolic rates performing an optimization onto the phylogeny (using Least Squared Parsimony) of the values inferred for the Notosuchia analyzed in this study and the values quantified in the sample of extant tetrapods. Considering that the resting metabolic rate is a reliable proxy to infer the thermometabolism of extinct taxa, we will discuss hypotheses about the state (endothermic or ectothermic) of Notosuchia.

Functional Disparity in Triassic-Jurassic Archosaur Hind Limbs, and Implications for Musculoskeletal Modelling

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The late Triassic to early Jurassic was a time of high terrestrial diversity and disparity in archosaurian reptiles, initially with the pseudosuchians and then dinosauromorphs. However, the modern diversity of archosaurs is restricted to crocodilians and birds. Here, we investigated the functional disparity of archosaur hind limbs, widely seen as remarkable, using biomechanics. Skeletal models of fossil and extant species of pseudosuchians (*Batrachotomus*, *Poposaurus* and Nile crocodile) and dinosauromorphs (*Marasuchus*, *Coelophysis*, *Mussaurus*, and elegant-crested tinamou) were digitized, and muscles added to these models in musculoskeletal modelling software. We then calculated ranges of motions (ROM) and normalized muscle moment arms of the hip, knee, and ankle. Pseudosuchian taxa generally had the greatest ROM in hip flexion/extension, whilst dinosauromorphs had the greatest ankle extension (due to absence of the enlarged calcaneal tuber). Across the other joints, ROM was similar between the taxa. Muscle moment arms varied widely depending on the method of size-normalization. When the cube root of body mass was used, smaller taxa had larger moment arms around most joint axes. When scaled against femoral length, *Mussaurus* had the largest hip flexion/extension moment arms for the M. caudofemoralis longus, but the smallest for M. flexor tibialis externus. Extinct pseudosuchians had some of the largest M. gastrocnemius moment arms, as expected from the calcaneal tuber; and comparable to birds. Hence there is a tradeoff in ankle mobility and leverage in archosaurs. The fossil taxa and crocodile retained ancestral hip abduction/adduction moment arms, contrasting to the patterns in birds. By using 3D-musculoskeletal models we can explicitly quantify functional disparity in (and evolution of) archosaurian hindlimb function, and we discovered important lessons about tradeoffs between different methods of normalizing muscle moment arms.

Form-Function Relationships in Squamate Eggshells: Insights from Evolution and Biomechanics

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Eggs are multifunctional structures that enabled early tetrapods to colonize the land millions of years ago, and are now the reproductive mode of over 70% of land vertebrates. Egg morphology is at the core of animal survival, mediating the interactions between embryos and their environment, and has evolved into a massive diversity of forms and functions in modern reptiles. These functions are critical to embryonic survival, have had profound effects on vertebrate evolution and may serve as models for new antimicrobial and/or breathable materials. Nevertheless, we lack essential knowledge on the basic properties of eggs, including their chemical composition, ultrastructure, and material properties. This is particularly true of non-avian reptiles. These data are critically needed if we are to understand their effects on vertebrate evolution and diversification. In this project the goal was to determine the relative contributions of structural constituents and chemical composition of eggshells to their biomechanical performance using squamate eggs as study system. First I characterized eggshell structure using X-ray micro Computed Tomography (μCT) coupled with scanning electron microscopy, then I analyzed eggshell chemical composition using FTIR and conducted experiments to determine eggshell functional properties (optical, mechanical, interaction with water and microbes). I show that squamate eggs display larger diversity in egg phenotypes than previously thought and that this diversity is coupled with a large range of functional properties, some of which might serve as inspiration for biomimetic materials. The inferences generated in this project are of great relevance to evolutionary biologists, paleontologists as well as bioengineers interested in biomimicry and bio-inspired design.

Sonic Hedgehog and Ectodysplasin in the Development of Teeth in Mice

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Eda is a gene for a transmembrane protein from the TNF family - Ectodysplasin A. This protein plays an important role in the development of ectodermal derivatives, such as teeth. We focus on the development of incisors and of adjacent epithelial structures in mice with a spontaneous mutation in the Eda gene through tracking Sonic hedgehog (Shh), an important signalling molecule involved in the initiation of tooth development. We performed a comparative study of tooth development in Eda mutants and WT using epithelial dissociation and fluorescent microscopy. According to our results, the development of teeth in Eda mutants seems to be approximately one day delayed. Using Shh whole-mount *in situ* hybridization in Eda mutants, we showed that the position of Shh signalling areas which are appearing during tooth development correspond to those in WT mice, but they were noticeably reduced in size. In order to determine possible changes in the expression of Shh we also mapped the expression of SHH using immunohistochemistry and evaluated the levels of SHH protein using western blot in Eda mutant mice and compared these results to WT. According to our results, the area of its expression seemed to be reduced in size, but the level of SHH protein expression in Eda mutants was similar to that in WT mice. Western blot analyses did not reveal any quantitative reduction of SHH expression in Eda mutants. Descendants of the Shh expressing cells, traced using the Cre-loxP system, showed that the density of cells expressing Shh was changed in Eda mutants compared to controls. Thus in WT mice Eda expression could be a limiting factor for the restriction of the signalling center during tooth development. Its deficiency in Eda mutants could lead to enlarged density of cells in the smaller signalling center without final reduction of Shh gene expression product. Financial support: 18-04859S.

Vertebral Development and Congenital Vertebral Malformations in Plethodontid Salamanders

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The vertebral column is composed of serially repeating chondrified and ossified vertebrae that surround the spinal cord and the notochord. While amniotes display a rather conserved vertebral development, centrum formation and ossification sequence of the vertebral centra and neural arches are highly variable in lissamphibians. To determine if and how vertebral development is influenced by morphological, ecological and ontogenetic parameters, growth series of different plethodontid salamanders were examined. This group of derived salamanders is particularly interesting as members of the group are adapted to a wide range of habitats (terrestrial, fossorial, aquatic), are highly variable in size (from 2cm body size up to 23cm), and as they display complex life cycles (direct development, aquatic larval stage with metamorphosis). Here, in all 18 species, the following chondrification and ossification sequences are observed: chondrification first of the neural arches and then of the centra, followed by ossification first of the centra and then of the neural arches. Vertebral development starts early in ontogeny and the chondrification and ossification pace of neural arches and vertebral centra is fast. Regenerated tails are characterized by a reverse order of development: the cartilaginous centra develop prior to neural and hemal arches. Furthermore, congenital vertebral malformations (wedge and block vertebrae) and posttraumatic deformities are observed in some specimens of *Desmognathus fuscus.*

Sources of Variation in the Tooth-Bearing Vomer Bone in Spelerpini Salamanders (Caudata: Plethodontidae)

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The vomer is an important tooth-bearing cranial bone in the lungless salamanders (Caudata: Plethodontidae) that serves different functional roles in aquatic *versus* terrestrial feeding. Vomerine tooth rows parallel with the maxillary teeth are thought to help grasp prey while expelling water from the mouth, while posterior extensions of the tooth row may help terrestrial taxa bring prey down the throat. Based on these factors, we may hypothesize that these two general morphological types will correlate with the habitat of the adult salamander. Alternatively, variation in form may be due to taxonomic effects, such that closely related species will have similar vomer morphology regardless of adult habitat. In this study, we examine these two influences on vomerine shape on a set of species of the morphologically diverse tribe Spelerpini, in which two of the five genera (*Eurycea* and *Gyrinophilus*) present both aquatic and terrestrial species. Data were collected using micro computed tomography (microCT) scans from specimens from the Field Museum of Natural History and the Illinois Natural History Survey; additional data was obtained from public online repositories including Morphosource.org. Geometric morphometric analyses were performed to capture shape variation of both the vomer and the vomerine tooth row. Individuals were plotted in morphospace to determine if aquatic and terrestrial morphologies clustered. Although all individuals we scanned appeared to be post-metamorphic adults, some individuals had vomers that retained a few juvenile characteristics. Body size proxies were compared to the morphometric data to investigate if there were ontogenetic effects in the analysis.

Evolution of the Branchial Musculature in Ray-Finned Fishes, with Emphasis in Pre-Acanthomorphs (Osteichthyes, Actinopterygii)

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The musculoskeletal branchial system is one most intricate and sophisticated anatomical complexes of ray-finned fishes. Despite recent progress, many doubts persist as to the evolution of the 17 main groups of muscles associated with the actinopterygian gill arches. The present study explores the anatomy, homologies, and evolutionary origins of all branchial muscles and their significance for the higher-level phylogeny of pre-acanthomorphs. Comparative analyses indicate that the obliqui ventrales and transversi ventrales are serially homologous and this nomenclatural distinction is artificial and potentially misleading. Rectus communis and rectus ventralis IV are subdivisions of a single primitive muscle, herein termed rectus primordialis. The branchiomandibularis was primitively present in bony fishes and was completely lost in teleosts. The dorsoposteriormost branchial muscle of ostariophysans and most clupeiforms is homologized with the levator posterior, which independently evolved in euacanthomorphs. The term rectus dorsalis has been inappropriately applied to specialized subdivisions of at least three distinct primitive muscles. New evidence suggests that the retractor dorsalis evolved from ligamentous connections of the sphincter esophagi with the roof of the abdominal cavity. New synapomorphies derived from the branchial musculature are proposed for several major actinopterygian lineages. Notably among these findings are the support for the sister-group relationship between siluriforms and gymnotiforms and between alepocephaloids and argentinoids, both of which are corroborated by previous anatomical analyses but rejected by recent molecular phylogenies. This study was funded by the São Paulo Research Foundation (FAPESP #2010/18984-9 and #2016/19075–9).

A New Structure-Function Relationship in Bone Histology Allows Tracking the Origin of Warm-Bodied Teleost Fishes

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Warm-bodied physiologies sharing some features of bird- and mammal-like endothermy evolved in several groups of marine vertebrates. These include two groups of teleosts, the tunas (Thunnini) and opahs (*Lampris* spp.). Based on comparative study of bone histology, we propose a new osteological correlate of endothermy in fishes, and use it to constrain the timing of origins of this key physiological innovation using fossil bone histology. The majority of modern teleosts possess a peculiar type of "acellular" bone, in which osteocytes (the most widespread bone cells) are missing entirely. Acellular bone is a derived trait predominantly found in the clade Neoteleostei, which comprises more than 18,000 species. We recently found that tunas and opahs are the only neoteleosts known to have cellular bone, implying a secondary acquisition of osteocytes in both lineages. We propose that this histological feature correlates with endothermy in tunas and opahs, and can be used to infer it in their fossil record. We sectioned bone samples of two early to middle Eocene (56-40 Ma) teleosts: *'Thunnus' abchasicus* and *Whitephippus tamensis*. They are the oldest known representatives of the tuna and opah lineages, respectively. Osteocytes appear to be absent in the bone of both taxa, like in ectothermic relatives of tunas (e.g., mackerels) and opahs (e.g., oarfishes). Thus, we hypothesize that they were ectothermic, meaning that endothermy is a more recent innovation in both lineages. Including more recent fossil tunas and opahs will be needed to detect their oldest endothermic representatives. We will target Oligocene and Miocene fossils in particular, since these periods correspond to a global cooling of oceanic waters, potentially linked with the appearance of endothermic physiologies in marine teleosts.

Morphological Adaptations of Gliding Geckos

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Gliding, or unpowered flight, has evolved in several tetrapod groups, including frogs, mammals, birds, snakes and lizards, and at least five extinct reptile groups, including the non-avian dinosaurs. Unpowered flight can be classified as falling, parachuting, and gliding flight. Geckos have evolved parachuting at least 3 times, and unlike other groups, some gecko species have closely related relatives that show gradual acquisition of gliding traits. Here, we study the skeletal structure of two groups of gliding geckos (*Ptychozoon* and *Hemidactylus*) who developed parachuting under similar ecological conditions. Our results indicate that both glider groups include extreme flattening of the body, and *Ptychozoon* and some closely related species of the genus *Luperosaurus* have evolved more elaborated body flaps that increase drag during falling. Gliding in the genus *Ptychozoon* has resulted in several skeletal adaptations including: very low neural arches in the dorsal vertebrae; expanded wrists; and elongated ribs. Some of these features are also seen to some extent in other gliding lizards such as the gliding agamid, *Draco*. Gliding has produced a diversity of non-homologous morphologies among tetrapod groups, but despite this phenotypical heterogeneity, all groups are arboreal. Considering gliding as an initial stage for powered flight, the universal arboreal behavior of gliding tetrapods offers support to the origin of flight in birds from tree dwelling dinosaur ancestors, instead of bipedal cursorial dinosaurs.

Allodaposuchid Patterns of Cranial Morphospace Occupation within Modern Crocodiles (Crocodyliformes, Eusuchia)

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The patterns of cranial morphospace occupation in crocodiles have been explored among extant species, but there are still few studies in which fossils are included. In the case of allodaposuchids, the fragmentary nature of the available specimens until the last decade prevented them to be actively included in these analyses. During this period, new exceptional cranial remains have been discovered and new allodaposuchid taxa have been described, offering the opportunity to explore their poorly known patterns of morphospace occupation within that of eusuchian crocodiles. A total of 96 skulls, representing some of the major eusuchian clades (Alligatoridae, Allodaposuchidae, Crocodylidae, Gavialidae and Hylaeochampsidae) and including 21 extant crocodylian species, were used in the analyses. Allodaposuchid taxa included were *Allodaposuchus precedens*, *Agaresuchus fontisensis* and *Lohuecosuchus megadontos*. Two new 2D-sets of landmark configurations were developed for the ventral (20) and dorsal (34) cranial views. These datasets were subsequently divided in two sections, the rostrum and postrostrum, to analyze them separately. Each dataset was subjected to Procrustes superimposition, and afterwards to principal component analyses (PCA) to generate a morphospace of skull shape variation. PC-scores accounting for 90% of the total variance were subjected to a pairwise multivariate analysis of variance (NPMANOVA) to explore morphospace occupation patterns among the analyzed clades. PCA showed that allodaposuchids partially overlap their morphospace occupation area with that of alligatorids and/or crocodylids. However, the results from the pairwise NPMANOVAs reveal that allodaposuchid morphospace occupation area significantly differs from that of alligatorids. Furthermore, pairwise NPMANOVAs indicate that the shape of the rostrum in ventral view represents the most distinct structure of allodaposuchids with regard to the analyzed clades of crocodylians.

Comparative Morphology of Oral Glands of New World Coral Snakes Focusing on Labial and Rictal Structures

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Despite the wide diversity and obvious medical importance of the New World coral snakes, little is known about their glandular morphology. We compare the morphology of oral glands (especially labial and rictal) in all three genera (*Micrurus*, *Leptomicrurus* and *Micruroides*) of Neotropical elapids and selected outgroups. In addition to dissection and conventional histology of sections, snake heads were stained with iodine to enhance contrast in soft tissues and submitted to computed tomography (diceCT). Venom and accessory glands are similar to those described for other elapids, with some variation in the attachment of compressor musculature. Of fifteen studied ingroup species, supralabial glands occupied the entire region under the supralabial scales only in *Micrurus mipartitus* and *Leptomicrurus narduccii*, while in other species and outgroups they are divided in anterior and posterior portions. Small superior rictal glands were observed only in *Micruroides euryxanthus*, *Leptomicrurus narduccii*, *Micrurus frontalis* and *M. spixii*. All ingroup species and close relatives possess inferior rictal glands composed of serous acini, with single large ducts extending along their medial surfaces to the corners of the mouth. In *Micrurus* and *Leptomicrurus*, inferior rictal glands occupy the posterior halves of the mandibles under the supralabial scales, whereas in *Micruroides euryxanthus* rictal glands are very small, occupying only the posteriormost region of the mandible. Infralabial glands comprise mostly mucous cells with pocket-like structures in the mandibular region associated with the front-fangs. We have discovered substantial morphological variation in oral glands of Neotropical coral snakes and structural evidence for protein-secreting inferior rictal glands, which may suggest additional functions besides the usual mucus production of typical labial glands. FAPESP Process N° 2018/093017.

The Road to Parasitism in Trichomycterid Catfishes: Phylogenetic and Ontogenetic Transformations of the Feeding Apparatus, from Copionodontinae to Vandelliinae (Teleostei: Siluriformes)

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The neotropical catfish family Trichomycteridae comprises the most diverse range of trophic adaptations in Siluriformes. Members of the group include taxa which are predators of aquatic invertebrates, carrion feeders, mucus- and scale-eating, and exclusively hematophagous species. Such range of variation is reflected in equally diverse morphologies, especially in the jaw and branchial complexes. Such modifications are particularly pronounced in the semi-parasitic forms, with some adaptations without parallel in bony fishes. In this paper, we describe and trace the sequence of trophic morphological change in various lineages of Trichomycteridae, from basal representatives of Copionodontinae and Trichogeninae to the most highly modified Vandeliinae. Our hypotheses of character-state transformations are based on observed ontogenetic changes in representative taxa mapped against known components of trichomycterid phylogeny. Most of the developmental data are new, and provide a detailed assessment of morphological change and hypotheses of homology. Developmental data are particularly detailed in Copionodontinae and Vandelliinae. In the latter, ontogenetic changes are so extreme that they qualify as metamorphosis of the feeding apparatus. Results provide a scenario about trophic evolution in Trichomycteridae and allow inferences about the role of such adaptations in the diversification of the family. Funding FAPESP 2015/26804-4.

Retro-Deformation Using Thin Plate-Spline (TPS) Method on Asymmetric Objects: Inquiry on Perissodactyl Femora

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Fossils are generally discovered with post-mortem deformations that unavoidably alter their biological information. Because digital visualization allows paleontologists to perform high precision measurements, biomechanical models, 3D-reconstructions, and quantitative comparative analyses, it appears essential to estimate as accurately as possible the original shape of a fossil organism. Today, 3D-tools offer a wide range of possibilities for the retro-deformation of deformed objects. The use of 3D-geometric morphometrics and thin-plate splines (TPS) interpolation as a retrodeformation tool is already used but only for symmetrical objects such as fossilized skulls. In this study, we propose to quantify the effectiveness of TPS interpolation as a retrodeformation method for asymmetric long bones. To do so, we proceeded in two phases: 1) 3D-digital taphonomic degradations (stretching, flattening, bending and twisting) were performed in 3D on a horse femur. The deformed objects were then retrodeformed and quantitatively compared to the original model; 2) The same process was finally performed on a sample of femurs of white rhinos, in order to evaluate the retrodeformation based on an averaged morphology for the species, by comparing the retrodeformed object with the original shape of the bones. Results show that affine deformations – flattening and stretching of the whole bone - are the best estimated. Retrodeformations performed on the rhino sample confirm the previous observations, despite the fact that the retrodeformation is performed on an object different from the original one. This highlights the possibility to reliably use this retrodeformation approach on bones showing the best handled deformations. This could enable to incorporate numerous deformed fossil bones in quantitative analyses such as biomechanical modelling and morphometrics.

Avian Facial Bristles, are they Analogous to Mammalian Whiskers?

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While the sense of touch in mammals has been well explored by researchers, it has been relatively understudied in birds. For example, the avian counterpart of mammalian tactile whiskers, called facial bristles, have been almost entirely overlooked. Facial bristles are a type of feather above the upper beak of many nocturnal species of birds that look, morphologically at least, like mammalian whiskers. Thus, perhaps facial bristles could carry out a similar tactile function to mammalian whiskers, by guiding navigation and foraging in dark, complex environments. If they do convey tactile information, facial bristles need to have mechanoreceptors around their follicles, to receive and transmit environmental information to the brain. Consequently, to provide a first understanding of facial bristle function, this study examined the morphology and follicle anatomy of prominent facial bristles in several representative species of the caprimulgiform order. Foraging behavior was also compared. Results demonstrated variation of facial bristles morphology, follicle anatomy and foraging behavior between the species. Mechanoreceptors were not always present, and their organization and number were not identical between species. Nocturnality appeared to be a possible predictor of mechanoreceptor presence, number and organization around the follicles. This study gives insights into avian sensory systems, and helps us to understand more about these species of Caprimulgiformes, of which relatively little is known.

Limb Bones Microstructure in Rauisuchia (Archosauria: Pseudosuchia): New Insights in the Growth Strategies

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Recently discovered specimens of "Rauisuchia" have boosted interest in this enigmatic group of pseudosuchians, because they provide crucial information on major patterns and processes in continental Triassic archosaur evolution. Here, we analyze limb bone histology of *Decuriasuchus quartacolonia* MCNPV10.005b-X (humerus, ulna, radius, tibia) and *Prestosuchus chiniquensis* BSPG AS XXV 10, 11b, 35 (humerus,

femur, fibula) from the Middle Triassic (Santa Maria Supersequence), southern Brazil, to establish their ontogenetic stage and infer growth dynamics. Both taxa exhibit cyclically deposited highly vascularized cortices. Whereas a maximum of four lines of arrested growth were recorded in *Prestosuchus*, only one is preserved in *Decuriasuchus*. While the cortical bone is formed by fibrolamellar tissue in *Decuriasuchus*, parallel fibered bone predominates in *Prestosuchus*. Evidence of secondary remodeling is only observed in *Prestosuchus*. An outer circumferential layer (indicative of somatic maturity) is absent in all samples. Furthermore, since no clear reduction of the distance between growth marks is observed, sexual maturity also seems to not be achieved. Comparing with the large bodied "rauisuchian" *Batrachotomus* which exhibits a higher proportion of fibrolamellar bone, the relative growth rate of *Prestosuchus* appears to be lower. Comparison with *Decuriasuchus* is difficult, due to the younger condition of the sampled individual. Other pseudosuchians such as *Effigia*, *Terrestrisuchus*, and *Postosuchus* grew fast in early development, as shown by fibrolamellar bone matrix in the inner cortex, changing to lamellar-zonal after reaching sexual maturity. This condition is also evident in the taxa sampled here, likely reflecting the primitive condition for archosaurs. Bone histology thus argues for rauisuchians reaching massive body size during early development instead of protracted longevity. Funding: PICT 2016-0159 (JBD)& 2014-0609(JBD/IC).

Paleoneuroanatomy: 3D-Digital Endocasts of *Desmatosuchus* Reveal Endocranial Diversity within Aetosauria (Archosauria: Pseudosuchia)

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The paleoneuroanatomy of aetosaurs was previously reported only for *Desmatosuchus* based on the physical endocast (UMMP 7476) described by Case (1921, J. Comp. Neurol. Neurology 33: 132-147), though new materials of *Neoaetosauroides engaeus* contributed new knowledge of the encephalon, inner ear, and middle ear sinus. Using CT-scanning, we developed new digital endocasts of two specimens of *D. spurensis*, UCMP 27408 and 27410, which provided novel information about its inner ear, vasculature, and cranial nerves, enabling us to rectify previous interpretations of some anatomic structures and recognize interspecific variations within Aetosauria. The systematic assignment of the UCMP specimens was also revised because UCMP 27408 was previously referred to *D. haplocerus* by Small (2002, Zool. J. Linn. Soc.136: 97 – 111), despite the type material lacking cranial material, so we refer both UCMP 27408 and 27410 to *D. spurensis* based on the following characters identified by Parker (2008, PaleoBios, 28: 1-40): transversely oriented groove on the parietals between the supratemporal openings, deep median pharyngeal recess, and almost no gap between basal tubera and basipterygoid processes. The new digital endocasts allowed us to reinterpret the exits of cranial nerves (CN) VII, VIII, and XII in the physical endocast UMMP 7476, and confirm the structure of the hypophysis, the passage of the internal carotid arteries, and CN VI of *D. spurensis*. The inner ear of *D. spurensis* has a marked difference between the anterior and posterior semicircular canals and a proportionally long lagena, in contrast to the short lagena and similarly sized anterior and posterior canals of *N. engaeus*. Another difference between these species is that the olfactory tracts are short in *D. spurensis* and the olfactory bulbs are as wide as long, being more similar to the situation in other herbivorous archosaurs, than in the animalivorous *N. engaeus*. Funding: PICT 2016-0159 (PB/JBD) & 2014-0609(JBD); NSF IOS-1050154 & 1456503 (LMW).

Automatic Landmark Identification in a Genetically Diverse Sample of Adult Mouse Skulls using Multi-atlas Label Propagation and Joint Landmark Fusion

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The allure of landmark coordinate data is its ability to represent biological information in a sparse, precise, and statistically meaningful form. Yet, manual landmark identification is tedious, time-consuming, and biased within and between observers. Atlas-based phenotyping, an image-processing paradigm situated between biology and machine learning, holds the promise of overcoming each of these concerns via automated landmark identification. The present work investigates the effects of highly variable adult mouse (*Mus musculus*) skull morphology on automatic landmark identification, then optimizes such landmark configurations via joint label fusion. We test the hypothesis that deforming each individual observation to a library of genetically diverse atlases (n=10) spanning a wide range of normal and mutant shape will improve the registration and offer an array of landmark configurations that can be fused into an optimal configuration. Using a test set (N=225) of micro-computed tomography images from 225 unique strain-genotype combinations, we linearly and non-linearly deformed each image to the atlas library. The resulting ten landmark sets for each specimen were fused and optimized into a single configuration using global and local image information, as well as Procrustes distance. Our results indicate that automatically derived landmark coordinates are significantly different from manual landmark coordinates, with a mean difference between 0.11 and 1.37 mm. Extreme cases of skull morphology are highly correlated with automated error. The most poorly identified landmarks are located on the zygomatic arch and on the anterior portion of the face, with errors exceeding 0.25 mm. However, the multi-atlas approach locates error prone landmarks with significantly higher precision. Principal axes of skull shape covariation are highly correlated across methods despite landmark differences. This work was supported by the McCaig Institute for Bone and Joint Health.

Morphology, Performance, and Anti-predator Strategies of Gobiid Fishes across Predator Regimes

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Anti-predator strategies facilitate the survival and fitness of prey species. Such strategies for avoiding attacks include: 1) avoiding areas with predators, 2) eluding predator detection, or 3) escaping predator attacks. Assessing habitat use, morphology, and escape performance can provide insight into the factors that underlie which strategies species implement. For prey species that evade predator attacks, kinematic escape performance is pivotal for survival. These species are likely to have morphologies that enhance escape performance. Alternatively, prey species that can avoid areas with predators or avoid predator detection may show lower escape performance than prey species living with predators. For such species, escape-enhancing morphologies would not be expected as their survival does not necessarily depend on this performance. Amphidromous gobiid fishes from Hawai'i and La Réunion provide an opportunity to test these predictions. These fishes develop in the marine environment but migrate into island streams to reach adult habitats. On Hawai'i some species can climb waterfalls to reach predator-free habitats, but non-climbers must evade predators throughout their life. On La Réunion some predator species can also climb, so climbing does not eliminate predation. We compared morphology and escape performance in six species of gobies: three that climb to avoid predators, two that experience predation after climbing, and one that does not climb and lives with predators. Using linear body measures, we found similar morphologies among all climbing species, regardless of predator regime. Moreover, species that overlap with predators had slower escape responses than species that migrate to predator-free habitats. These results suggest gobies that overlap with predators may avoid predator detection, rather than rely on kinematic escapes. These comparisons improve insight into the factors underlying anti-predator strategies.

The First Pseudothumb Identified in a Primate

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Several mammalian lineages – including bears, elephants, moles, and rodents – are known to have independently evolved accessory digits. These digits are interpreted as serving diverse purposes, from increasing pedal stabilization and digging efficiency to enhancing grip dexterity. For the first time, we present data on the presence of a 'pseudothumb' within a primate taxon – the enigmatic aye-aye (*Daubentonia madagascariensis*). This digit contains both bony and cartilaginous elements, and is associated with three distinct muscles. Collectively, these muscles cause abduction, adduction and opposition of the pseudothumb. Combining digital and physical dissection techniques, we present a three-dimensional visualization of these structures *in situ* and explore their functional role. The discovery of this anatomy also informs our understanding of the mechanisms by which a pseudothumb may emerge. Unlike the panda's pseudothumb (which is interpreted to have evolved as a result of the hypospecialization of the ursoid manual digits) or the mole's pseudothumb (which likely arose to broaden the hand), the aye-aye's pseudothumb likely arises as a result of the hyperspecialization of this taxon's hand, which is highly derived and features long, elongated digits that are impractical for grasping but coopted for percussive "tap-foraging". The aye-aye's pseudothumb may help to compensate for the poor grip capacity of these digits by providing additional dexterity to the palm, likely enhancing both postural stability on narrow substrates and the ability of the aye-aye to manipulate smaller items. As such, this discovery significantly broadens our understanding of one of evolution's most iconic anatomical traits.

Traversing the Water-Land Transition: Morphofunctional Evolution of the Tetrapod Humerus across an Adaptive Landscape

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The evolution of terrestrial tetrapods from their aquatic fish ancestors was an important transition in vertebrate evolution as it revolutionized terrestrial ecosystems. The origin of limbs is one key innovation that allowed tetrapods to invade the land; although the fossil record suggests that limbs evolved in aquatic animals and were later co-opted for terrestrial locomotion. There has been much debate on which stem tetrapods were capable of moving on land and how well, with little consensus achieved. Recent efforts to unravel the water-land transition have utilized musculoskeletal reconstruction, bone histology, trace fossils, and 3D-modelling; however, detailed quantitative analyses of locomotor traits have generally been limited in taxonomic scope. In this study, we capitalized on the abundance of fossil humeri preserved across the water-land transition – from tetrapodomorph fishes to crown tetrapods – and applied quantitative trait modelling techniques to provide novel insight into terrestrialization. We characterized the 3D-shape of 50 humeri (including newly discovered fossils) and assessed various functional parameters, including stress under mechanical load. These data were then used to generate a water-land adaptive landscape to explore the locomotor capacity of stem tetrapods. Our data show that the shape of the humerus follows a strong phylogenetic trend that is aligned along an ecological gradient. Further, stem tetrapod humeri are morphofunctionally diverse with some species better adapted to aquatic, and others to terrestrial life. By using a comprehensive taxonomic sample and quantitative techniques we demonstrate broad-scale ecological experimentation early on in tetrapod evolution, further details of which will be discussed.

Optical Computed Tomography of Large Specimens - Cleared and Stained in 3D

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X-Ray computed tomography (CT) scans are used to study the internal anatomy of organisms in great detail. More recently the ScanAllFish and OVert (Open Vertebrate) projects have made hundreds and thousands of scans of museum specimens free to download. These projects are a great way to make generally difficult to access collections available to everyone around the world. This technique works well for specimens preserved in ethanol, but more delicately preserved specimens are difficult to digitize and share. Cleared and stained specimens, for example, cannot be scanned the same way, so studies using them have been limited to 2D. We have addressed this problem by writing software to "scan" and digitize cleared and stained specimens in a way that allows us to make a 3D-model similar to the result of a CT-scan. We use a series of standard light photographs taken of a specimen fixed in a glycerin-gelatin mix and rotating on a turntable. The photo series is imported into software written in MatLab, and then digitally reconstructed using X-Ray CT-reconstruction techniques. The resulting reconstruction can be opened in 3D-Slicer, Amira, or any other software designed to open CT-scans. These methods can be used to make cleared and stained specimens easier to handle, and more widely available.

A New Lizard from the Jurassic of China

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The Jurassic record of lizards in eastern Asia is poor in comparison with that of the Cretaceous. In China, to date, the only confirmed records from this period are an armored lizard from Shishugou, Xinjiang Uygur Autonomous Region, of probable Oxfordian age, and two unnamed juvenile specimens from the slightly older, Callovian-Oxfordian, Nei Mongol locality of Daohugou. A new, well preserved lizard skeleton was found from the locality of Guancaishan, Jianping County, Liaoning Province, which is considered to be of similar age as Daohugou. It is distinguished from other Jurassic-Cretaceous lizards by a unique combination of derived characters, notably a long frontal with posterior processes that clasp the short parietal; cranial osteoderms limited to the lower temporal and supraocular regions; and an elongated manus and pes. In this new lizard, the relatively low number of sharp, well-spaced teeth suggests a diet of large insects. The deep maxilla, fused nasals, and extended frontal, in conjunction with the temporal osteoderms, may all have helped to strengthen the skull during feeding. And its large manus and pes, coupled with relatively long limbs, suggest it may have climbed or scrambled on uneven surfaces. Phylogenetic analysis using morphological data alone places the new taxon on the stem of a traditional 'Scleroglossa', but when the same data is run with a backbone constraint tree based on molecular data, the new taxon is placed on the stem of Squamata as a whole. Thus, its position, and that of other Jurassic and Early Cretaceous taxa, seems to be influenced primarily by the position of Gekkota.

Mammalian Whiskers and the Euler Spiral

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Mammal whiskers are often used as a model for understanding the sensory circuits in the brain. Signals from the whiskers, especially their forces, are processed throughout the brain, particularly in the somatosensory "barrel" cortex. Before attempting to interpret the neuronal signals, it is imperative to understand the signals received by the whisker follicles themselves and therefore accurately modelling whisker mechanics is important. Previously, whiskers have been modelled as a parabola based on Cartesian coordinates of the whisker centerline, but we propose that an Euler spiral model is a simple way to capture many aspects of whisker shape. In this study, we model 516 rat (*Rattus norvegicus*) whiskers as plane model curves with a linear relationship between arc length, s, and curvature, k, such that k(s) = A(s) + B and show that any original rat whisker can be mapped onto a normalized Euler spiral. The Euler spiral provides a convenient and highly accurate model for analytical studies, particularly intrinsically curved rods such as whiskers. The simplistic description in terms of coefficients A and B allows average whiskers to be created from data sets. In addition, vibrissae of many different species, such as pygmy shrew or grey seal, can be readily compared based on their shape alone.

Dynamics of the Postnatal Skull Disparities in Rodents

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The skull is a complex structure because of its numerous constituent bones and its involvement in many essential tasks. At the same time and somehow paradoxically, this unit is highly evolvable and presents a high diversity of shapes. Epigenetic interactions in response to mechanical stimulations will compensate and coordinate the growth of the different organs constituting the head, in order to acquire and/or to maintain certain functions. The importance of these interactions in the expression of inter-specific differences and at a large time-scale in the dynamics of clades remains nonetheless poorly understood. This study aims at observing the onset of craniofacial disparity during rodent ontogeny using 3D-geometric morphometrics. The variations in shape within ontogenetic series and the young and grown-up disparities will be observed using different juveniles and adults from European museum collections.

Variation in Patterns of Craniofacial Integration and Modularity across a Teleostean Species Complex Including Asexual Hybrids

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Epigenetic mechanisms shape developmental constraints and evolutionary trajectories. Epigenetic variation can produce phenotypic variation even in the absence of genetic variation. This additional source of variation may thus significantly affect phenotypic variability and, subsequently, ecology at the scale of species and populations. Hybrid organisms are interesting models for the study of epigenetics as hybridization disrupts genomic coadaptation, which may produce new developmental constraints in hybrids relative to parental species. Additionally, recombined genomes potentially offer novel epigenetic patterns and interactions absent in parental populations. The *Chrosomus eos-neogaeus* hybridization complex harbors asexual hybrids known to display genotype-dependent differences in phenotypes and ecology, and impressive phenotypic plasticity. *Chrosomus eos-neogaeus* hybrids also display genotype- and environment-dependent epigenetic marks which may lead to phenotypic novelty. This study aims to investigate how differences in genotype-dependent epigenetic variation and developmental constraints affect phenotypic variability in *C. eos-neogaeus* hybrids. Morphological variation and covariation in the craniofacial skeleton were assessed and compared across three hybrid genotypes and their parental species using μCT-imaging and three dimensional geometric morphometric analyses. Results reveal differences in morphology and in the structure of phenotypic covariation, between hybrid lineages and between hybrids and parental species. Hybrids seem to benefit from relaxed constraints, allowing for the expression of transgressive phenotypes. Hybrid lineages also display phenotypic variation that is equal and, sometimes, greater than that displayed by parental species. It remains unclear whether changes in developmental constraints in hybrids are the cause of the increased variability they display, and whether this affects the ecology of a given hybrid genotype.

Evidence for Modularity of the Weberian Apparatus in the Zebrafish *Danio rerio* Using MicroCT-Technology and 3-D Geometric Morphometrics

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Complex morphological systems are subject to constraints that divide the phenotype into modules (i.e., discrete units of variation), which influence their developmental and evolutionary trajectories. Some constraints are intrinsically developmental, and some arise due to functional and mechanical restrictions. The covariance structure of objects can be used to investigate the modularity of a system and test hypotheses based on functional, ecological, developmental or other factors. This approach is often used in geometric morphometrics and allows for in-depth investigation of developmental and evolutionary constraints. The Weberian apparatus, a crucial system for the auditory function of otophysan fishes (e.g., minnows, suckers, catfishes), is known for its complexity and its variability across taxa. Some authors even attributed the ecological success of otophysans to the evolution of the Weberian apparatus. Despite this, little is known about what shapes the evolution of the Weberian apparatus and how variable it is within taxa. The objective of this project is to test modular partitioning of the Weberian apparatus, and its modularity as distinct from cranial and trunk skeleton. Here, we assess phenotypic variation and modularity of the Weberian apparatus and associated elements in the zebrafish, *Danio rerio*, using micro-computed tomography and three-dimensional geometric morphometrics. Our results show high levels of phenotypic variation in the Weberian apparatus. Maximum-likelihood analyses suggest modular patterning based on functional groupings. This modular patterning also involves strong covariational tendencies between modules that constrain their variability. This approach could provide new insights into the evolution of complex structures such as the Weberian apparatus and how the space of possible phenotypes is constrained during evolution.

Filling the Olson's Gap? A Re-appraisal of *Raranimus dashankouensis* (Synapsida, Therapsida) using CT-Scanning Technologies

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Non-mammalian Therapsida is a paraphyletic group of Permian-Jurassic amniotes closely related to mammals. Understanding the origin of Therapsida is complicated by the existence of a phylogenetic gap in the fossil record termed Olson's gap. Because of its assumed low stratigraphic occurrence and basal phylogenetic position, *Raranimus dashankouensis*, from the Dashankou fauna, Qingtoushan Formation, China, is the best candidate to fill this gap. However, its phylogenetic position as the basal-most therapsid is the subject of debate. In addition, the age of the Qingtoushan Formation is poorly constrained. Enhancement of CT-scanning technology offers new ways to investigate the skull of extinct species and provides access to characters which were previously out of reach (e.g., internal cranial features such as cranial nerves) which can be useful for phylogenetic analysis. Our results show that *Raranimus* has five therapsid synapomorphies, the most obvious being the short contact between the maxilla and the prefrontal. However, the presence of plesiomorphic characters, such as the presence of a precanine caniniform tooth, manifest retention of typical “pelycosaur” grade features. The maxillary canal morphology of *Raranimus* is comparable to that of the "pelycosaur" *Varanosaurus* and the biarmosuchian *Herpetoskylax*. Overall, this suggests a very basal position for *Raranimus* in the therapsid phylogenetic tree. New data on the age of the Qingtoushan Formation indicates a Roadian age for *Raranimus*, hence filling Olson's gap and confirming that the genus is an important taxon for understanding the evolutionary origin of therapsids. The project is financially supported by the National Research Foundation, the DST-NRF Centre of Excellence in Palaeosciences, the Palaeontological Scientific Trust (PAST), and the Postgraduate Merit Award program of the University of the Witwatersrand, Johannesburg, South Africa.

Structural Adaptations to Flight in the Skeletons of Bats

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Bats are the only mammals capable of flapping flight. Bats belong to the order Chiroptera and are incredibly diverse, in terms of species number (> 1000), diet, size, trophic niches and flight behavior. Surprisingly, the structural adaptations of their skeleton, as a flying mammal have rarely been studied. Such adaptations can of course also vary within Chiroptera; for example, as a result of their differences of size, which probably affects their skeleton, bone micro-architecture and mechanical properties could be very different between megabats and microbats. In the same way, great disparity should exist between poor crawler bats and the vampire bat, which is a most adept terrestrial walker. The aim of this study is to characterize the different structural features of specific bones in a few bat species, compare them to typical terrestrial mammal bones in order to better understand their adaptation to flight. We investigated limb bones of several bat species: the large fruit Egyptian bat (Pteropodidae), the pipistrelle (Verpertilionidae), the mouse-tail bat (Rhinopomatidae) and the common vampire bat (Phyllostomidae). The bones were all scanned in a microCT and bone analysis (cortical and cancellous) was performed. We also studied transverse cortical bone sections with light microscopy, scanning electron microscopy, polarized light microscopy and confocal microscopy and perform some mechanical testing. The combination of these different technique permits us to better understand the structural adaptations and structure-function relationships in Chiroptera.

Assessing the Functional Evolution of the Semicircular Duct System at the "Fish"-Tetrapod Transition: Insights from Living Vertebrates

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The transition from aquatic to terrestrial lifestyle is accompanied by drastic changes in the physical constraints to which organisms must adapt. The invasion of land hence required a reorganization of the body plan and major changes in the feeding and locomotor functions. In this context, how the changes in body plan are associated with the evolution of terrestrial locomotion represents a central question for our understanding of the origin of land-dwelling vertebrates. The membranous semicircular duct system of jawed vertebrates is made of three interconnected ducts located inside the bony labyrinth of the inner ear. This organ is essential to monitor head motion, and thus represents a key sensorial component for the detection of body motion and orientation. As such, investigating the function of the semicircular duct system is likely to bring important insights into the evolution of the locomotor behavior during the transition from water onto land in vertebrates. We here present preliminary results on the comparative function of the semicircular duct system between five living vertebrates: the basal actinopterygian *Polypterus*, the coelacanth *Latimeria*, the terrestrial salamanders *Dicamptodon* and *Eurycea*, and the lizard *Podarcis*. Specimens were either scanned using PPC-SRμCT at the ESRF (ID19), or μCT-scanned after staining in PTA to generate high-resolution 3D-reconstructions of the inner ear and of the delicate membranous semicircular duct. Then, we used the Ariadne toolbox to analyze quantitatively the morphology and function of the semicircular duct system in each taxon. Time constants, sensitivity and spatial configuration of the semicircular duct system were calculated and compared. Future work will involve the inclusion of fossils to determine the temporal pattern of the functional evolution of the semicircular duct system, and how it relates to the evolution of tetrapod body plan and terrestrial locomotion.

Comparative Musculoskeletal Anatomy and Function between Fishes and Amphibians

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The colonization of land during the Devonian represents a major environmental transition in the evolution of vertebrates. The dramatic differences in the physical properties of water and air imposed a major restructuring of the skull between "fishes" and tetrapods, that is now well-documented. However, how and when the changes in skull shape across the fish-tetrapod transition were associated with a shift towards a terrestrial feeding system still remains unanswered. Tackling this question first requires gaining a deeper understanding of the skull anatomy and function in extant taxa. Here, we present preliminary results obtained for the musculoskeletal anatomy and function of the head in three living vertebrates that bracket fossil early tetrapods: the basal actinopterygian *Polypterus*, the coelacanth *Latimeria*, and the fire salamander *Salamandra*. Specimens were μCT-scanned prior to and after staining, allowing for the 3D-reconstruction of both hard and soft tissues of the head. These detailed virtual models were complemented by dissections in order to obtain further morphological observations, and to quantify important muscle parameters, such as muscle fiber length and muscle physiological cross-sectional area. In addition, we collected *in vivo* bite force measurements for *Polypterus* and *Salamandra*. These data were then used as input parameters to build and validate numerical biomechanical simulations of the cranial musculoskeletal system for each of these taxa. Using inverse dynamics we calculated muscle activity, bite force, and joint reaction forces during biting. These multibody dynamic models allowed us to compare quantitatively how the musculoskeletal function and skull kinematics relate to biting performance. This deeper understanding of the anatomy and function of the cranial musculoskeletal system in living taxa will serve to reconstruct the morphological and functional evolution of the cranial musculoskeletal system in fossil lobe-finned fishes and early tetrapods.

Gonad Structure Related to Insemination in the Teleost *Pantodon buchholzi* (Pisces: Teleostei: Osteoglossomorpha: Pantodontidae)

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Pantodon, a representative of a primitive Teleostei group, Osteoglossomorpha, shows unique features of reproductive biology, especially in the presence of a complex introsperm structure. This contrasts with other species of this group, possessing flagellate or aflagellate aquasperm. Therefore, the aim of our study was to analyze gonad structure and gametogenesis in both sexes of *P. buchholzi*. In contrast to other osteoglossomorphs characterized by external fertilization and possession of a single gonad, gonads in both sexes of *P. buchholzi* are paired and exhibit features described in the literature only in inseminating teleost species. Each of the testis consists of seminiferous anastomosing tubules and is divided into an anterior part, where spermatogenesis occurs, ending with packet formation; and a posterior, aspermatogenic area, transformed into testicular gland, in which naked sperm packets, named spermatozeugmata, are stored in secretion filling tubules of the testicular gland. Ovaries in *P. buchholzi* contain oocytes in different stages of oogenesis without signs of synchronous development, observed among other Osteoglossomorpha. Differentiating oocytes exhibit unusual features connected with the presence of a Balbiani body, including the formation of clusters of organelles, e.g., nuage arranged into net structure keeps elongated mitochondria together, forming a mitochondrial aggregation. During oogenesis the cytoplasm displays different degrees of electron density; from electron-dense cytoplasm dominating in previtellogenic ovarian follicles to electron-lucent cytoplasm filling vitellogenic oocytes. Moreover, the mucosa bordering the ovarian cavity is deeply folded and creates numerous crypts, while the epithelial cells show apical specializations forming microvilli and cilia. The extremely different structure of gonads and gametes in *P. buchholzi* suggests Pantodontidae branched off very early from other osteoglossomorph taxa.

Optimizing diceCT-Staining Protocols to Mitigate Potential Degradation of Museum Specimens

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Diffusible iodine-based contrast-enhanced computed tomography (diceCT) techniques allow visualization of soft-tissues of fluid-preserved specimens in three dimensions without dissection or histology. Two popular diceCT-stains, iodine-potassium iodide (I_2KI) dissolved in water and elemental iodine (I_2) dissolved in 100% ethanol (EtOH), yield striking results. Requests to apply these stains to anatomical specimens preserved in natural history museums are increasing, yet curators have little information about the potential of the various stain solutions to degrade the condition of specimens under their care. Typically, vertebrate wet specimens are stored in 70% EtOH, which differs in make-up and concentration from the aforementioned popular stain solvents. To assess for effects of stain solvent on typical museum specimens, we compared popular stains to two relatively unexplored stains (I_2KI in 70% EtOH, I_2 in 70% EtOH) that allowed specimens to remain in 70% EtOH throughout. House sparrows (*Passer domesticus*) were collected and preserved under uniform conditions following standard museum protocols (i.e., IACUC approval, formalin fixation, ethanol preservation), and each was then subjected to one of the stains. Results show that three of the four stains (I_2 in 70% EtOH, I_2 in 100% EtOH, I_2KI in 70% EtOH) worked equally well (producing fully stained, life-like, publication quality scans) but in different timeframes (five, six, eight weeks, respectively). The specimen in I_2KI in water took the longest to stain and exhibited anomalous degradation. We conclude that staining in I_2 in 70% EtOH can yield high-quality soft-tissue visualization in a timeframe that is as short, or even shorter, than better-known iodine-based stains, without subjecting museum specimens to changes in solvent concentration or type. Funding: NSF DGE 1645419 to CME; Alexander Wetmore Fund of the Smithsonian National Museum of Natural History Division of Birds.

Comparative Morphology of the Laryngeal Soft Tissue in Testudines by Means of Contrast Enhanced μCT and its Role in Vocalization

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Our current understanding of form and function of the structures employed for vocalization in Testudines remains notably limited. To gain insight into their possible interactions, we carried out μCT-scans on the larynx of *Testudo horsfieldii* (Testudinidae) and *Emys orbicularis* (Emydidae), which serve as examples of the two turtle clades with the greatest number of vocalizing species. Phosphotungstic acid (PTA) was utilized for contrast enhancement. We measured position, dimensions, orientation and association of the laryngeal muscles and cartilage. For outgroup comparison, we carried out the same procedure on the larynx of the lizard *Lacerta agilis*. Our results present the first μCT-scans and 3D-visualization of the laryngeal soft tissue in Testudines. Several findings exceed basic laryngeal functions (i.e., protection from aspiration). The organization of the Musculus constrictor laryngis and the Musculus dilatator laryngis indicate a coordinated action in laryngeal retraction comparable to a mechanism described in crocodiles. Moreover, an anteroposterior gradient in cartilage thickness and association is likely to locally affect rigidity. Both of these aspects might enable the laryngeal cavity to modulate its shape, as known from psittaciform birds. Furthermore, we detected different possible modes of laryngeal closure and generating longitudinal tension in the vocal folds. In *T. horsfieldii*, laryngeal diverticula and a tracheal reduction were observed, of which we infer a possible benefit for vocalization. Overall, we were able to show remarkable similarities to crocodiles and birds. Since the evolution of vocalization in Testudines and their sister taxon, Archosauria, still remains to be clarified, we performed an ancestral state reconstruction based on the latest phylogenetic data. We found that vocalization appears to be plesiomorphic for all Testudines, indicating a potentially shared acquisition of vocalization for the two clades.

Quantification of the Influence of Fossoriality on the Inner Bone Structure of the Cranium in Burrowing and Surface-Terrestrial Lizards (Squamata)

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Vertebrate ecology has been successfully inferred from bone microstructure in the past, but a systematic approach to quantify differences of the inner bone structure in the skull of squamate reptiles, i.e., lizards and snakes, has never been undertaken. In head-first-burrowing squamates, for example, the cranium is the structure exposed to the greatest strain, so one would expect that a distinct fossorial ecology might be reflected in the thickness and compactness of cranial bones. In this respect, lacertoid lizards appear particularly attractive as a model system since they contain closely related taxa with pronounced differences in cranial bone structure and ecology. Within Lacertoidea, the fossorial Amphisbaenia possess thick and compact cranial roofing bones whereas their surface-terrestrial sister taxon, the Lacertidae, seem to be lacking such traits, but these differences have previously not been quantified. We employed microCT-scans and the image analysis software ImageJ to generate a comprehensive data set including thickness and compactness of premaxilla, nasal, frontal and parietal of different lacertoids. Taking into account the different positions of homologous bones along the anteroposterior skull axis, we were able to plot the distribution of these parameters over a cranial profile. These profiles differ consistently in amplitude, slope and position of maxima according to fossoriality, with amphisbaenians showing a greater thickness and compactness in the anterior region of the skull. Our next steps include a phylogenetically informed analysis of fossorial and non-fossorial taxa across Squamata as a whole, in order to test our findings in a larger systematic context and to investigate if there are general patterns that repeatedly evolve under similar ecological conditions.

On the Morphogenetic Historiography of the Archosaur Femur

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The downward directed leg posture is one of the key innovations for dinosaurs. The main rationale for this derived posture is the modification of hip joint morphology, which must have taken place necessarily through the modification of its morphogenesis. Thus, understanding its morphogenetic evolution enables us to reconstruct the concrete transitional process of dinosaurian morphological evolution and provides us with a mechanistic viewpoint on it. Hence, we studied the key modification of the dinosaurian hip joint, the acquisition of the inward-directed head of the femur (thigh bone), by using embryos of extant organisms and the fossil record and reconstructed the evolutionary process of hip joint morphogenesis. First, we compared the 3D-shape of the femoral anlagen and their morphogenetic processes between alligators (with the ancestral state) and quails (with the dinosaurian state). We found that the incipient shape is so conservative while the following morphogenetic processes are quite different, which results in the difference of the femoral head direction. Second, we listed adult phenotypes of the femoral bone (e.g., the position of protrusions and depressions) available to distinguish the morphogenetic types (alligator-type or bird-type) and found the non-avian dinosaurs would have developed the femora through a small modification of the alligator-type morphogenesis, not through a bird-type one, although non-avian dinosaurs had inward-directed femoral heads like birds. Based on these results, we hypothesized an evolutionary scenario in which the inward-direction of the femoral head was firstly acquired through a small modification of the alligator-type morphogenesis and was later substituted by a bird-type one during bird evolution. In this way, we demonstrated that the combinational analysis of embryos and fossils enables us to reconstruct even the counterintuitive, elusive, and complex evolutionary history of dinosaurian morphogenesis.

Differences in Position of the Cotylar Fossa on the Astragulus and its Function in the Proximal Talar Joint between Primates and Other Mammals

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The cotylar fossa on the astragalus is not a common characteristic among mammals but is known to be present in phylogenetically distant taxa such as primates, many afrotherians, and kangaroos. I examined morphological differences of the cotylar fossa among these groups and its functional significance in the ankle joint. The observations were carried out using skeletal specimens. The cotylar fossa articulates with the medial malleolus of the tibia, serving as part of the articular surface of the proximal talar joint. In primates, the cotylar fossa is located at the medial wall of the astragalar body. The space between the medial malleolus of the tibia and the fibular malleolus is much wider than the astragalar trochlea; thus, the medial malleolus and the cotylar fossa do not make a firm contact during usual dorsoplantar flexion. The contact between the fossa and the malleolus is observed when the foot is dorsoflexed as well as everted. In afrotherians, the cotylar fossa is located at the base of the astragalar neck and/or the distal end of the medial wall of the astragalar body. The distal surface of the medial malleolus fits to the fossa, and the maximum fit is achieved at the dorsoflexion of the ankle joint. In kangaroos, the cotylar fossa is a groove-like structure parallel to the astragalar trochlea. A flat surface of the distal end of the malleolus is pushed into the groove at the dorsoflexion of the ankle joint. Because of the firm contact, eversion or inversion does not occur in a dorsoflexed ankle of afrotherians and kangaroos. In conclusion, the possession of the cotylar fossa has been treated as the same characteristic in phylogenetic analyses; however, this study indicates morphological and functional differences of the cotylar fossa between primates and other mammals, and suggests that this structure may have developed under functional demands of different joint motions among different mammalian taxa.

Signal Evolution and Morphological Complexity in Hummingbirds (Aves: Trochilidae)

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The origins of morphological and functional novelty remain central questions in evolutionary biology, and rapidly-evolving sexually selected traits are particularly understudied in this regard. Hummingbirds have some of the brightest and most iridescent colors in nature. Their feathers contain optically complex stacks of hollow, platelet-like, melanin-filled organelles called melanosomes, but neither has how these produce colors, nor their evolution been systematically studied. We first used nanoscale morphological measurements and optical modeling to identify the physical basis of color production in 34 hummingbird species. We found that in general the melanosome stacks function as multilayer reflectors, with platelet thickness and air space size explaining variation in hue (color) and saturation (color purity). Additionally, the outer keratin cortex both affects saturation (through modulating primary peak width) and, in conjunction with small, previously-undescribed melanosomes that lie below it, produces secondary reflectance peaks. We then compared evolutionary rates of both, the morphological components and the colors (at a wavelength-specific level) they produce. The outer keratin cortex evolved at a faster rate than the other morphological traits, likely because of its evolutionary independence. Intriguingly, shorter wavelength colors evolved faster than long wavelength colors, perhaps due to sensitivity biases in bird vision or because of a developmental process that enables greater lability of smaller melanosomes. Together, these data demonstrate that morphological complexity enables greater evolutionary lability and potential for new functionality.

Geographical Variation of the Skeletal Morphology in Red Jungle Fowl and its Morphological Changes in Domesticated Populations

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The skeletons of the red jungle fowl (*Gallus gallus*) were osteometrically compared among the populations from Vietnam, Laos and Bangladesh. We used 44 museum specimens, including the three traditional subspecies, to clarify the geographical differences in *G. gallus* from the Southeast and South Asian Districts. One of the subspecies, *G. gallus murghi* from Bangladesh, was clearly distinguishable from the other subspecies using canonical discriminant analysis of osteometrical data. We did not confirm the morphological differences of the skull between the subspecies *G. gallus gallus* population from South Vietnam and the subspecies *G. gallus spadiceus* of North Laos. In the canonical discriminant scores morphological similarities were demonstrated in the skulls of the populations from North Laos and South Vietnam. As a result, it was concluded that red jungle fowls shows no obvious osteometrical variations between geographical localities on the Indochinese Peninsula, although previous studies had pointed out that these subspecies show various external morphological differences. These studies also suggested that zoogeographical barriers between the North and South Districts of the Indochinese Peninsula may affect the variations among subspecies of the red jungle fowl. Next, the osteometrical data of the skull from the red jungle fowl were compared with those from the domesticated populations, with the aim to understand patterns of morphological changes during domestication. The changes of the frontal bone area were noticeable in the domesticated fowl. The characteristics of the domestication enhance the positive allometric growth in width of the frontal bone in the case of the fowl. It is also shown in the domestication process in mammals. In addition, the volume of the brain is being examined in fowls using three-dimensional image analysis. We expect a relative decrease of the volume of the brain from red jungle fowl towards domesticated breeds.

Optimizing Segmentation and Surface Generation of Bones from μCT-Scans Using Synthetic Image Stacks

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In biology and related fields measurements are commonly derived either directly from micro computed tomography (μCT) scans or polymesh surfaces derived secondarily from such scans. Workflows of measurement acquisition comprise the step of image segmentation. Various studies indicate that a precise segmentation is crucial for obtaining accurate measurements either from the volume data or derived surfaces. Aiming at minimizing error in the segmentation of scans and in derived surfaces, a synthetic image stack that mimicked a μCT-scan of the pectoral girdle bones of frogs was generated and the quality of different segmentation and surface generation strategies was assessed. Results indicate that the most accurate segmentation is obtained by the application of automatic local thresholding algorithms to a version of the μCT-stack in which the histogram range has been adjusted such that it lays symmetrically around the average of the mean gray values of bone and soft tissues. Surfaces derived from the result of such an adjusted segmentation process are most accurate if a careful and moderate surface simplification (reduction of polygon count and smoothing) is applied; obtaining surfaces with sub-voxel accuracy is possible (maximum vertex

deviations: of 0.4-0.8 voxel depending on scan and segmentation quality; outliers: 8-9 voxels). In the case of an error-free segmentation, surfaces with a maximum vertex deviation of less than 0.2 voxel (with outliers deviating up to 7 voxels) are achievable. If the segmentation result is too inaccurate, surface simplification generally has a negative effect on the accuracy of surfaces. Future studies are needed to validate the results for real μCT-scans and different specimens. This work was funded by the Deutsche Forschungsgemeinschaft (HA 2323/14-1).

Making Sensory Hair Cells from Ectodermal Placodes: The Development of the Paratympanic Organ in Chick

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In this study, we are using the development of the paratympanic organ in chick to better understand how sensory hair cells develop from ectodermal placodes. Sensory hair cells are ciliated mechanosensory receptors that are critical for hearing, balance and our sense of motion. In tetrapods they are mainly situated within the inner ear, although in some groups they can also be found outside the inner ear. An example of this is the paratympanic organ (PTO), an enigmatic structure found in the middle ear of crocodiles and birds. It is a small sack-like organ, filled with sensory hair cells in the medial wall of the middle ear cavity and attached to the tympanic membrane via Platner's ligament. The function of this organ has not yet been elucidated, although it has been speculated that it is involved in barometric sensing. The developmental origin of the PTO in chick has been traced to a Sox2-positive ectodermal placode just dorsal to the geniculate placode of the first pharyngeal pouch. Cell-tracing studies has shown that all the cells of the PTO are derived from this placode; sensory hair cells, supporting cells and even the afferent neurons. This makes the PTO an attractive system for understanding the development of sensory hair cell producing placodes. In this study, we describe the development of the PTO from ectodermal placode to fully functional organ. To analyze the molecular pathways that are required for sensory hair cell development, we analyze the gene expression at various stages of PTO development using RNA-seq. This information can then be compared with similar studies of sensory hair cells in other organs such as the inner ear to get a better understanding of how ectodermal placodes give rise to sensory hair cells.

The Effect of Mass and Habitat Preference on Limb Long Bones: an Investigation in Bovidae (Mammalia, Cetartiodactyla)

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In tetrapods, limb long bones are essential for movement and body support, notably by providing attachment for the muscles. The shape of long bones is therefore expected to be heavily impacted by a variety of factors, e.g., the environment in which an animal lives, its mass, its morphology and body proportions, and its evolutionary history. Understanding the influence of these various factors necessitates the investigation of limb bone shape in a highly diverse group. Bovids are excellent in that regard. They comprise about 280 species that are found in Africa, Eurasia and North America, in a diversity of environments from hot, dry deserts to dense rainforests, steep mountains and tundra. They present a wide range of mass, from approximatively 2 to 1200 kilograms, and include some of the earliest species domesticated by humankind. Despite all these variations, they retain a relatively homogeneous morphology. Here, we studied each of the limb long bones (humerus, radius-ulna, femur, tibia-fibula), across 51 species of bovids belonging to ten of the twelve recognized tribes. We sampled the species in order to encompass a great diversity of masses and habitats. We quantified the shape of the bones and its variations, using 3D-geometric morphometrics. We characterized the influence of the various morphological, biological, phylogenetic, and ecological factors using multivariate analyses. Beyond testing and analyzing the impact of these various parameters on the shape of the various limb bones, these analyses enabled us to notably characterize the shape changes associated with high body mass and with habitat preference in bovids, and to make comparisons with what is known for other lineages.

A Universal Power Law for the Growth and Form of Teeth, Claws, Horns, Thorns and Beaks

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An immense diversity of pointed structures is found throughout biological systems, including teeth, claws, horns, thorns and beaks. While the shapes of some of these structures have been attributed to a logarithmic (or equiangular) spiral, these structures generally do not fit this pattern very well. Here, we show a new model of growth and shape based on a power law that generates accurate representations of teeth from all vertebrate groups (e.g., Mammalia [Marsupialia, Carnivora, Cetartiodactyla, Chiroptera, Primates], {Reptilia [Squamata, Dinosauria, Sauropterygia, Ichthyosauria], Aves [*Ichthyornis*]}, Osteichthyes and Chondrichthyes). For instance, growth of unicuspid teeth as diverse as those found in humans (R^2 = 0.998), *Smilodon fatalis* (R^2 = 0.999), *Tyrannosaurus rex* (R^2 = 0.998), and *Carcharocles megalodon* (R^2 = 0.997) are extremely well described by the model. We can also use it to describe the growth of individual cusps on multicuspid teeth, and variation of tooth shape along the tooth row, in tooth families and within species. It represents the shape of cusps more accurately than existing *in silico* models of tooth development, and can be used to predict the original shape and length for worn and broken teeth. This new model of cusp shape is the third general model of tooth development, adding to the patterning cascade that describes cusp position and the inhibitory cascade that predicts tooth size. Beyond dentitions, the model also depicts the growth of claws in Mammalia, horns in Cetartiodactyla, beaks in Aves, and thorns from Plantae. This model provides a mechanistic basis for the generation of these structures across the tree of life.

Cracking the Evolutionary and Developmental Link between Brain and Skull in Archosauria

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The brain has a primacy in early cranial development. Extant birds underwent an enlargement of the brain in comparison to other reptiles. This process caused important changes to the bird skull, in particular the skull roof. However, a link between the brain regions and the skull roof elements has never been formally addressed. CT-scanning, immunofluorescence and confocal imaging were combined to track mesenchymal condensation and ossification patterns of the skull roof along the development of the brain in a developmental series of diapsids, including squamates, stem and crown crocodilomorphs, dinosaurs and crown avialans. Correlation tests between the boundary of brain regions and the suture between frontal and parietal were statistically significant, suggesting a deep evolutionary link. Mesenchymal cells condense early in organogenesis between the forebrain and midbrain and midbrain and hindbrain. However, it is only after establishment of the facial region and its chondrogenesis that the mesenchymal condensations of the skull roof start to express Collagen I. We found no support for Sox9 and Collagen II expression in these mesenchymal condensations. Moreover, we found no proliferation center in the skull roof, suggesting that physical variables, such as the pressure in the ventricle of the brain, are driving ossification of the dermatocranium surrounding the brain. Birds show a delayed patterning of the skull in comparison to reptiles. We suggest that this is due to the positive allometry of the bird brain, contrary to the negative trajectory observed in reptiles. We regard the skull roof as an example of non-independence character, because strongly influenced by the evolution and development of the brain. This could explain why several bones composing the braincase and not in direct contact with the brain were lost along the evolution of the main branches of Amniota.

3D-Atlas of the Embryonic Human Heart

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Recent publications of 3D-models of the human embryo and fetus have shown that there is a need for digital 3D-anatomical learning tools for students, developmental biologists, and clinicians. Heart development is highly complex and many cardiac anatomical changes have not been illustrated by the current models. In the coming years, we aim to elucidate the normal cardiac development of the human heart in an annotated 3D-atlas. The atlas will cover weeks 3 to 8 of development (Carnegie stages 9 to 23). It will be based on histological sections, reconstructed with Amira software, culminating into interactive models that facilitate understanding of the complex 3D-morphogenesis. The sections used are immunofluorescently stained for several transcription factors and ion channels that are key in heart development and cardiac physiology. These stains will be used to clarify structural and functional borders in the tissue. We will annotate structures according to current medical curricula for heart anatomy and development. All annotations can be converted to volumetric readouts whereby growth, and the timing of it, can be measured. By this, we can for example, analyze growth of mesenchymal tissues in the completion of septation and the extent of trabeculations to the ventricular walls. Our project will result in a quantitative framework for physicians and researchers to evaluate development that complements the qualitative measures that are prevailing today. So far, an early and a late embryonic heart have been comprehensively labelled and in parallel we are keeping an extensive matrix of temporal changes.

Morphological Integration of the Head in Salamanders: Impact of Developmental Strategy and Ecology

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Caudata display a great diversity of developmental strategies directly impacting their morphology and the exploitation of their environment during their ontogeny. Several different developmental strategies have evolved independently during the evolution of Caudata. For example, some species exhibit direct development, hatching directly as terrestrial miniature versions of the adults, whereas others are paedomorphic, retaining aquatic larval traits even if they are reproductively active. Other species have a complex life cycle with bi-phasic development, allowing them to exploit different environments during morphologically different life history stages. The aim of this study is to test the impact of the complexity of life cycles and ecology on cranial shape evolution. To do so, high-density geometric morphometric and integration methods were used to characterize the shape of 14 regions of the cranium for 150 species spanning the full phylogenetic, ecological, and developmental breadth of Caudata. Each cranial region was analyzed separately to detect mosaic evolution and test for a relationship between magnitude of integration, morphological disparity, and evolutionary rate. Morphological integration, modularity, and disparity analyses were carried out in order to test if a complex life cycle promotes phenotypic disparity and modularity, whereas paedomorphic or direct development strategies may instead promote morphological integration and constrain shape variability. Our results show that head shape can be differentiated based on life history, with paedomorphic species having higher rates of shape evolution and disparity than biphasic or direct-developing ones. Species with direct development have the lowest disparity and rate of morphological evolution. The latter can possibly be explained by the loss of larval structures and ontogenetic repatterning.

Convergences Toward a New Mammalian Jaw Muscle System among Three Oceanic Island Lineages of Worm Eating Rats

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Most spectacular shifts in morphology and ecology seem to result from major historical events, such as mass extinctions or island emergences. The repeated shift from omnivory to vermivory (the consumption of earthworms) among Indo-Pacific rodents constitute one of the most spectacular dietary changes, both in terms of ecology and morphology. Their peculiar morphological characteristics led early taxonomists to group some of these genera in their own subfamily, the Rhynchomyinae Thomas 1898. We combined classical and virtual dissections to study the craniomandibular system of these atypical insular rodents. We observed that the dietary shifts toward vermivory involved major morphological rearrangements of the cranio-mandibular system including the elongation of the rostrum and jaws, the loss of cheek teeth, a high mobility of the jaw symphysis, and some modifications of the alisphenoid region. The reduction of the masseteric region associated with the loss of gnawing and chewing capacities also induced a major reshaping of the classical mammalian cranio-mandibular muscle system. Notably, we found that these rodents have extremely large pterygoid muscles associated with both an increased propaliny and medio-lateral jaw movements. These morphological changes likely enable these worm-eating rats to use their jaw as a tool like a tweezer to manipulate and ingest earthworms.

Species Specificity of Tooth Roots in Bats (Chiroptera, Vespertilionidae)

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Bone remains of six bat species (*Eptesicus nilssonii*, *Plecotus auritus*, *Myotis brandtii*, *Myotis mystacinus*, *Myotis daubentonii*, *Myotis dasycneme*) were found in Holocene sediments of caves in the northeast of the Perm Pre-Ural. The last three species are represented only by single bones. The degree of the preservation of the teeth in the fossil maxillae of three species [*E. nilssonii* (1,319 maxillae), *P. auritus* (66), *M. brandtii* (129)] and morphological features of roots of a large premolar (P4) and molars (M1, M2, M3) were investigated. In all three species the roots of P4 are curved in shape and are located in different planes relative to each other - this allows the tooth to be retained in the maxillae of the fossils (the percentage of the fossil maxillae with this tooth: *E. nilssonii* – 87.0%, *P. auritus* – 81.8%, *M. brandtii* – 79.8%). The wide angle between buccal roots M2 of all three species of bats also holds the tooth relatively firmly in the maxilla (76.3 %; 75.8 %; 82.2 % - in each species respectively). M1 of *E. nilssonii* is most weakly retained in maxillae (50.0 %) since its roots are located almost in parallel. However, this tooth is preserved better in the maxillae of other fossil taxa - there is a wide angle between roots M1 of *M. brandtii* (64.3 %), parallel buccal roots and lingual root M1 of *P. auritus* are bent in different directions (80.3 %). M3 of *P. auritus* is the most vulnerable tooth to be lost (27.3 %), primarily because of the parallel arrangement of its roots in the anteroposterior plane and their very slight curvature. Roots of M3 of *E. nilssonii* are located at a wide angle (61.1%), while the roots of M3 of *M. brandtii* are relatively close together (50.4%). The orientation of roots relative to each other can serve as an additional characteristic for species identification of isolated fossil teeth in bats. This study was funded by RFBR, research project № 18-04-00982a.

Generating and Testing Hypotheses of Dinosaur Foot Motions Using 3D-Digitized Tracks and Large-Scale Granular Simulations

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The evolution of modern birds from their dinosaur ancestors is a major transition, well known in the classroom and in popular media. Unfortunately, being extinct makes it difficult to study dinosaur movements and compare their terrestrial locomotion with extant birds, which retain the bipedal, tridactyl-foot anatomy, but differ in limb proportions and in lacking the large muscular tail. Whilst bones present a static view of extinct animals, fossil footprints are a direct record of the activity and motion of the track maker. Deep footprints are a particularly good record of foot motion. Such footprints rarely look like the feet that made them, the sediment being displaced by the foot motion. Because of this, such tracks are often overlooked or dismissed in preference for more foot-like impressions. However, the deeper the foot penetrates the substrate, the more motion is captured in the sediment volume. We have used deep, penetrative, Jurassic dinosaur tracks which have been naturally split into layers, to reconstruct foot motions of animals living over 200 million years ago. We consider these reconstructions to be hypotheses of motion. To test these hypotheses, we use the Discrete Element Method, in which individual particles of substrate are simulated in response to a penetrating foot model. Simulations that produce virtual tracks morphologically similar to the fossils lend support to the motion being plausible, while simulations that result in very different final tracks serve to reject the hypothesis of motion and help generate a new hypothesis. Not only does this workflow shed light on how individual feet moved, but our ability to digitally look inside the footprint throughout its formation process (a process we have dubbed 'track ontogeny') has enabled us to identify emergent sedimentary features common to certain motions and foot morphologies, particularly regarding exit structures which secondarily deform entrance deformations.

Characterizing the Deep-Time Shifts during Pan-Pleurodira (Testudinata) Body Size Evolution

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The Pleurodira encompass 93 out of 356 extant turtle species and are currently restricted to the freshwater habitats of the Southern hemisphere. The group's fossil record, often neglected in macroevolutionary studies, indicates greater species richness, broader distribution and occurrence in different habitats. The group also exhibits a remarkable body size disparity throughout its more than 160-million-year evolutionary history, which remains to be quantitatively characterized. In this study, we employ phylogenetic comparative methods to identify the patterns of body size evolution in pan-Pleurodira. We measured dorsal carapace length (as a proxy for total body size) from 118 pan-pleurodiran species, and used a time-scaled phylogenetic tree to fit a set of evolutionary models. Our results show that a multi-peak OU-based model (i.e., SURFACE) received significantly higher support (based on AICc scores) over all other models fitted to our data, suggesting that different clades experienced shifts towards distinct body size optima during their evolution. Most SURFACE model fits identified evolutionary regime shifts towards larger body sizes in relation to the ancestral regime, such as in Taphrosphyini (theta, θ = 606.75–562.13 mm of carapace length) and in a clade that includes Podocnemididae, Peiropemydidae and some podocnemidoid taxa (θ = 429,13–370,02 mm). These regime shifts occurred predominantly during the beginning of the Late Cretaceous, suggesting that environmental conditions may have impacted on body size regime shifts by the end of the Mesozoic. In particular, the frequent identification of independent shifts with the same body size optima (θ = 606.75–562.13 mm) in two different lineages of Chelidae (in *Mendozachelys* and in an extinct clade within *Chelina*) suggests that Southern South American environments could have more influence on chelid body size regimes than their evolutionary history.

Nasal Chambers of the Bowhead Whale (Cetacea: *Balaena mysticetus*): Embryology and Histology

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Whales, dolphins, and porpoises are generally considered to have a very poor sense of smell. However, some baleen whales have well developed olfactory bulbs and dozens of olfactory receptor genes. The purpose of this study is to investigate the presence and distribution of olfactory epithelium in the nasal chambers of a baleen whale, the bowhead. Additionally, we describe the shape of the nasal chambers, turbinate bones, nasal passages, and olfactory bulbs through fetal development. We CT-scanned the nasal chambers and surrounding anatomy of bowhead whales: a postnatal individual, a nearly full-term fetus, and a fetus approximately halfway through gestation. By reconstructing the lumen of the respiratory tract, we documented changes in this anatomy through ontogeny. We examined the distribution of epithelium in the postnatal nasal chambers using histology and immunohistochemistry. We stained for olfactory marker protein (OMP), which is expressed in mature olfactory sensory neurons. On the CT-reconstruction of the same animal, we mapped the location of the epithelium that was examined histologically within the nasal chambers. The respiratory tracts of the fetuses are similar morphologically. The connections from the nasal chambers to the nasal passages are not as wide in the fetuses as they are in the postnatal individual. Additionally, their turbinates project less far into the chamber. The pseudostratified columnar epithelium of the postnatal nasal chambers has characteristics of olfactory epithelium. Additionally, we found that particularly the cilia on the lateral wall of the nasal chamber, rostroventral to the cribriform plate are OMP-positive. Taken together, this evidence supports a sense of smell in bowhead whales and lays the foundation for determining what these whales smell.

Distribution of Morphological and Phylogenetic Diversity of Freshwater Fishes of the United States

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The freshwater fauna and hydrography of the United States has been the subject of intense study for more than a century, resulting in an abundance of data concerning the environment and composition of these freshwater communities. We harnessed existing species distribution and phylogenetic resources and joined them with a novel body shape dataset for more than 900 species of freshwater fishes native to the contiguous United States to determine how the spatial distribution of species richness relates to morphological and phylogenetic diversity. Species richness of freshwater fishes in the United States follows the drainage patterns of major river basins, with the most diverse communities in the lower Mississippi River basin and southeastern Appalachia. Analysis of phylogenetic diversity revealed a similar pattern, with a small number of phylogenetically over-dispersed communities localized to the Mississippi delta and the southern Atlantic coast. Consistent with previous studies, morphometric analysis of body shapes revealed strong phylogenetic signal in patterns of morphological diversity. Accordingly, morphological diversity largely followed the spatial distribution pattern of phylogenetic diversity. More than 40% of morphological variation in the species sampled was summarized by an axis describing differences in position of the pelvic fins, associated with the divergence between spiny-finned teleosts and other ray-finned fishes.

Birds Like It Hot: Diversification of Skull Shape in Birds during the Past Climatic Changes

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There is enormous variation in morphological diversity across modern vertebrates. However, how this diversity has evolved through geological time is still much debated and has been mostly assessed through the study of simple traits such as body-size, despite morphology being inherently multi-dimensional. This continuing reliance on easily characterized (univariate) traits comes from the computational and statistical challenges of studying high-dimensional phenomic datasets. Here, we build on recently proposed phylogenetic models of traits evolution that relate evolutionary rates to past climatic events along with new methods that are capable of handling high-dimensional datasets through penalized likelihood techniques to tackle the question with geometric morphometrics datasets. We used intensive simulations to assess the performances of the approach and applied it to a recently-published high-density 3D-geometric morphometric dataset for the avian skull. Our dataset samples 352 species spanning the extant diversity of birds with 757 landmarks and sliding semi-landmarks. Overall, we found that the skull morphology is best fit by a climatic model where rates of evolution are positively correlated to past climatic temperatures, meaning that rates of cranial evolution increase during warmer periods of the Cenozoic. This result is in contrast to that found in previous analyses of body size using similar methods, which suggested that higher rates were observed in colder periods. Although a substantial part of the shape diversity is not explained by these models, as would be expected for the shape of a structure as complex as the avian cranium, these results suggest that past climatic changes – and in particular climatic optimums – have left a significant imprint on the morphological diversity of modern birds.

Biomechanical Implications on the Evolution of Turtle Skull Architectures Using Finite Element Analyses

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In extant turtles, a large quadrate is strongly fused to the braincase and a broad temporal skull coverage imposes space constraints for their jaw musculature. Posteriorly elongated squamosals and supraoccipitals, however, provide additional insertion sites. A trochlear mechanism redirects jaw muscle fibers around the large otic chamber developed first on the outer surface of the chamber itself (most stem-taxa, cryptodires) and second on a lateral projection of the pterygoid (in pleurodires). Several changes related to the loss of skull mobility, incl. the omission of the basipterygoid articulation by a sutural contact and the closure of the interpterygoid vacuity, also appeared, and diverse marginal reductions of dermatocranial bones developed in different taxa. To assess the biomechanical implications of these morphological changes to the skull of turtles, we conducted a series of Finite Element Analyses (FEA) in eight extant and three extinct turtles. We modeled skulls with and without the trochlea and, in the earliest shelled turtle *Proganochelys*, a skull with movable and stiff basipterygoid articulations. Our results show an increase in overall stress in the clade including extant turtles and baenids with stiffened skulls and unambiguous trochlear mechanisms in relation to earlier taxa. Expansion of the ventrolateral emargination appears to be related to a more stressed quadrate, but posterodorsal emarginations do not seem to reflect distinct stress patterns. Suturing the basipterygoid process relieves stress on the basicranium, which may have allowed muscles related to neck retraction to expand onto this area. Additional analyses, modelling hypothetical pterygoid trochleae and temporal crests in stem turtles helps understanding the relation between the morphological evolution and function of the diverse turtle skull architecture permitting the emergence of a variety of feeding behaviors.

Covariation Patterns in the Skull of Ant-Eating Placentals

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The evolution of complex anatomical structures results from the coordinated variation (integration) of semi-independent groups of traits (modules) and reflects developmental, functional, and genetic constraints. The modular organization of the vertebrate skull represents trade-offs between interacting functions such as hearing, sight, smell, mastication, and breathing, as well as its embryonic origins. Adaptation to myrmecophagy (ant- and termite-eating) drove the convergent evolution of the morphology of the skull of a few placental lineages resulting in extremely long rostra, a reduction or total loss of teeth, and a modified masticatory apparatus. Using the ant-eating model, we aim to test if the convergent evolution of such drastic dietary specializations affected cranial covariation patterns in independent lineages. A landmark-based approach enabled us to compare patterns of cranial modularity across more than 600 specimens including anteaters, pangolins, giant armadillos, aardvarks, and aardwolves. We use Euclidean Distance Matrix Analysis (EDMA) and community detection network approaches to explore intraspecific modular structures without a priori. We further test multiple a priori hypotheses of cranial modularity using maximum-likelihood model selection and covariance ratio tests. Additionally, we assess the effect of full configuration Procrustes superimposition in trait integration by calculating covariation within and between independently aligned modules. Our results show evidence that between-modules covariation is affected by Procrustes superimposition. Nevertheless, all approaches recovered modular patterns consistent with previous studies on placental mammals, partitioned in six modules. Surprisingly, most of the myrmecophagous species presented a strongly integrated oral-nasal module, despite the absence of incisor and canine dentition. The palatine/molar region remained moderately integrated despite the loss of functional teeth and chewing.

Exceptional Mesozoic Fossils Reveal the Mosaic Assembly of the Crown Bird Skull

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The distinctively modified skull of crown birds is strikingly different from the condition of their dinosaurian antecedents. Bird skulls exhibit an enlarged, toothless premaxillary beak and a linked, multi-bone kinetic system incorporating the mobile palate and jaw suspensorium. The expanded neurocranium of crown birds protects an enlarged brain and is flanked by jaw adductor muscles substantially reduced relative to those of carnivorous theropod dinosaurs. Understanding the order of appearance of these distinctive crown bird features, and the nature of their earliest manifestations among Mesozoic Avialae remain unclear, due to a fossil record characterized largely by fragmentary and distorted fossils. The Late Cretaceous toothed avialan *Ichthyornis* sits in a pivotal phylogenetic position outside crown bird diversity: close to the extant avian radiation, despite retaining numerous ancestral characters. Although its evolutionary importance is clear, no substantial new cranial material has been described beyond incomplete remains recovered in the 1870s. We report four three-dimensionally preserved specimens of *Ichthyornis* as well as two previously overlooked elements from the holotype and present a virtually complete 3D-reconstruction of the *Ichthyornis* skull using high resolution microCT. We show that *Ichthyornis* had a small transitional beak—lacking a palatal shelf and restricted to the tips of the jaws—coupled with a kinetic system essentially indistinguishable from that of living birds. The brain of *Ichthyornis* appears relatively modern compared to stemward avialans, but the temporal region of the *Ichthyornis* skull was unexpectedly plesiomorphic, retaining a large adductor chamber bounded dorsally by substantial bony remnants of the ancestral upper temporal fenestra. This combination of features illustrates that important characteristics of the avian brain and palate evolved before the reduction of jaw musculature and the full transformation of the beak.

Phenotypic Integration in the Vertebral Column of Mammalian Carnivores

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In a previous work, we demonstrated that vertebral column disparity (=morphological variability) in mammalian carnivores increases in an antero-posterior direction along the presacral region; while the cervicals exhibited the lowest values of disparity, the lumbars exhibited high disparity values, as recently demonstrated for all mammals. However, changes in phenotypic integration along the presacral region of the spine has not been investigated in the order Carnivora as a whole. Here, we investigate phenotypic integration along the vertebral column of carnivores using a sample of all presacral vertebrae in 50 species belonging to different families and also having different locomotor strategies (i.e., pursuit *vs* ambush predators). We use pairwise comparison of vertebral shape covariation and we test our results with different hypotheses of developmental and functional modularity from three-dimensional symmetrized aligned-Procrustes of vertebral shape. Our results indicate the presence of more integrated subsets of vertebrae within regions but disintegrated transitional vertebrae among regions. In the light of this new evidence, we discuss the link between phenotypic integration, locomotor adaptation, and evolvability.

Examining the Relationship between Tooth Size and Food Size: the Functional Consequence of Dental Reduction

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Molar teeth can vary considerably in morphology between species. Whilst the effect of dental shape on food breakdown has received some attention, the role of dental size in efficient food breakdown is not understood. This is especially relevant for our own species: the size of the molar teeth has reduced significantly during the course of human evolution. However, little is known about the impact of dental reduction on food breakdown performance and diet. To examine this relationship, stainless steel dental models of a modern *Homo sapiens* upper and lower dental row were manufactured and attached to a universal physical testing machine. The dental models were isometrically scaled up, producing a series of models with increasing surface areas. Using a 3D-printer, spherical hard brittle food replicas were produced in small (10mm diameter), medium (15mm), and large (20mm) sizes. Spheres of each size were crushed between each dental size using the physical testing machine, and the peak force at initial fracture, energy required to induce fracture and fragmentation were recorded. The smaller teeth were slightly more efficient, reducing the force required and energy for all sizes of food. However, compared to the effect of changes in food size and the location of the bite on the tooth, performance differences between the different tooth sizes were minimal. The results suggest that individuals could access different stress resistant food resources by simply changing how they position a food item, but also suggest that dental reduction during human evolution may have had a minimal impact on the ability of the individual to break hard food items of varying sizes. Further consideration is now needed into how such dental reduction would impact on tooth fracture risk and dental performance with foods of different material properties.

Scaling with Scales: Analysis of Armor and Swimming Through Ontogeny in the Bay Pipefish, *Syngnathus leptorhynchus* (Syngnathidae: Actinopterygii)

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Syngnathid fishes provide an unusual opportunity to examine dermal armor development throughout ontogeny and quantify the influences of sex-role reversals on the morphology of teleost fishes. Individuals of the Bay Pipefish, *Syngnathus leptorhynchus* (n=16), were filmed, CT-scanned, and measured to analyze swimming kinematics and dermal armor characteristics. These analyses indicate that individuals do not scale proportionally during ontogenetic growth in terms of body diameter, cross-sectional area of the body, or surface area of dermal armor. Instead, larger individuals have a more slender body shape with a much smaller cross-sectional area than is predicted by an isometric growth model. Further, swimming speed and estimated Reynolds number scales with total length to the power of 1.8 and 2.7, respectively. Thus, juveniles of *S. leptorhynchus* become proportionally faster as they grow in size, and swim at lower Reynolds numbers than mature individuals. Mature Bay Pipefish adults, regardless of sex, have proportionally larger scales that cover a greater percentage of their body when compared with small juveniles. There are also distinct shape differences in the dermal armor between sexes; these differences are likely related to reproductive roles, because male brooding requires specialized bony structures along the abdomen and tail. In summary, body shape and dermal armor in *S. leptorhynchus* change with size and sex, and these variables likely influence the functional characteristics such as Reynolds number and swimming speed.

Incisor Modifications in Euarchontoglires (Mammalia: Placentalia): A Morphological Survey Informed by the Fossil Record

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Euarchontoglires, a large clade of placental mammals, which includes primates, scandentians, dermopterans, and Glires (lagomorphs and rodents) has at least 65 Ma of documented evolutionary history, with the representatives of primates and Glires both present in the early Paleocene. The morphology of lower cheek teeth across the group shows a 'common denominator' of an uncomplicated tri- (or two-) cuspidate trigonid and a broadly basined talonid, fitting well within the tribosphenic molar paradigm. On the other hand, the incisor portion presents a wide variety of loci number and morphology. Large and open-rooted incisors of the second deciduous pair are one of the major synapomorphies of Glires. They share the enlargement of the lower mesial incisors with the Late Cretaceous eutherians, Zalambdalestidae (although it is not necessarily a homologous feature). The elongated, frequently ever-growing permanent incisors are known to appear also in many lineages of euarchontans, such as plesiadapids (stem primates), plagiomenids, and *Daubentonia* (a lemur), indicating the evolutionary potential for modifications of this segment. The elongated, although to a lesser extent, incisors appear in some anagalids, a basal group of Paleogene Euarchontoglires endemic for Asia. These observations highlight the general plasticity of the incisor segment in Euarchontoglires. This is further underscored by variability in shape (a frequent formation of lobes and grooves) as adaptations to food ingestion or grooming. The observations across the phylogenetic tree show a recurring convergence of incisor elongation in many lineages of Euarchontoglires (including potentially ancestral Zalambdalestidae). In our broad review of the incisor size and form we focus on early Paleogene Glires, noting the shortening of lower incisors very early in some Glires; although convergent with crown Lagomorpha, this trait is generally opposite to that in fossil and extant Rodentia.

Evolution of Tendon Shape in Diphyabatrachia is Influenced by Size, Phylogeny and Locomotion

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Tendons are viscoelastic elements with unique mechanical properties. With a close relation to movement, tendon function is mainly related to the transmission, amplification and recycling of energy. In Anura, jumping is the principal locomotor challenge, and most related anatomical specializations have been observed in the pelvic girdle and hind limbs. Despite a greatly specialized body plan, locomotor variation in anurans goes beyond jumping, including specializations for swimming, burrowing, and climbing. In this study, we apply geometric morphometrics to test for morphological adaptation in three tendinous elements associated with the urostyle and hind limb joints. Variation in 99 species of the Diphyabatrachia clade was analyzed as a study case, taking into consideration functional and ecological aspects of species and their phylogenetic history. The Diphyabatrachia include jumping and climbing species of arboreal habitats (Centrolenidae) and jumping species of long and short distances with terrestrial and aquatic habitats (Leptodactylidae). We found significant differences between locomotor modes and habitat use regarding tendon shape, especially in the patellar tendon of jumping-arboreal species when compared to others. In all analyzed tendons, locomotor modes and habitat use showed interaction with size. Optimization and reconstruction of tendon shape revealed two putative synapomophies, a broad tendon of the longissimus dorsi for Leptodactylinae and an elongated patellar tendon for Centrolenidae. In addition, there was significant covariation of shape between the knee and the heel tendon shapes, which led us to propose a functional analogy between these two structures. All evidence points to an adaptive significance of tendon variation, yet the results also showed a great influence of phylogeny. Therefore, it is possible to conclude that a combination of factors, rather than one determinant variable, is influencing tendon evolution in Dyphiabatrachia.

Exceptional Preservation in a Pennsylvanian Ray-Finned Fish and the Limits of Neuroanatomical Inference from Actinopterygian Cranial Endocasts

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Key evidence for ray-finned fish monophyly and interrelationships derives from brain anatomy. While the endocavity in most modern actinopterygians—especially teleosts—does not bear a close correspondence to the enclosed brain, endocasts in Paleozoic ray-finned fishes are widely assumed to provide a faithful record of neuroanatomy. For several decades, rare natural endocasts and a handful of models from physical tomography yielded the only constraints on brain structure in early actinopterygians. A diversity of computed tomographic endocranial models now complement older examples, and provide new data bearing on longstanding uncertainties concerning the placement of fossils relative to one another and modern lineages. We used micro-computed tomography to examine the three-dimensionally preserved *Coccocephalichthys wildi* from the Pennsylvanian (Bashkirian; ca. 315 Ma) of the UK. Consistent with past phylogenetic interpretations, *Coccocephalichthys* shows derived endocast features widely distributed among Carboniferous actinopterygians but lacking in earlier taxa: anteriorly directed olfactory tracts, a long common olfactory canal, and widening attributed to expanded optic lobes. The specimen also preserves two large, pear-shaped otoliths, broadly similar to the few examples described from Paleozoic actinopterygians. More significantly, this specimen shows extensive preservation of apparent soft tissues within the cranial endocavity, including features interpreted as remains of the brain and cranial nerves that can be compared directly to modern examples. Putative neural structures do not fill the endocavity in *Coccocephalichthys*, calling into question the fidelity with which early actinopterygian endocasts record neuroanatomy more generally. Although it could require re-evaluation of existing interpretations of fossil endocasts, *Coccocephalichthys* provides a remarkable snapshot of brain anatomy in the actinopterygian stem group.

Propping on Forelimbs Carries a High Risk of Rib Fractures in *Tyrannosaurus* (Dinosauria: Theropoda)

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Tyrannosaurus (Theropoda, Dinosauria) is one of the largest bipedal tetrapods of all time. Despite its iconic status, the use of its small forelimbs remains uncertain. A recent study proposed that *Tyrannosaurus* have propped on the forelimbs for supporting the body when rising up from a crouched posture. However, the rib cage supporting the forelimbs is subjected to vertical compression between the downward gravity and upward ground reaction force via the serratus muscles, which originate on the lateral wall of the thoracic ribs and insert on the scapulae. According to a three-dimensional finite element stress analysis on the rib cage that assumes vertical compression, the rib cage of *Tyrannosaurus* can bear up to 20–40% of the body weight, while the pubis can bear about six times its body weight. The weakness of the rib cage in *Tyrannosaurus* stands out among the other terrestrial tetrapods, including quadrupeds and birds with flight ability, whose rib cage can bear more than twenty times their body weight, and obligate bipeds whose rib cage can bear no more than ten times their body weight. Therefore, *Tyrannosaurus* have a high risk of rib fracture in rising up by propping on the forelimbs. The strength of the rib cage in relation to the body weight can be one of the indicators on whether the animal can support its body on forelimbs or on thorax, especially in theropod dinosaurs which retained a bipedal posture.

Robotics-inspired Biology: Simple Decentralized Control Mechanism Reproduces Versatile Gait Patterns in Quadruped Locomotion

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Quadrupeds exhibit versatile gait patterns (i.e., interlimb coordination) depending on locomotion speed, body properties, and circumstances. While quadrupeds have a large diversity in their morphology, different species have similar gait patterns, suggesting that there is some common principle to generate adaptive locomotion patterns. Although neurophysiological studies show that adaptive interlimb coordination is partially generated by decentralized control mechanisms, e.g., central patterns generator (CPG) and local sensory feedback, it is still unclear how body properties induce adaptive interlimb coordination. To this end, our research group has developed a simple interlimb coordination mechanism that allows simple quadruped robots to generate flexible locomotion patterns in response to body properties. For example, a robot with front-heavy body exhibits lateral-sequence walking gait, while a robot with rear-heavy body exhibits diagonal-sequence walking gait (Owaki et al. 2013, J. Roy. Soc. of Interface 10: 20120669). As another example, different inertia of the robot's body induce different running gait patterns: a robot with a pendulum on its backside shows a pacing gait while a robot without the pendulum shows a trotting gait (Owaki et al., 2014, Proc. of Dynamic Walking 2013, 2013, 5, 11). Furthermore, the same control mechanism can allow quadruped robots to adapt to changes in locomotion speed by gait transition (Owaki & Ishiguro, 2017, Sci. Rep.7, 277: 1-10). These robotics case studies show that adaptive locomotor patterns can emerge from the interactions between the controller, body, and environment, suggesting the significance of body properties in the generation of versatile quadruped gait patterns. We believe that robotics can produce useful tools for morphology to interpret form and function underlying vertebrates' adaptive behaviors, leading to an interdisciplinary study which can be called "Robotics-inspired Biology."

Open Science : 3D-Vertebrates Scan of the Paris Museum

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The Paris national museum of natural history (MNHN) is implementing an open science data policy as recommended by EU policies on research data. There are still obstacles, which make that the data may not be findable, accessible, interoperable, and reusable ('FAIR'). The slowness of digitization is probably the prime factor in hampering implementation of open access. In the case of morphology, the MNHN developed two different strategies based primarily on 3D-images. Although abundant and widespread in the natural sciences, 3D-imaging methods relevant to these issues turn out to be little adapted to the broad sampling of skeletons of large dimensions (acquisition time, processing time, data quality). In March 2016 scanning was performed of exhibited specimens from the galleries of paleontology and comparative anatomy of the Paris Natural History Museum, where over 200 large skeletons were globally scanned by Global Digital Heritage. These mounted skeleton are composed of hundreds of different bones, tedious to accurately digitize in 3D because many surfaces remain hidden to the scanning device. The cloud point already usable will be completed. An explanation how to design and implement a mathematical model of the bone surface deformation through optimization will be presented elsewhere (Gailliègue et al., this conference). Beside this program, organizing a common repository is our second objective. The MNHN have several hundreds of scientists, which make digitizations, organized in 18 research teams, which may also have scanning platforms. Both for their conservation and for valorisation of our collections, we have implemented simple and standardized tools for a 3D-repository. In connection with the scientific databases, 3D-imaging files of the Museum's collections from the different digitization platforms of the institution, or from external sources are thus made available to the community for new research programs or for any other use related to the missions of the Museum.

Automatic 3D-Mesh Reconstruction of Mounted Skeleton Point Clouds

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In the collections of natural history, mounted skeletons, composed of hundreds of different bones, are among the most complex objects. To produce a virtual representation of many vertebrates, the Gallery of Palaeontology and Comparative Anatomy of the National Museum of Natural History of Paris was globally scanned, which resulted in a digitized 3D-point cloud of more than 200 large mounted skeletons. However, the use of this data to investigate large vertebrates' body shape requires a mesh triangulation, instead of isolated points in space, to obtain consistent and accurate biomechanical models. The aim of the present work is to develop a mathematical model of the bone surface deformation and to produce a 3D-surface reconstruction, adapted to the geometric properties of a given skeleton point cloud (e.g., morphology, shape and number of bones, noise artifacts, density defects, parasitic points). Each skeletal feature from the point cloud is reconstructed by deforming and adjusting a generic representative surface from a common skeleton template, based on morphological synapomorphies. This morphing leads to the definition of a closed orientable surface and to the preservation of specifically labeled components, and also allows the mathematical extrapolation of the unknown articular surfaces, which were not covered during the data acquisition. The results will be validated using numerical simulation from the anatomical point of view, in order to conduct derivative morphofunctional studies. Collections of natural history are a huge research infrastructure, limited by their accessibility. New digital tools, like an automatic 3D-reconstruction of mounted skeleton point clouds, represent a major step forward for their massive digitalization. Moreover, the ability to model the biomechanical behavior on comparative series of complete large vertebrate skeletons will allow to improve the reliability of functional interpretations about changes in body shape for adaptation.

Armor in the Invasive Lionfish, *Pterois volitans*: Head Morphology Varies Across Ontogeny

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Fish head armor has many uses including protection, defense, and displays in mating rituals. Previous work showed that head spine number increased with ontogeny in the native *Pterois brevipectoralis*; juvenile and young specimens have a simple nasal spine with a spinous point, while larger fish have additional spinous points. *P. volitans* have eighteen venomous spines on three fin locations: dorsal, pelvic, and anal; and have sharp facial/head spines similar to *P. brevipectoralis*. The goal of this study was to quantify differences in the bony head armor of *P. volitans* over ontogeny and between sexes. We hypothesized that the facial spines would increase in number over ontogeny, and *P. volitans* develops additional armor as it grows. We hypothesized that facial spines would not be sexually dimorphic since no morphological characters have been found to date. Controlling for fish total length, we measured lengths and widths of the largest facial spines: 5 (coronal), 7 (parietal), and 8 (nuchal) for 34 lionfish ranging in size (83.3mm - 381mm) using digital calipers. We found no difference between total length of the fish and sex ($p=0.532$) or total number of head spines and sex ($p=0.336$), suggesting that the total number of facial spines is not a sexually dimorphic trait in *P. volitans*. We did find significant differences in facial spine number as total length increases ($F_{1,33}=62.87$, $p<0.0001$). Thus, the number of facial spines does increase over ontogeny for *P. volitans*. Finally, linear regressions showed that length and width of the coronal, parietal, and nuchal spines varies significantly with total fish length. These data suggest that the large coronal, parietal, and nuchal facial spines of *P. volitans* increase in width and length as the fish grows. Overall, these data show that the invasive lionfish develops a robust, sharp facial morphology over ontogeny, even though this extremely invasive fish has limited natural predators in its invasive range.

Convergent Evolution of Flight Morphology in Frugivorous Bats

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Flight ecomorphology studies typically concentrate on the relationship between wing shape and diet. For example, the slender and curved wings of swifts and swallows are a classic case of convergent evolution for insect hawking. However, correlations between diet and flight morphology are not limited to the wings, with bats also utilizing ear and tail membranes in flight. Yet, studies of convergent evolution in bat flight morphology are rare, despite a diverse array of diets beyond hawking insects. In particular frugivory is common not just in the well-known large Pteropodidae (fruit bats), but also in other phylogenetically distant families such as the New World Phyllostomidae. Given that selective pressures for an efficient foraging strategy are likely different for frugivorous and insectivorous species, we hypothesize that frugivorous bats will exhibit diet-related morphological adaptations of their flight structures. Furthermore, these adaptations will converge in morphospace between phylogenetically-distant species. To test these hypotheses, morphological data from the flight structures of 280 species were gathered, including metrics such as ear, thumb and tail membrane length. Dietary classifications were assigned from the literature and data analyzed using a phylogenetically-corrected principal component analysis. Additionally, the presence of convergent evolution towards frugivory in flight morphology was tested. Our results indicate that flight morphology strongly correlates with diet, with frugivory associated with short (or no) tail membrane, long thumbs and small ears. Furthermore, convergent evolution in flight morphology for frugivory was identified, with New World frugivorous Phyllostomidae sharing morphological adaptations with Old World Pteripodidae, distinct from their insectivorous ancestral form. These results highlight the importance of considering all flight structures beyond just the wings when studying the ecomorphology of bats.

Foot Morphology In, Print Morphology Out: A Biplanar X-ray Approach for Studying the 3-D Dynamics of Human Track Formation

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The number of known Plio-Pleistocene hominin track sites has increased dramatically in the past decade. These data can inform long-standing debates about hominin locomotion, but researchers still deliberate over exactly how pedal anatomy and gait biomechanics should be inferred from track morphology. This lack of consensus stems from our limited understanding of the complex interactions among anatomy, motion, and substrate that generate track shape. Insights from living taxa are elusive because 1) data from stiff-surfaced instruments cannot be extrapolated to deformable substrates, and 2) direct visualization is hindered by foot and substrate opacity. We developed a variation in methods based on X-ray Reconstruction of Moving Morphology to analyze the foot-substrate interface. Seven human subjects were recorded at 50 fps as they walked across radiolucent artificial substrates (three deformable muds and a rigid carbon fiber plank). Using the coordinates of 70 skin markers applied to the sole and toes, we constructed a dynamic mesh of 112 polygons to animate the 3D-shape of the foot during each step. Foot motion was then compared to photogrammetry-derived 3D-models of the final track morphology. We found that foot dynamics were significantly influenced by substrate deformability. Both the heel and medial longitudinal arch deformed to greater extents as substrates became more rigid. In very soft muds, we found that the 3D-topography of resulting tracks did not directly reflect foot motion. Specifically, deformations from the heel and arch in early stance were reworked later in stance as the forefoot and toes were maximally loaded. These results highlight the complexity and dynamic nature of track formation and offer a path forward for more accurately inferring foot anatomy and motion from fossil hominin tracks. Supported by the U.S. NSF, the Chatham University Research and Sabbatical Committee, and the Brown Undergraduate Teaching and Research Awards program.

Evolution of Carpal Morphology during the Land-to-Water Transition in Whales

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During the land-to-water transition in the Eocene, the cetacean skeleton underwent modifications that are well-documented in the fossil record. The forelimb changed from a weight-bearing pentadactyl structure to a flipper with an immobile carpus. Extant mysticetes, baleen whales, maintain six carpals, ossification of which is delayed or absent. Carpal number and morphology vary in odontocetes, toothed whales. Modern artiodactyls, which share a common ancestry with cetaceans, alter their carpal number in relation to the reduction of metacarpals. The most archaic artiodactyls have digit morphologies similar to Eocene whales. We used CT-imaging to assess evolutionary changes in the articulation of the carpus within Eocene taxa associated with the limb-to-flipper transition. In particular, we compared *Ambulocetus natans*, a well-preserved amphibious archaeocete taxon, with other semi-aquatic archaeocetes. The pisiform of *A. natans* is robust and projects laterally, an orientation shared with extinct and extant cetaceans. However, articulation of the pisiform and trapezium vary among archaeocetes. The pisiforms of *A. natans* and *Dorudon atrox*, another Eocene cetacean, articulate with the ulna and cuneiform. This carpal is small in *Maiacetus inuus*, an Eocene cetacean, and lacks contact with the ulna. The trapezium of most mammals articulates with metacarpal I and the scaphoid. Both the trapezium and trapezoid lie distal to the scaphoid and medial to the magnum in terrestrial mammals. *M. inuus* differs from this pattern; the trapezium articulates with the radius. Moreover, *M. inuus* and *A. natans* display an additional carpal that lacks an artiodactyl homologue. The trapezium is lost in pentadactyl cetaceans, leaving direct contact between the scaphoid and metacarpal I. These morphological changes may relate to functional shifts from weight-bearing locomotion to a mediolaterally expanded flipper that acts as a control surface.

Development of Feeding and Airway Protection in Preterm Infant Mammals as a Model of Altricial Evolution

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Variation along a precocious-altricial axis has evolved multiple times in vertebrates, especially in mammals. However, functions such as feeding and respiration must be in place at birth. In mammals, these behaviors require the coordination and integration of multiple systems, as well as neural control beyond the reflex level, as respiration can only be briefly interrupted. Preterm infant mammals represent a natural experiment in the limits of altriciality, and the level of performance necessary for survival. We tested the hypothesis that preterm infants lack coordination in oropharyngeal kinematics, which in turn compromises performance, both in feeding and in airway protection. We obtained 21 preterm infant pigs through C-section, at the youngest age where independent respiration was possible. We measured oropharyngeal and laryngeal function during feeding in these animals and in 17 term infants using high-speed digital videofluroscopy from birth through weaning. Preterm infants are capable of intraoral transport and swallowing, although the kinematics of tongue and hyoid that generate these behaviors are not well coordinated. The correlation of epiglottal movement and pharyngeal arch contraction, a hallmark of airway protection that characterizes term infants prior to weaning, was significantly delayed in preterm infants. Despite poor oropharyngeal coordination, preterm infants were capable of successful feeding, growth, and weaning and showed substantial postnatal development in the coordination of their oropharyngeal kinematics. We conclude that functional variation associated with gestation time is a potential substrate for natural selection.

High-Resolution Episcopic Microscopy (HREM): A Tool for Three-Dimensional (3D) Visualization of Vertebrate Embryos

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"High resolution episcopic microscopy" (HREM) is a *post-mortem* 3D-imaging technique based on physical sectioning of tissue samples embedded in resin. Stacks of up to 5000 inherently aligned digital images are captured directly from the surface of the resin block during sectioning on a microtome. The single images of an HREM image series nearly match the quality of digitized images of hematoxylin/eosin stained histological sections. Volume data generated from HREM image series have a typical voxel size of $2 \times 2 \times 2\ \mu m^3$ and are available within a few hours after starting the HREM sectioning and data generation process. We provide information on the HREM data generation process and show examples of 3D-computer visualizations generated from mouse, chick, quail, clawed frog, horse, ferret and zebrafish embryos and of tissue material harvested from adult mice, pigs and humans. The results demonstrate that HREM is a powerful technique for 3D-visualization and highly detailed spatial analysis of the morphology of whole embryos, placenta and tissue material harvested from a broad range of vertebrate species.

Opening up the Treasure Chest: Mass Digitization of Historic Histological Slides

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Histological slides were the high-tech morphological approach during the nineteenth and early twentieth century. The field of embryology is closely linked to this technology, resulting in the production of large collections of sectioned specimens. Since their initial production, these have represented an important source for research and the Embryological Collection housed at the Museum für Naturkunde, Berlin, Germany, remains a well sought-after resource for vertebrate morphologists up to this day. The collection encompasses the research collections from numerous scientists, including those from A.A.W. Hubrecht and J.P. Hill. However, there are constraints linked to the use of this resource, formed by travel requirements of the user and the conservation status of the specimens. Due to aging processes, a slow decay of the slides is apparent in many of these specimens. To facilitate use and to preserve the information contained in the specimens that may be lost otherwise, digitization of these objects has started. Embedded in an international co-operation (Digital Embryology Consortium) to digitize part of the slides in the Embryological Collection, a workflow for the slide scanning of these historical objects at the museum was developed. This ultimately results in the online publication and access of these slides in a virtual microscope environment. Thus, the inherent information of the slides is preserved and access for interested researchers is facilitated.

Endoskeletal Trabecular Bone in a Placoderm from the Early Devonian of Mongolia

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Endochondral bone is widely considered a derived trait of osteichthyans—the clade comprising the bulk of modern vertebrate diversity. The absence of endochondral bone in chondrichthyans and jawless fishes is therefore considered the retention of an ancestral vertebrate condition. By contrast, the fossil record strongly suggests that exoskeletal bone is a ancestral gnathostome trait that was lost in the lineage leading to modern chondrichthyans. Recent evidence has reinforced this, linking the facial skeletal armor of osteichthyans to that of placoderms—an assemblage of armored jawed vertebrates from the Silurian and Devonian periods. Here, we report the first substantial evidence of endochondral bone in a placoderm from the Early Devonian of Mongolia. The primary specimen consists of a partial skull roof and braincase. The braincase shows a clear lack of osteichthyan synapomorphies, and lacks features common to early crown-group gnathostomes such as an otico-occipital fissure. However, the inter-perichondral space is filled with a rich network of bony trabeculae comparable to those observed in early osteichthyans. Using synchrotron tomography of a stem-group chondrichthyan with a highly calcified endoskeleton, we demonstrate profound differences between this type of tissue and the endoskeletal ossification in the new placoderm. While this fossil represents a single occurrence, it fits into the now rapidly closing gap between placoderm and osteichthyan morphology. It highlights questions about both the origin of bone, early gnathostome phylogeny, and the geographical centres for gnathostome evolution.

Using Morphological Techniques to Reveal the Ecology of Miniature Coral Reef Fishes

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The abundance and diversity of vertebrates on coral reefs is exceptionally high, with each square meter of reef housing up to 80 individuals and 14 species of fishes. While abundant and diverse, the majority of these fishes are very small and remain hidden from view for most, if not all, of their lives. These small fishes, primarily in the families Gobiidae (gobies) and Blenniidae (blennies) are collectively known as cryptobenthic reef fishes (CRFs). All evidence points to CRFs playing important roles in coral reef trophodynamics, acting as a critical step in the recycling of waste materials back into the food web. However, the cryptic behavior of these fishes means that directly quantifying the functions of CRFs is almost impossible. Ecomorphological techniques using microCT-scanning, linear and geometric morphometrics, offer the potential to reveal the function of difficult-to-study organisms, and have been used to reconstruct the feeding modes and ecological structure of extinct reef fish assemblages. These same techniques show promise in identifying feeding modes and functional roles of CRFs. However, there are potential complications as miniaturization, a defining characteristic of CRFs, is often associated with developmental truncation/paedomorphism, which could limit differences among taxa, and hinder comparative morphological analyses. Here, I will present the results of a morphological analysis of functionally important traits, which reveals surprising morphological variability in CRFs, highlighting the potential utility of morphological analyses in elucidating their ecological roles. I will then move on to propose novel applications of microCT-data to identify functionally important traits and provide direct evidence of previously unknown feeding modes in these small coral reef fishes.

Morpho-Functional Diversity of the Masticatory Apparatus in Extinct South American Ungulate Mammals

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During their evolutionary history, mammals underwent numerous events of diversification that resulted in a large variety of shapes and spectacular examples of morphological convergence. Notoungulates are a clade of endemic South American mammals, which appeared during the Late Paleocene and became extinct during the Pleistocene. They present a large diversity of cranial and dental sizes and shapes, including numerous convergences with extant groups of mammals (e.g., rhinos, horses, rabbits, and rodents). However, their ecological and functional affinities remain to be discussed. Here, we explore the biomechanical and functional diversity of the masticatory apparatus in notoungulates mainly focusing on the last diverging and most specialized families. We performed a comprehensive study integrating analyses of dental enamel microstructure, and quantification of cranial shape with 3D-geometric morphometric analyses, in 21 and 25 genera of notoungulates respectively. We found that late diverging families present some strikingly convergent and complex enamel microstructure patterns associated to high-crowned teeth. Interestingly, comparisons with perissodactyls, their putative closest extant relatives, showed that these notoungulates paralleled horses in some aspects related to abrasion resistance. Our morphometric analyses of the masticatory apparatus document the main morphological changes in areas of functional interest (rostrum, insertions of masticatory muscles, glenoid fossa), accompanying these repeated dental innovations. After comparisons with extant analogues, involving notably rodents, rhinos, and horses, we discussed the main convergences observed.

External Morphological Diversity of Uropeltid Snakes

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Fossoriality holds a special place in debates about snake origins and early evolution. Although knowledge of especially non-caenophidian, extant burrowing snakes might inform these debates, these taxa generally remain poorly studied. One group exemplifying this is the shield-tailed snakes, Uropeltidae, a family of eight genera and approximately 60 species endemic to Sri Lanka and peninsular India. Understanding of uropeltid diversity and diversification has been greatly hampered by a confusing taxonomy resulting partly from unclear documentation of (especially tail shield) morphology, and a lack of integration of observations of animals in life with observations of historical museum specimens, but most of all by lack of study. However, in contrast to general perceptions about fossorial taxa, uropeltids are clearly morphologically diverse as well as speciose. While undertaking taxonomic revisions of Uropeltidae, we examined the external morphology of >1,300 specimens, including all described species and most of the types. We generated meristic and morphometric data, covering head, body and tail features, and we reassessed the homology of tail shield structures. These phenotypic data have been examined in light of a new molecular phylogeny for the group. The new data provide a morphological basis for resolving several long-standing taxonomic problems, which is resulting in the resurrection of species hidden in synonymy and also in descriptions of new taxa. Convergence in head scalation patterns is confirmed for some species of the two most speciose genera. Sexual dimorphism is prevalent in features including body segmentation, tail size and shape, and presence of multiple ridges on body and tail scales, but the presence and extent of dimorphism varies among taxa. Structures referred to as tail 'shields' are not homologous across all uropeltid genera, so that a new terminology is required to more accurately describe the morphological variation.

The Acanthomorph Fish Genus *Polymixia*: Morphological Analysis, Re-described Type Species, Assessment of Disparity among Species, and Origin of a Unique Body Plan

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Polymixia is the only extant genus in the acanthomorph fish order Polymixiiformes, with about ten species inhabiting moderately deep waters of continental slopes and the flanks of submarine seamounts and oceanic islands. For many years *Polymixia* was thought to be a beryciform, but we now understand it to be a basal paracanthopterygian. We also now have a working hypothesis of the phylogeny of its species, which are distributed among five species-group clades. Often cited as a 'living fossil', the last survivor from a Cretaceous radiation, *Polymixia* retains ancestral traits not seen in other acanthomorphs. Despite its importance for understanding acanthomorph evolution, the anatomy of *Polymixia* has been studied seldom and never with a comprehensive sampling of its lineages. Here, we present results from a detailed redescription of the type species *P. nobilis* as well as comparisons of morphological disparity among all available valid species. Our approach is multidimensional, with examination of cleared-and-stained preparations, dried skeletons, X-radiographs, μCT-scans, 3D-reconstructions, and 3D-multivariate morphometrics of both adult and developmental material within a phylogenetic framework. Unique morphological features of *Polymixia* discussed here include unusual patterns of cephalic sensory canals, posterior skull novelties, simplified supramaxillae, modified anterior branchiostegals, enlarged first intermuscular bone, pipe-shaped first anal radial, and oar-shaped neural and hemal spines. Many of these features constitute a mosaic of traits that can be recognized in Cretaceous fossil polymixiiforms, supporting their ordinal placement. An important question addressed in this study is whether the primitive features of *Polymixia* have been retained from the origins of acanthomorphs or whether some more advanced traits have been lost, resulting in convergence and an appearance of primitiveness.

Comparing the Morphology and Musculature of Mammalian Whiskers

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One of the most striking features on the faces of many mammals are the presence of their long whiskers, or vibrissae. Primarily, these are used for touch sensing, and can be employed to guide behaviors such as foraging, navigation, and social interactions. Whiskers are thick, tapered hairs that are enclosed by an innervated follicle. Most mammals have whiskers at some stage of their life, and these have a common muscle architecture of intrinsic muscles. While similarities in whisker position and muscle architecture suggest a common mammalian ancestor with whiskers, variations in morphology and anatomy reveal that whiskers are also adapted to function in many species. This presentation will describe similarities and differences in mammalian whisker morphology using histological and CT-scanning techniques. It will also consider these findings in terms of movement abilities from high-speed video recordings, and propose functional associations. We find that whiskers are especially prominent in nocturnal, arboreal and aquatic mammals that also tend to move their whiskers. These whisker specialists have more regularly organized whiskers and intrinsic muscles, as well as an established system of extrinsic muscles that enable fine scale whisker positioning, during movement. As well as diversity in muscle structure, whiskers themselves can vary, including

differences in cross-sectional shape, curvature and the presence of undulations. The size of the infraorbital foramen is also somewhat bigger in whisker specialists. Understanding more about these differences, especially how they interact with other sensory modalities, will provide important insights into mammalian sensory biology.

Ontogeny of Southern Cassowary Casques (Aves: Paleognathae: *Casuarius casuarius*): Setting an Osteo-Developmental Baseline for Evolutionary and Functional Studies

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Studies of avian cranial phenotypic complexity often center on bill morphology and its relationship to taxonomy and diet. Relatively little attention has been given to bony cranial ornament variation and functional morphology despite the appearance of such structures in at least 11 orders of extant birds. Perhaps the best-known cranial ornaments among birds belong to cassowaries (*Casuarius*), which have spade-like casques that have been superficially implicated in numerous functional roles (e.g., display, vocalization, thermoregulation). Cassowary casques have been studied since the 1800's, but comprehensive documentation of their internal and external cranial ontogeny has never been conducted, hampering functional interpretations. To gain insight into osteo-developmental correlates of proposed functions, we track the 3D-development of individual casque elements across an extensive growth series of southern cassowaries (*C. casuarius*), compare casque size to skeletal and sexual maturity, and describe phenotypic variation of this unique ornament in adults. Because cassowaries are the only known paleognaths to possess bony cranial ornaments, we additionally compared anatomies to casqued neognaths (e.g., *Macrocephalon maleo*, *Numida meleagris*). In cassowaries and neognaths, we find that most of the casque growth occurs in the period prior to sexual maturity. These groups differ, however, in that cassowaries have substantial individual variability (i.e., in part due to non-sex-specific asymmetries in casque shape) and a unique bony composition. Neognathous species show ornament configurations that consist of dermatocranial bones only, while those of paleognathous cassowaries consist of dermatocranial bones along with a primary, midline chondrocranial element. This work now sets the stage to formally address the biological role(s) of the cassowary casque by targeting the morphologies that might contribute to its hypothesized functions.

Embryonic Development of Adhesive Lizard Digits: Comparisons Between Independent Evolutionary Origins (Reptilia: Squamata)

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One goal of evolutionary developmental biology is to understand the role of development in the origin of phenotypic novelty and convergent evolution. One example of morphological convergence is the repeated independent origin of digital adhesion in lizards. Digital adhesion has evolved at least 14 times in lizards, 12 of which occurred in geckos. The toepads of *Anolis* lizards typically consist of expanded, undivided lamellae; however, geckos exhibit immense diversity in toepad shape and size, including toepads superficially similar to those of *Anolis*; medially divided pads; and distally-enlarged pads or "leaf-toes". Despite being considered a key innovation, very little is known about the developmental origins of adhesive toepads in lizards. Here, we describe the digital development of four lizard taxa, each representing an independent evolutionary origin of adhesive toepads, three geckos and *Anolis sagrei*. We collected embryological series from all four species, identified the time in which toepads develop, and then examined the morphology of the developing digits using scanning electron microscopy (SEM). We compare and contrast the development of these independently derived adhesive digits in a phylogenetic context. Due to different overall toepad morphologies and independent evolutionary origins, we hypothesized that all taxa investigated would exhibit different patterns of toepad lamellae formation throughout development. We found striking similarities in the early development of toepad lamellae between geckos and *A. sagrei*, suggesting developmental constraint in the evolution of digital adhesion. Later in embryonic development, patterns of lamellar formation diverge to produce distinct toepad morphologies. We discuss how early similarities may relate to deep homology of digital development among lizards. We also discuss the subsequent mechanisms of morphological divergence.

Hips Don't Lie: Facultative Bipedality, Substrate Use and their Link to Pelvic Anatomy in Lepidosaurs

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Facultative bipedality is a high energy locomotor mode, and is traditionally considered an enigmatic transitionary state in the evolution of obligate bipedality. Traits associated with this locomotor mode are largely found in the hind limbs and tail. The pelvis-sacrum unit articulates with these structures and is essential for hind limb powered locomotion. The pelvis-sacrum unit is likely subject to selective pressures for locomotor adaptations that are reflected in its morphology. We investigated how pelvic anatomy is linked to locomotor mode and substrate use in 34 species of extant lepidosaurs. 3D-models of the ilium, ischium and pubis were constructed using X-ray micro-computed tomography in the open-source imaging software 3DSlicer. A 3D-landmark-based geometric morphometrics approach was used to quantify osteological morphology. Using principal component analysis and MANOVA tests on generalized Procrustes distances we compare morphology with locomotor mode and substrate use. Anatomical dissections of soft-tissue specimens were also conducted to investigate the function of these osteological variations. Locomotor mode correlates strongly with changes in the preacetabular process of the iliac blade and with arboreal substrate use, clustering both substrate and locomotor mode together. Terrestrial lepidosaurs, however, exhibit a far more varied morphology, occupying a larger region of morphospace suggesting a more generalist morphology. Functional interpretation of ligamentous and muscle structures in the pelvic girdle indicate that similar soft-tissue morphologies are present in arboreal species as in those that are capable of a facultatively bipedal locomotor mode when moving terrestrially. These quantifiable anatomical changes promote better understanding of the function of the lepidosaur pelvis during facultatively bipedal behavior and may aid in our understanding of the evolution of reptilian bipedality as a whole.

Diverse Morphology in the Forewings of Flapping Rays

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Batoids (skates and stingrays) exhibit swimming modes that can be characterized on a spectrum from undulation (>1 wave present along the fin) to oscillation (<0.5 wave present along the fin). The latter is a derived mode of locomotion that characterizes a group of charismatic pelagic batoids, the Myliobatidae (manta rays, cownose rays, eagle rays). Oscillatory swimming is associated with specific pectoral fin morphology, including laterally elongated pectoral fins (wings), posterior redistribution of pectoral fin rays, and the evolution of modified anterior pectoral fin domains called cephalic lobes. These anteriorly extended appendages are used primarily for feeding in this family. We quantified the number of fin rays that articulate with the three primary cartilages of pectoral fins and cephalic lobes. There is no evidence that additional anterior fin rays evolved in association with the origin of cephalic lobes. Rather, we found variation in the abundance and morphology of the anterior pectoral fin rays, these configurations are likely associated with the separation of swimming and feeding functions in myliobatids. The Myliobatidae also have a derived skeletal feature in the anterior pectoral fin - the "jointed-plate". We used microCT to quantify the morphology of the plate within and across species. The separation of cephalic lobes from the pectoral fins in myliobatids has allowed both structures to functionally diversify. With prey acquisition no longer being a constraint, the pectoral fins developed a number of novel adaptations for oscillatory flight. The forewings of these flapping rays are stiff relative to other batoids. Reinforcement in the leading edge of the wing is provided by thicker fin rays that lack terminal bifurcations and exhibit cross-bracing or stacking of joints. Overall, these unique traits enable myliobatids to generate the necessary lift and thrust power for efficient aquatic propulsion and life in a pelagic environment.

Functional and Developmental Diversity in Mammal Body Wall Composition

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Four ventrolateral muscular layers support the thorax and abdomen of most tetrapods, while only two muscular layers support the perineum. However, many, if not all, placental mammals have four ventrolateral muscular layers supporting the perineum. These additional layers function to allow precise muscular control of the structures that develop as part of full septation of the cloaca into urogenital and anorectal portions, including the rectum, anal canal, urethra, vagina, vulva, and paired vascular erectile tissues. While the organization and function of muscular layers of the thorax and abdomen are consistent across taxa, the muscular layers of the perineum serve a diverse set of functions and are thus more varied in structure. In general, from superficial to deep, the perineal subcutaneous layer usually regulates orifice closure; the external layer usually supplements erectile and micturition function; the internal layer usually provides primary micturition and defecation regulation, and the transversus layer provides structural support for pelvic organs. Yet, in our mammalian perineal dissections, we observe that some well-known muscles that are present across many mammals may derive from different muscle layers. For example, in dogs, the retractor penis/clitoris muscle derives from the external layer, but in horses and goats, the retractor penis derives from the transversus muscle. In dogs, constrictor vulvae and constrictor vestibulae both derive from the external layer, but in horses the constrictor vulvae derives from the subcutaneous layer and the constrictor vestibulae derives from the external layer. Here, we identify perineal muscular homologies and analogies in a variety of mammals, including humans, lemurs, monkeys, dogs, cats, goats, horses, and pigs. Our findings suggest that variations in perineal muscle layering of the mammalian taxa examined likely represent independent evolutionary adaptations that serve specific reproductive and excretory functions.

SEM Study of the Lingual Papillae in the Lesser Hedgehog Tenrec (*Echinops telfairi*; Mammalia: Afrosoricida)

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The lesser hedgehog tenrec (*Echinops telfairi*) is an endemic African insectivore that is found only in Madagascar. In the past, tenrecs were classified as Eulipotyphla. Recently, the nucleotide sequence data shows their closer relationship to Infraorder Afrotheria. Lingual papillae located on the tongue of the tenrec were evaluated by scanning electron microscopy (SEM). Four types of papillae were distinguished: filiform, conical, fungiform and vallate. Appearance of the filiform papillae varied considerably in specific parts of the tongue (apex, corpus, radix). Rostrocaudally, the number of their spikes increased. Filiform, crown-like papillae were found on the radix. Large conical papillae with a wide base and a caudally bent single spike were located on the dorsal surface in a caudal part of the lingual radix. Fungiform papillae were randomly scattered on the dorsal surface. Three vallate papillae in an inverse triangular layout were formed on the lingual radix. The results were compared to the lingual morphology of other Afrotheria and Eulipotyphla. This is the first description of the lingual morphology of the species that belongs to the Order Afrosoricida.

Cdk13-/- Mice Exhibit Developmental Delay and Craniofacial Malformations during Embryonic Development

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Cyclin-dependent kinase 13 (CDK13) belongs to the family of transcription regulating kinases. Together with its binding partners, cyclin K or L, they form a complex which regulates phosphorylation of RNA Polymerase II, or control alternative splicing. Large numbers of different mutations of this gene cause various developmental defects. In humans, these mutations cause developmental delay, intellectual disability, autism, seizures, facial dysmorphisms, structural heart, brain and digital abnormalities. Our mouse strain with mutation in Cdk13 gene has very similar phenotypic manifestations including developmental delay, craniofacial and heart abnormalities, plus defects in kidney morphology. The aim of this study is to precisely describe morphological changes in the craniofacial region of Cdk13-/- embryos and to reveal what cellular and molecular processes are responsible for these changes. According to macroscopic and microscopic analysis, the most obvious morphological differences between wild type and mutant embryos in the craniofacial region are a generally smaller head, cleft palate and smaller and dysmorphic incisor tooth germs. Alizarin red and Alcian blue staining showed differences in morphology of bones and cartilages of the head between wild type and mutant embryos. For deeper analysis of bones and teeth, we performed μCT-scanning. Analyses were performed on embryos from E11.5 to E16.5. Precursor cells normally migrate along the axons to their final destination in order to differentiate and form a specific tissue or can serve there as a source for eventual renewal. Our goal is to reveal whether migration of craniofacial-forming cells is impeded if axonal outgrowth in Cdk13 mutants is defective. CDK13 is known to be responsible for axon outgrowth *in vitro*. This hypothesis will be verified using IHC on slides and on wholemount embryos, and on PCR arrays specific for mouse neurogenesis markers. This work was supported by the Czech Science Foundation (grant 17-14886S).

Unlocking the Vault: Mass Digitization and Imaging of Historical Slide Collections for Use in Vertebrate Morphology

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Natural history museums hold vast collections of glass microscope slides amassed from numerous sources over the last 100 or more years. These slides were prepared in association with a variety of botanical and zoological studies, which ranged from comparative embryology, to wood anatomy, to taxonomy, but they were especially important for studies of vertebrate morphology. While such collections represent a unique and irreplaceable resource for studies of integrative and comparative biology, most are fragile or otherwise difficult to access and work with; even their existence is poorly known. Hence, they are largely ignored by contemporary researchers. We have developed a cost-effective, high-throughput and semi-automated workflow for digitally scanning and displaying slides of many different sizes characteristic of the collections of the Harvard Museum of Comparative Zoology and the Harvard University Herbaria, which is applicable to like collections at other institutions. The resulting high-resolution digital images, each depicting the contents of an entire slide, may be accessed via a customized web application that allows a variety of kinds of image analysis, data capture and visual display. Ready access to these historically and scientifically rich data sources will enable fruitful and timely collaborations between natural history museums and other branches of biology, such as neuroscience, physiology, developmental biology, functional morphology and ecology, and complements the growing number of digital-image repositories available via the Internet. We demonstrate our workflow with digital scans from the historic Harvard Embryological Collection amassed by Charles Sedgwick Minot at the beginning of the 20th century.

The First Three-Dimensional Reconstruction of the Skull and Musculature of a Cretaceous Toothed Bird, *Hesperornis regalis* (Avialae: Hesperornithiformes)

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Cranial kinesis in birds is a remarkable anatomical specialization involving the development of novel joints resulting in a complex biomechanical system that allows the bill to move independently of the braincase. The early evolutionary history of the specialized musculoskeletal structures necessary for a fully kinetic skull, however, is poorly understood. Whereas nearly all Mesozoic bird skull fossils are crushed flat, the fossil marine toothed bird *Hesperornis regalis*, from Late Cretaceous Kansas, is the closest fossil taxon to crown Aves known from nearly complete, undistorted skull material, making it crucial for understanding the emergence of kinesis in birds. The three-dimensionally preserved skull material can be integrated with osteological correlates to musculature and mobile joints from living species to reconstruct the cranial kinetic system of *Hesperornis*. We μCT-scanned and digitally prepared *Hesperornis* skull elements to construct a model for comparative and functional studies. We used contrast-stained μCT-scans of palaeognathous and neognathous birds, and a crocodylian, to precisely identify osteological correlates to the cranial kinetic system and cranial musculature. With these comparative data, we developed a reconstruction of cranial muscles in *Hesperornis*. The palate, rostrum, and some correlates to musculature compare favorably with palaeognaths, lacking mobile interpterygoid joints or a nasofrontal hinge, and kinesis relying on elastic deformation of the rostral bones. We also identify a suite of osteological correlates to jaw adductor muscles on the braincase resembling those in disparate clades of extant pursuit-diving birds, showing a mosaic of deeply plesiomorphic characters occurring in concert with remarkable convergence and specialization.

An Extraordinary Enigmatic Structure in the Middle Ear of Acrobatid Marsupials

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A ventral ectotympanic bony process (VEP) occurs in the middle ear of all living members of the marsupial family Acrobatidae including the gliding *Acrobates pygmaeus* of Australian and New Guinean open forests, and the non-gliding *Distoechurus pennatus* of New Guinea's closed forests. The VEP arises from the ventral portion of the ectotympanic and almost completely blocks the auditory passage lateral to the tympanum. Because this structure is unique among mammals to acrobatids, its impact on auditory perception is an enticing mystery. Aitkin and Nelson (1989, Brain Behav. Evol. 33: 325–333) hypothesized that it might create a Helmholtz resonator in *A. pygmaeus*. Because they did not realize that the same structure occurs in the non-gliding *D. pennatus*, they hypothesized that this may relate to gliding behavior. In our effort to determine the function of this structure and test previous hypotheses, microCT-scans of the middle ear region and microMRI-scans of the brain of both species were produced. Using 3D-models generated from scan data, we have clarified how this system functions. In terms of habitat correlations, *D. pennatus* occupies the phylogenetically ancestral closed forest habitat in which gliding might be unnecessary to move between trees. All of Australia's six living marsupial gliders occur only in open forests. However, new species of both acrobatid genera have been found in Miocene closed forest deposits of the Riversleigh World Heritage Area of northern Australia. Hence, rather than evolving to assist gliding behavior, we suggest that it may have better enabled early acrobatids to discriminate their own vocalizations within the biologically hyperdiverse and undoubtedly very noisy mid Cenozoic closed forest communities of Australia.

Retention of Fish-like Odontode Overgrowth in Tetrapods and Implications for Outside-in Theory of Tooth Origins

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Teeth are often only thought of as structures that line the margins of the mouth; however, tooth-like structures called odontodes are commonly found on the surface of the dermal bones of many Paleozoic vertebrates including early jawless fishes. Odontode is a generalized term for all tooth-like dentine structures which have homologous tissues and development, and this definition includes true teeth. Teeth are often split into two broad categories, marginal and non-marginal dentition, based on their position in the dental arcade. Non-marginal dentition is present in most Paleozoic tetrapods as coronoid teeth in the lower jaw and palatal teeth. Despite their prevalence, non-marginal tetrapod dentition has received little attention, especially from the histological and developmental perspectives. Our histological examination of several terrestrial Paleozoic tetrapods revealed that their palatal dentition had an unexpected pattern of development and replacement, a pattern previously documented only in fish odontodes and palatal teeth of one Triassic stereospondyl. Here, we show that unlike the well-known one-to-one replacement patterns of marginal dentitions, the palatal dentition of the early Permian tetrapods, including the dissorophoid amphibian *Cacops* and the early reptile *Captorhinus*, is overgrown by a new layer of bone to which the newest teeth are then attached. This pattern is referred to as 'over-growth' when documented in the odontodes and scales in fish. This same overgrowth pattern has been well documented in dermal and oral odontodes of early agnathan fishes. We propose that this pattern represents the primitive condition for vertebrates, and that it predates even the origin of jaws. Therefore, this pattern transcends the fish-tetrapod transition, and the retention of this ancestral pattern in the palatal dentition of early terrestrial tetrapods provides strong support for the 'outside-in' hypothesis of tooth origins.

Morphometric Measurements of the Equine Hoof: How is Hoof Shape Altered by Trimming?

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Foot shape is associated with lameness in horses. Farriery has a significant role in managing hoof shape. This study aimed to observe the effect of farriery on hoof shape. Digital photographs were taken of dorsal, lateral, medial and solar views of the forefeet of 45 horses before and after trimming by qualified farriers. Comparisons were made using Wilcox sum rank test or Mann-Whitney test as appropriate. Increases in Centre of Rotation-Frog Apex ($p<0.001$), Centre of Rotation-Centre of Pressure ($p<0.001$) and Heel Buttress-Centre of Pressure ($p<0.001$) were associated with trimming. Frog apex-toe distance reduced post-trimming ($p<0.001$). Median dorsal hoof wall length: heel length was 1.9 (IQR=2.1-1.7). Average dorsal hoof wall angle-heel angle difference was 4.9° (IQR=9.35-0.13); greater difference was observed on the medial view ($p=0.03$). A reduction in solar width ($p<0.001$) and medial solar width ($p<0.05$) were associated with trimming. An increase in medial hoof wall angle ($p<0.05$) was associated with trimming. Lateral: medial sole width did not change significantly following trimming ($p>0.05$). Medial hoof wall angle was significantly more acute ($p<0.001$) than lateral hoof wall angles in pre- and post-trim conditions of the left forelimb, but not the right forelimb. From these results we can conclude that hoof trimming results in palmar heel migration and reduction in length at the toe. Most

horses maintain toe length: heel length within previously described limits, but large variation in dorsal-heel angle difference is evident, which may affect wear on structures in the foot. Differences in trimming and angulation of medial and lateral walls of the hoof may indicate differing growth during the shoeing interval and have implications for mediolateral balance of the hoof before and after trimming. This study gained ethical approval from University of Liverpool Veterinary Ethics Committee (VREC538). Informed consent was gained from all horse owners prior to data collection. Sources of Funding: The Horse Trust Competing Interests: None declared.

What the First DiceCT Fascicle-by-Fascicle Dissection can Tell us about the Primate Masticatory Apparatus

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Fascicle architecture determines the contractile properties of a muscle; longer fascicles permit increased excursion, while fascicle quantity relates to contractile force. Studying fascicle architecture has traditionally involved destructive gross and chemical dissection. In recent years, however, new imaging modalities have permitted muscles to be visualized non-destructively. Here, we present data from a primate (*Callithrix jacchus*) in which, for the first time, muscle fascicles are individually digitally “dissected” (segmented and reconstructed) using non-destructive, high-resolution diffusible iodine-based contrast-enhanced computed tomography (DiceCT) techniques. In addition to this 3D-visualization we present quantitative data on the length and orientation of these fascicles within ten jaw adductor and abductor muscle divisions and compare these measurements to lengths collected through traditional dissection of the same specimen. Digitally- and traditionally-derived fascicle lengths correspond well. Moreover, our analyses of fascicle orientation across the adductor complex enable us to visualize new levels of detail, and highlight significant variation between adjacent muscle layers within muscle groups (e.g., between superficial, deep and zygomatic portions of masseter and temporalis). This technique offers great potential for the visualization and quantification of obscured and often-overlooked muscles such as the pterygoid muscles. The digital visualization also allows us to study the compression that most adductor fascicles are under at near occlusion, as demonstrated by their substantial curvature. Most importantly, combining corrections for this gross fascicular compression and sarcomeric measurements (also collected on the same specimen) of cellular compression, this technique will allow the creation of the most accurate models of the primate masticatory system yet to be constructed. This project was supported by the NSF (IOS-15-57125 and BCS-14-40599).

Sniffing out Covariation Patterns in the Olfactory System of Myrmecophagous Mammals

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Myrmecophagous (ant-and termite-eating) mammals represent a textbook example of morphological convergence. These groups share a number of highly specialized features that have often been linked to feeding strategies, but only rarely to prey detection abilities. Yet, similar sniffing behaviors (rapid breaths in short sequence) have been observed in some ant-eating mammals. These behaviors may represent a convergence in olfactory performance, where olfaction is used to detect chemical signals emitted by ants and termites. Here, we used X-ray microCT to evaluate the extent of convergent evolution in the olfactory system of several myrmecophagous species (anteaters, armadillos, aardvarks, pangolins, and aardwolves), as well as their sister taxa. We hypothesize that potential convergences in olfactory performance might be reflected in the morphology of the different compartments of the olfactory system, and that these structures should covary with one another. Our anatomical comparisons focused on the variations of three distinct morphological units known to be involved in smell sensory abilities: turbinal bones, cribriform plate, and olfactory bulbs. We used complexity indexes, surface area, and volume as bony proxies for olfactory capacities, and then assessed correlation patterns using least squares analyses. Our results revealed a strong phylogenetic imprint in the anatomy of these olfactory structures, but no convergence to diet. We showed that these structures vary in concert with each other across taxa, so that trait integration might constrain the morphological evolution of their rostrum. The analysis of 3D-complexity and -morphology revealed a striking case of convergence between the giant armadillo and the aardvark, two species known to build complex burrows and spend less time above ground than other myrmecophagous mammals. The olfactory system of these two species may reflect the challenges associated with an underground lifestyle rather than prey detection.

Correlations between Lacrimal Bone Morphology and Behavioral Traits in Cervids and other Ruminants (Artiodactyla, Mammalia)

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The lacrimal bone of ruminants is larger than in other mammals; particularly in cervids, it is one of the key morphological skull characteristics. The lacrimal varies in shape, size and position. Most cervid species and some other non-cervid ruminants, especially male individuals, have a deep lacrimal fossa, which holds the preorbital gland in living animals. Secretions from this gland are used to mark territories and in some species also contain pheromones. We ask whether the dimensions and morphology of the lacrimal bone and the lacrimal

fossa could be used to infer certain behavioral traits in fossil cervids/ruminants. We examined the correlation of the lacrimal bone, the lacrimal fossa and skull length as a proxy for body size in all cervid genera and selected non-cervid ruminants. While length of these structures correlates well with body size, the area of the lacrimal or the lacrimal fossa shows a weaker correlation with body size, which is supported by comparative anatomy. This indicates that the lacrimal area, particularly the lacrimal-fossa-to-lacrimal-ratio, might best reflect behavioral traits. Further, the size of the lacrimal fossa was tested for correlation with the size of the preorbital gland. We investigated whether the gland size is linked to certain scent marking behavior, mating strategy, and/or territoriality, and reconstructed these traits along ruminant phylogeny.

Functional Constraints Lead to Decreased Disparity in Bird Limb Proportion Evolution

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Dinosaurs show tremendous disparity of limb proportions and locomotor modes, spanning massive quadrupedal sauropods, carnivorous bipeds, and small bipedal herbivores. Birds have wide variation in flight capability, from flightless kiwi birds to hyper-aerial swifts. Key questions about locomotor macroevolution in dinosaurs include whether locomotor innovations were pulsed or gradual, and to what extent increases in locomotor disparity correlate with changes in patterns of integration both between and within limbs. We conducted phylogenetic comparative analysis of disparity-through-time and integration on a database of limb proportions and body masses from 822 species of non-avian dinosaurs, fossil birds, and extant birds spanning 230 million years of evolutionary history. We found an increase in relative subclade disparity of limb proportions coincident with the origin of major non-avian dinosaur clades and a subsequent drop in disparity before the end-Cretaceous extinction. This resulted from a pulse-like pattern with early increases being from the divergence of proportions in major dinosaur subgroups. Mid-Mesozoic increases were derived from the origins of quadrupedality in multiple clades, and of flight in paravian theropods. Late Mesozoic increases resulted from expansion of forelimb proportions among crown-group birds. Flying taxa exhibit a double-pulse, having higher than expected subclade disparity during the origin of flight, and again, in the forelimb, among deep crown-group divergences. Shifts between locomotor modes were accompanied by restructuring of patterns of integration. Flightless bipeds had moderate integration between limbs and high integration within the hindlimb. In contrast, volant species had high integration within both limbs, and low between-limb integration. Our results suggest that functional constraints can lead to decreased morphological disparity even in one of the most recognized examples of an adaptive radiation, the origin of birds.

Modulation of Intraoral Processing in Salamandrid Newts: Effects of Prey Type and Environment

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Intraoral processing mechanisms are known for all major vertebrate clades, but form and function of systems used to crush, grind, or puncture food items in preparation for swallowing differ substantially between as well as within major clades. In most vertebrates, mechanisms of intraoral processing display flexibility and can be adjusted to demands of different environmental conditions or food types. Recently, we described a peculiar processing mechanism in newts and showed that they use cyclic loop-motions of the tongue to rasp prey against the palatal dentition. However, it is not known if newts can modulate their processing behavior in response to different conditions. Newts provide interesting models for studying functional modulation in response to different conditions due to their unique and flexible lifestyle: Newts seasonally change between aquatic and terrestrial habitats and consume a wide range of food types. Here, we test the effects of (i) the medium where feeding occurs (water/air) and (ii) food type (maggot, earthworm, cricket) on the processing behavior in the newt *Triturus carnifex*. Using x-ray high-speed recordings, anatomical investigations and behavioral analyses, we demonstrate that newts show little change in food processing between aquatic and terrestrial feeding. However, they adjust the number of processing cycles to different prey types. For example, while maggots are processed extensively, earthworm pieces are swallowed nearly unreduced. We conclude that sensory feedback such as smell, taste and material properties induce flexible processing responses, while the medium where feeding occurs appears to have less of an effect.

Body and Tooth Mass Estimates for the Earliest Bird, *Archaeopteryx lithographica* (Late Jurassic), and the Insiginificance of Tooth Mass in Bird Evolution

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Whole body and regional body mass estimates are made with four different restorations of the extinct early bird *Archaeopteryx lithographica* using digital, three-dimensional models. Densities assigned to the various regions of the models took lungs, air sacs and skeletal pneumatization into consideration. Complete sets of premaxillary, maxillary, and dentary tooth crowns and their associated roots were also represented as 3D-models, and their masses were computed using the observed density for dentine. It was found that the total mass of the teeth represents less than 1/100th of one percent of total body mass (less than 1/40th of the proportion measured in bats), and that a meal of a few of the insects found preserved in the same deposits with *Archaeopteryx* would weigh more than the teeth. The observations that many non-flying tetrapods of the past and present independently lost their teeth during the course of their evolution; that the approximately 1,200 species of living bats are all toothed; and that flying, toothed birds existed for approximately 85 Ma (more than half the time that birds have existed), all suggest that tooth loss as a weight minimization strategy during the evolution of powered flight in birds is extremely unlikely.

Insular Gigantism: Mandibular Allometry and Geographic Variation in Mediterranean Dormice

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Throughout history, several rodent and lagomorph species have had the tendency to increase in size on islands, particularly those in the western Mediterranean area. During the Pleistocene, the island of Sicily was the home of a gigantic dormouse, *Leithia melitensis*. This cat-sized species is the largest known dormouse, easily three times larger than its extant relative, *Eliomys quercinus*. Alongside this giant, other dormouse species occupied various Mediterranean islands, both during the Pleistocene and in the present. All these species have tended to become significantly larger than their mainland counterparts, though much smaller than the Sicilian giant. To understand this size adaptation and the allometric nature of this phenomenon, we digitized 88 mandibles of fossil insular dormice and 66 *Eliomys quercinus* mandibles using photogrammetry and microCT, and placed 19 anatomical landmarks on the 3D-models. Using generalized Procrustes analysis and principal component analyses, shape variation was quantified. Multivariate analysis of variance was used to identify any covariance between shape and centroid size. For the extant *Eliomys* dataset, major shape variations between populations are strongly associated with the increase in size ($r2= 83\%$). In the fossil dataset, the correlation between size and shape is less strong ($r2=63\%$), and is primarily a reflection of the huge size difference between *L. melitensis* and the other fossil species. Possibly, shape variance in this giant is an adaptation to a new ecological niche, associated with its significant increase in size. Biomechanical analyses suggest that the fossil giant has a relatively efficient temporalis muscle. Presumably, this giant was better adapted to biting with its incisors compared to its smaller relatives. The implications of this adaptation are unknown, however, it is clear that insular gigantism within dormice is associated with allometric shape variance, as well as a more powerful masticatory apparatus.

A New Method for Investigating Joint Mobility and its Relevance for Inferring Locomotor Evolution in Early Tetrapods

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Salamanders have often been used as a modern analogue (or even homologue) for musculoskeletal function in early tetrapods. To estimate whether early tetrapods such as the potentially more terrestrial Carboniferous form *Eoherpeton* were capable of salamander-like locomotion, we compare the osteological range of motion (RoM) at their joints. Additionally, we determine how well salamander osteological RoM corresponds to the RoM of intact joints (arthrological RoM) and *in vivo* RoM (in which behavior is also a factor), because we cannot measure the latter two in extinct taxa. Previous studies have quantified salamander osteological RoM by measuring minima and maxima in flexion/extension (F/E), abduction/adduction (AB/AD), and long-axis rotation (LAR). However, recent studies in birds have shown that the rotation around one axis affects the joint limits about the other axes. We quantified Fire Salamander (*Salamandra salamandra*) *ex vivo* (arthrological) RoMs for the knee joint using a new real-time visualization method that also measures passive joint stiffness. The salamander knee joint permits not only F/E but also substantial AB/AD and LAR. The largest arthrological RoM is around the F/E axis, corresponding to the dominance of F/E in the knee during salamander locomotion. Furthermore, we found that range of motion limits are inter-dependent. Strong flexion in the salamander knee decreases the potential for AB/AD. However, LAR limits stay relatively constant throughout knee flexion. We compare these results to salamander *in vivo* RoM (using scientific rotoscoping) and osteological RoM to determine the relative influence of arthrological *versus* osteological constraints on *in vivo* function. Finally, osteological RoM is compared to that of *Eoherpeton* to quantify limitations of hindlimb movement, and thus test whether some degree of terrestrial locomotor ability might have evolved in this taxon.

Reference Data of Mouse Developmental Morphology from Standardized 2D- and 3D-Images Produced in the Deciphering the Mechanisms of Developmental Disorders (DMDD) Program

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The Deciphering the Mechanisms of Developmental Disorders (DMDD) program was a systematic effort to characterize the phenotype of prenatally and perinatally lethal homozygous offspring from single gene knockout mouse lines. We aim to 1) introduce DMDD; 2) demonstrate the spectrum of abnormalities and normal phenotypic variation detected in the knockout mouse lines produced; and 3) show the usefulness and implications of DMDD data for identifying and studying mouse models for human diseases and basic research on developmental processes. 208 novel single gene knockout mouse lines, which produced prenatally lethal or sub-viable homozygous offspring, were generated for DMDD at the Wellcome Trust Sanger Institute by CRISPR/Cas9 technology. From those lines, about 700 embryos (homozygous and wildtype littermates) were harvested at embryonic day (E) 14.5 and E9.5, respectively, and digital volume data with an average voxel size of $3x3x3\ \mu m^3$ were imaged with the high resolution episcopic microscopy (HREM) method. Their phenotypes were comprehensively analyzed, using systematic and standardized protocols. The DMDD webpage (dmdd.org.uk) presents series of axial, sagittal, and coronal sections through the volume data of each embryo, with labelled morphological abnormalities. Thus, we present a valuable resource for researching the genetic basis of malformations. On average, E14.5 mutants showed up to 10 structural abnormalities, with cardiovascular defects occurring in most of the studied mouse lines. In most knockout lines, the severity of the detected malformations in each embryo ranged from harmless to prenatally lethal. Our wildtype mouse data represents a baseline for normal morphological variation, which can be used to compare data on novel mouse mutations or other vertebrate species.

Skull Shape Relations to Ecological Preferences of Side-Necked Turtles (Testudines: Pleurodira)

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Extant side-necked turtles (pleurodires) are restricted to southern hemisphere landmasses (Africa, Australasia, Madagascar and South America), with a diversity of nearly one third that of cryptodires (hidden-necked turtles). Ecologically, extant pleurodires also exhibit a more limited range of feeding strategies, being considered either aquatic herbivores or generalist carnivores, in contrast to the several diet specializations seen in cryptodires, such as durophagy and terrestrial herbivory, for example. Yet, the fossil record of the group suggests a different scenario, with broad-jawed (e.g., *Bothremys*) and robust-skulled (e.g., *Ummulisani*) forms possibly exploring different niches from those of living taxa. Here, we employ a 3D-geometric morphometrics approach (based on computed tomography data) to study skull shape variation in pleurodires and assess if (1) pleurodiran clades are well-differentiated in morphospace, suggesting phylogenetic constraints, or if (2) similar skull shapes evolved in distantly related taxa, indicating convergent ecological preferences. Our results show that most of the cranial variation in the first two Principal Components is explained by phylogeny, dividing chelids and pelomedusoids in two distinct areas of the morphospace, and with bothremydids separated from the remaining pelomedusoids. This might be the result of the influence that emarginations (both anterolateral and posterodorsal) have on shaping the skull. Regarding diet, gape-feeders and generalist carnivores are not placed close to one another, despite the phylogenetic affinities of the former group. Further analyses including more fossil and extant taxa, as well as cryptodiran taxa will help to better understand the relationships between ecology and skull shape among turtles. Funding statement: FAPESP scholarships to GSF (2014/25379-5) and MCL (2014/03825-3).

Botulinum-treated Mammalian Jaw Muscles Regain Strength by Compensation rather than Recovery

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Botulinum neurotoxins (BTX) cause temporary paralysis by preventing release of neurotransmitters. Widely used clinically for pain and cosmetic contouring, BTX is also popular for research on muscle hypofunction. The treatment is considered temporary and benign. We injected masseter muscles of rabbits (Lagomorpha, *Oryctolagus cuniculus*) with BTX unilaterally or bilaterally, using saline as a control. Electromyographic (EMG) activity during mastication and bite force produced by masseter stimulation were tracked periodically. EMG evoked by masseteric nerve stimulation was examined. Muscles were analyzed 4 and 12 weeks after one-time injection and after a series of 3 injections carried out every 12 weeks. In addition, one-time unilateral masseter treatment of pigs (Artiodactyla, *Sus scrofa*) was followed for 4 weeks. EMG-activity and bite force began returning to injected rabbit muscles at week 3 but remained slightly reduced even at week 11. Evoked EMG also remained low, but even the uninjected side was reduced relative to controls. Injected muscles had increased fatty and fibrous tissue. Hypertrophied as well as atrophied fibers were conspicuous. Sites distant from the injection site showed lessened effects. These deleterious changes were more prominent at 12 weeks than at 4 weeks after injection and were exaggerated in the 3-injection animals. Pigs were insensitive to BTX type A, but responded to type B with strong reductions of masticatory EMG and stimulated bite force. As in rabbits, milder reductions were seen in the uninjected masseter. Unlike rabbits, both injected and uninjected pig masseters featured greatly hypertrophied fibers. This bilateral compensation may relate to pigs' isognathic occlusion. These findings indicate that BTX-effects are not limited to the injected muscle, and that the return of EMG and force is due to hypertrophy of unaffected fibers rather than recovery of paralyzed motor endings. Supported by NIH DE018142.

Scaling in the Respiratory System of Varanid Lizards

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The aim of this study was to understand how respiratory parameters scale across a range of body masses in thirteen species of lizards of the genus *Varanus*. Data were collected using radiography and analyzed using Horos software. Linear regression of log transformed data showed that respiratory volume measurements, such as lung volume, primary bronchi volume, tracheal volume and dead space volume scale relative to body mass with a scaling exponent close to 1 (range 0.94 – 1.16). Calculations of Reynolds number in the lower trachea suggest laminar flow on both inspiration and expiration, and these values scale with body mass to the power of around one-third. There appears to be no difference in lung morphometry across different habitats, despite the wide range of ecological niches inhabited by varanids.

Different Airfoils, Different Joints: Skeletal Correlates of Wingtip Shape in Coraciimorph Birds (Aves: Coraciiformes + Piciformes)

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The continuum between pointed wingtips that optimize cruise efficiency, and rounded wingtips that optimize power in slower low-advance-ratio flight, forms one of the major axes of variation in extant avian flight. Understanding of the evolutionary dynamics of wingtip shape would enable more detailed modeling of the origin of flight, but wingtip shape is evolutionarily labile—modeling based on extant taxa alone becomes equivocal within the crown group. The aim of this study was to test skeletal features as correlates of wingtip shape, both as osteological correlates at sites of feather attachment, and in indirect relationships to joint shape and tendon routing. MicroCT-scans and feather length measurements were taken from ethanol-preserved specimens of 24 taxa of coraciimorph birds. Fixed and sliding surface semilandmarks were used to define flight feather attachment surfaces, joint surfaces, and tendon courses on the carpometacarpus and digits II & III. A phylogenetic coinertia analysis (two-block PLS) was used to assess coinertia between flight feather lengths and skeletal morphology. The first axis (89%) captured wing size allometry in the hand skeleton. Axes II & III (7% and 3%) show skeletal variation along differences in wingtip shape that have been previously described as pointedness and convexity. The most prominent skeletal loadings on axes II & III were not associated with feather attachment sites as initially predicted, but instead involved joint surfaces and tendon courses that are likely to influence elevation and long-axis rotation of the carpometacarpus and major digit. These expected range-of-motion limitations align well with known kinematic differences between flexed-wing and inverted-wingtip upstroke. The findings of the current morphometric analysis are in agreement with prior character-based analyses across neornithine birds, suggesting carpometacarpus and digit shape may record information on flight mechanics across Aves.

The Mammalian Face has Evolved by a Drastic Shift of Facial Prominences

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The amniote upper jaw is derived from two embryonic primordia, the frontonasal process (FNP) and the maxillary process (MXP). It is generally thought that their boundary has been identified by the position of the suture between the premaxilla and maxilla. Although it coincides with the soft tissue boundary between the innervation territories in almost all tetrapods, it is different only in mammals. Namely, the ophthalmic and maxillary nerves supply the premaxilla and maxilla, respectively, in amphibians and diapsids, whereas the maxillary nerve innervates the whole upper jaw region in mammals. It has been generally believed that the anatomical characters (e.g., nerves and skeletons) tightly coincide with the development of the facial prominences. Thus, the anatomical patterns of the adult face should reflect the compositional patterns of these embryonic prominences. Is this also true in the mammalian upper jaw? To clarify this, we conducted a comparative study of the craniofacial morphogenesis in mouse (*Mus musculus*), chicken (*Gallus gallus*), gecko (*Paroedura picta*) and frog (*Rana japonica*), and also compare the cleft lip/palate models (i.e. the primordial fusion is inhibited) by using these animals. As a result, we found that the premaxilla (the distalmost bone in upper jaw) is derived exclusively from FNP in diapsids and frog, while the lateral part of the "premaxilla" firstly develops in the MXP in mouse. This result is also supported by lineage tracing of MXP mesenchyme by using *Dlx1*-CreER^{T2} / R26R$^{LacZ/LacZ}$ mice. In summary, the FNP-MXP boundary appears to have been shifted in the mammalian lineage. We also have conducted comparative studies on the development of echidna (*Tachyglossus aculeatus*) and some fossil synapsids to discuss the evolutionary history of mammalian snout morphology.

Development of the Inner Ear in Hagfishes and Lampreys Reveals Evolution of the Vertebrate Semicircular Canals

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Jawed vertebrates have three semicircular canals in their inner ear to detect rolling in three-dimensional space. In contrast, lampreys, a modern jawless vertebrate, are generally thought to possess two semicircular canals and lack a lateral canal, whereas hagfishes, another jawless vertebrate, only have a single canal. As hagfishes diverged earlier than lampreys according to classical morphological studies, the single canal condition of the hagfish was thought to be more primitive than in the rest of vertebrates; the three semicircular canals evolved progressively from one, to two, to three. However, recent molecular and developmental analyses have strongly supported the monophyly of lampreys and hagfishes, and the process of inner ear evolution has remained unclear. In this study, we observed the developing inner ears of the inshore hagfish *Eptatretus burgeri* and compared them with those of lampreys and gnathostomes. We found that developmental patterning for anterior and posterior canals in both cyclostome species is similar to that in gnathostomes. In addition, we found another sensory epithelium and axon bundles in both cyclostomes, which are thought to be homologous to the gnathostome lateral crista. Thus, we suggest that the inner ears of the latest common ancestors of the extant vertebrates were more complex than previously thought. Specifically, ancestors possessed a developmental program for the two vertical canals and another detector for the future lateral canal crista. After the splitting of cyclostomes, gnathostomes newly acquired the lateral canal and its crista, which was diverted from the existing detector. Since *Otx1* knockout mice exhibit specific loss of the lateral canal, this phenotype was considered as 'phenocopy' of the lamprey situation. However, we detected four OTX genes from lamprey inner ear. We speculate that this acquisition of the lateral canal might have occurred by changes of a developmental program downstream of the OTX genes.

The Evolutionary Reconnections of Skeletal Muscles in Tetrapods

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Skeletal muscles acting for the facial expression and skin twitching in mammals are connected medially to the dermis, while most vertebrate skeletal muscles are connected to skeletal elements. It has long been considered that, in the evolution towards the turtles, the pectoralis muscle became reconnected from the sternum to the ventral bony shell, or plastron. Here, we show, through analyses on histological and gene expression signatures, that the turtles' pectoralis muscle develops to make a connection to the dermis, comparable with the dermal connections of mammalian muscles. Later in the embryonic development of the turtle, the plastron grows within the dermis eventually contacting with the attachment site of the pectoralis. Furthermore, we demonstrate that a comparable connection between a muscle and the dermis is involved in tongue muscle development, which evolved in the common ancestor of the crown tetrapods. Moreover, we found that the propatagialis muscle of birds controlling the wing shape during flight develops from two muscle anlagen, which extend from the shoulder and wrist respectively to be connected to the dermis of the propatagial membrane. Our findings indicate that the developmental mechanism connecting a muscle to the dermis has played a pivotal role in major evolutionary reconnections of tetrapod skeletal muscles, including the turtles' pectoralis that is uniquely encapsulated within the shell, the mammalian facial expression muscles, the avian wing muscle, and the tetrapod tongue muscles. The key innovations in the musculoskeletal system during tetrapod evolution have been created, hardly through bone-to-bone reconnections, but mostly through release from the musculoskeletal connections.

Large Clutch of Jurassic Stem-Mammal Perinates: Fossil Evidence on the Origin of Mammalian Reproduction

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Mammals are famously distinguished by the way they reproduce and raise their young. Along the 150 million year mammalian stem lineage, transformations in anatomy and physiology were accompanied by profound modifications to reproduction and growth, including the emergence of a reproductive strategy characterized by high maternal investment in a small number of offspring and heterochronic changes in early cranial development associated with the expansion of the brain. Because direct fossil evidence of these transitions is lacking, their timing and sequence are unknown. Here, we report the first fossil record of near-hatching young of any non-mammalian synapsid. A large clutch of well-preserved perinates of the tritylodontid *Kayentatherium wellesi* (Cynodontia: Mammaliamorpha) was found surrounded by a presumed maternal skeleton in Early Jurassic sediments of the Kayenta Formation. The single clutch numbers 38 individuals, more than twice the average litter size of any extant mammal. This discovery confirms that high offspring number is ancestral for amniotes and constrains the timing of a reduction in clutch size along the mammalian stem. The postcranial skeletons of the young exhibit a derived form of long-bone development that may have evolved in the first mammaliamorphs in connection with overall modernization of the skeleton. In contrast, skull growth is plesiomorphic: the perinates have overall skull shape similar to that of adults, with no allometric lengthening of the face during ontogeny. *Kayentatherium* diverged from the mammal line just before a hypothesized pulse of brain expansion that reorganized cranial architecture at the base of Mammaliaformes. The association of high offspring number with near-isometric skull growth is consistent with a scenario in which encephalization—and attendant shifts in metabolism and development—drove later changes to mammalian reproduction.

Comparative Study of Otoliths in Ray Finned Fishes

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Otoliths, ear stones of fishes, are important for equilibrium and hearing. They are also widely used for fish identification, growth and age estimation and can give information on the life history of individuals or population. Their role in equilibrium and hearing and correlations with ecology is discussed in several publications. However, information on otolith diversity is mainly based on size and form, but little is known about the orientation of the otoliths within the brain case. We have screened a large collection of CT-scans (obtained from the project oVert (ScanAllFish), NSF grant DEB-1701665 to Adam Summers et al.) and extracted size and orientation data from about 1200 species of ray finned fish contained in 180 families and 47 orders. There is a large diversity of all three otoliths (lapillus, sagitta, and asteriscus) that is often correlated with the systematic position of the species, but varies also within groups to a large degree. In most groups, the sagittae are the largest otoliths. They form an angle to each other that is open to the front. The asteriscus is the largest otolith in cyprinids and characins and is also angled. In all characins, however, the asterisci are opening to the back. An orientation of the otoliths may be an important factor for directional hearing. In a few groups, the larger otoliths (sagittae) are oriented parallel to each other which would be disadvantageous for directional hearing. The size of the otoliths also varies to a large degree within groups. In most studies, relative sizes are considered, but here, we pay attention also to absolute sizes since the physical properties of the otoliths depend more on absolute sizes. Many other properties of otoliths like form (straight or curved) and vertical orientations are discussed in the context of ecological and systematic correlations. All 3D-scans of the otoliths are available on a web site and can be inspected directly in a browser. Most data sets can be downloaded via MorphoSource.

A morphofunctional Study of the Tail in Sciuridae (Rodentia, Mammalia)

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Caudal vertebrae of mammals have been less studied morphofunctionally than other parts of the skeleton. Yet, the tail plays an important role in locomotion (e.g., balance, prehensility). Previous studies focused on the tail of arboreal Primates and Carnivora. Structural landmarks were used to define tail regions (proximal, transitional, distal), and similar patterns of anatomical character distributions were found in both orders. However, the applicability of tail regionalization and the similarity in features' distribution pattern have never been tested in other mammalian orders. We investigated the caudal vertebrae of 20 species of Sciuridae and six species of Gliridae to test if their anatomy is equivalent to that of arboreal Primates and Carnivora, and to check for relationships between tail morphology and locomotion. For our sample we defined three locomotion types: arboreal/scansorial, arboreal/gliding and terrestrial/fossorial. The position of selected characters was recorded for trait mapping and their distribution was compared with Spearman's rank correlation. Vertebral body length (VBL) was measured to calculate proportions of each tail region and to perform Procrustes analysis on the shape of VBL progressions. Our results show that tail regionalization can be applied to almost all squirrels, regardless of locomotion type. However, locomotion types can be distinguished by VBL progression and tail region proportions. In particular, among the investigated flying squirrels *Glaucomys* and *Hylopetes* show an extremely reduced transitional region. In contrast, the tail region proportions of the flying squirrel *Petaurista*, phylogenetically more basal than the former, are similar to those of arboreal/scansorial squirrels. These observations mirror previous results based on the inner ear morphometry of squirrels. Further morphofunctional research focusing on the tail of other rodent clades is ongoing to confirm the applicability of the Primates/Carnivora model to all rodents.

Heterogeneity of Fiber Types in the Anterior Temporalis Muscle in Papionins

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Previous work in baboons has shown that superficial and deep portions of the temporalis muscle are recruited differently during feeding depending on the material properties of the food. This regional functional heterogeneity has been correlated with intramuscular variation in fiber type distribution and myosin heavy chain (MyHC) composition. Here, we compare variation in fiber type composition of the superficial (SAT) and deep (DAT) anterior temporalis between baboons (*Papio anubis*) and three closely related papionin primates (*Cercocebus atys*, *Macaca mulatta*, *M. fasicularis*). Immunohistochemistry was used to determine the presence of MyHC-I and MyHC α-cardiac (Type I: slow-contracting, fatigue resistant) and MyHC-II and MyHC-M (Type II: fast-contracting, fatigable) myosin proteins. In all four species, the DAT is dominated by Type I fibers (88%-100%) while the SAT comprises larger proportions of Type II fibers (33%-76%). Notably, proportions of MyHC-M, a jaw-specific myosin capable of developing high force at a moderately fast rate, are 20%-70% higher in the SAT than the DAT. These results confirm earlier findings of a higher proportion of Type II fibers in the SAT compared with the DAT in baboons and rhesus macaques and further demonstrate that this same pattern is observed in *M. fascicularis* and *C. atys*. EMG-studies have shown that the DAT is recruited similarly during both soft- and hard/tough-object chewing while the SAT is strongly recruited only during chewing on hard/tough objects, when rapid production of high bite force is needed. The consistent pattern of a higher proportion of Type II fibers in the SAT compared with the DAT suggests we should expect functional heterogeneity of the anterior temporalis in macaques and *C. atys*. The range of variation in Type II expression of the SAT may be functionally linked to fine tuning the SAT during the power stroke of hard/tough object chewing. Support: NSF BCS 1719743.

A Novel Scenario for the Evolutionary Origin of Feathers: Implications for the Evolutionary History of Avian Flight from Small Leaping Arboreal Reptilian Ancestors

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Current hypotheses derive feathers from reptilian scales, but a more plausible explanation posits that feathers evolved from bristled sensilla on imbricated scales of small arboreal reptilian ancestors. This scenario is based on a gradual series of complex functional-morphological adaptations, integrates known biological and selective processes, and is testable through extant models. In extant small arboreal reptiles, sensilla are situated at the caudal rim of imbricated scales and bear bristles with branching setules. They are supplied with mechanoreceptors and are indirectly controlled by the dermal muscles of the scales. They are positioned to monitor airflow and serve as microturbulators to ensure laminar airflow during aerial locomotion. In extant small volant birds, feather follicles are similarly supplied with mechanoreceptors and controlled by dermal muscles, and feathers serve as airflow sensors as well as microturbulators. Reduced or experimentally generated feathers are situated on the distal rim of scales at the transition to the feathered parts of the legs, thereby supporting the scenario of feathers evolving from reptilian bristled sensilla under the selection for improved aerial locomotion. This scenario maintains the original function of the reptilian sensory organs while gradually integrating emergent roles of avian feathers, such as aerodynamic streamlining, thermal insulation, and visual signaling. Since the skin of reptiles with tuberculate or plate-like scales lacks bristled sensilla and dermal muscles, crocodilians and dinosaurs lack the accessory structures necessary for a gradual evolution of feathers. Based on the novel scenario of feather evolution and other supporting data, powered flight is inferred to have evolved gradually in small birds from small arboreal lizard-like ancestors leaping powerfully among tree branches rather than from putative archosaurian or dinosaurian ancestors gliding down from trees or running up inclines.

Amelogenesis of a Tribosphenic Molar: Patterns and Variation

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The tribosphenic molar presents the phylotypic stage in mammalian dental evolution. A study of its enamel microarchitecture in several clades (Chiroptera, Afrosoricida, Eulipotyphla, Didelphomorhia, Cetartiodactyla) revealed, apart from a considerable taxon-specific variation, a set of structural (i-iii) and developmental (iv-x) characteristics common to all: (i) patterning crown shape by shearing crests of major cusps, the basic structural modules of tribosphenic design, (ii) heterotopy of enamel thickness at individual modules (thick enamel on the convex *vs* its lack on concave sides of shearing crests), (iii) radial prismatic enamel (PE) with interprismatic matrix (IPM) and aprismatic surface enamel (AE), (iv) heterochrony of amelogenetic processes (establishing PE scaffold as primary amelogenetic product during the secretory stage, infilling the between-prism spaces by IPM at late maturation stage, termination of enamel maturation with AE related to amelotin secretion prior to eruption), (v) initiation of PE by intervention of odontoblastic processes, (vi) gradual growth of PE crystallites with abrupt drop of microstrain and increase of mechanical resistance at late maturation, (vii) extensive growth of the tooth during PE formation with considerable heterotopies and heterochronies among particular structural modules (as revealed by different patterns of prism curvatures), (viii) prolonged perieruptional stage enabling (ix) terminal enlargement of tooth and (x) refinement of shearing effect by growth heterotopy under control of first occlusion efforts of matured crests. Particular clades differ mostly in dynamics of tooth enlargement (vii), afrosoricids and shrews being the most derived. The results suggest that the developmental processes producing tribosphenic molars include a complex set of amelogenetic apomorphies prefiguring the potential of tremendous dental evolution already at the early onset of mammalian history.

On the Nature of the Trabecula Cranii

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The trabecula cranii comprises major paired elements that constitute the cartilaginous basis of the rostral embryonic skull. The trabecula was initially recognized as belonging to segmental elements of the pre-mandibular visceral arch, but more recent works suggest the trabecula to be an evolutionary novelty of gnathostomes with no relationships to ancient visceral arches of early vertebrates. We tested whether the trabecula can be considered as visceral arch elements utilizing embryos of basal actinopterygian fishes (African bichirs, European sturgeons, and Tropical gars), in which the pharyngeal pouch-like component in the premandibular head segment was recently described. This preoral gut might represent a pharyngeal counterpart of the rostral-most head, and we thus thoroughly examined the relationships of the trabecula and preoral gut during early stages of development with the aim to contribute to our understanding of the nature of the trabecula cranii.

Individual Variations in the Upper Molars of *Saguinus*: Comparative Study of Dental Wear on the Hypocone-like Cusp

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Many mammals have a cusp called the hypocone in the distolingual portion of the upper molar. In the platyrrhines (New World Monkeys), hypocone development is important for discussing classification and phylogenetic position. In addition, different forms of dental wear produce microwear features near the cusp and ridge line of the upper and lower teeth. On the hypocone, wear is noted along the distolingual, mesial, and buccal region of the cusp. A past report found that a hypocone-like cusp can be seen in the genus *Saguinus* (Natori M., 1988, Primates 29: 263-276). Generally, this is in the distolingual region of the upper molar of Callitrichinae including *Callithrix* and *Saguinus*, although Callitrichinae has a lingual cingulum instead of a hypocone. However, there is little information (frequency of appearance, degree of development, wear, etc.) pertaining to the hypocone-like cusp in *Saguinus*. In addition, its influence on chewing and jaw movement is unclear. We used materials obtained from six extant species of *Saguinus*, and the closely-related *Callimico*, *Leontopithecus*, and *Saimiri*, all examined under scanning electron microscopy (SEM) and digital microscopy (20-500×). We compared the frequency and development of the hypocone-like cusp and characteristics of the wear facet and microwear. We found that individuals with a distinctive hypocone-like cusp existed in *S. labiatus* and *S. fuscicollis*, with characteristic wear facets and microwear. Examination of cusp development, wear facet formation, and microwear features suggests that individuals with a hypocone-like cusp appear to demonstrate chewing or jaw movement patterns that are different from those associated with the normal lingual cingulum. To move forward, particularly when analyzing microwear, features of the extant species and fossil species, including jaw movement, tooth evolution, and relationship of the lineage within the Callitrichinae as a whole should be examined.

Functional Adaptation of the Shape and Inner Structure of the Patella – An Investigation in Perissodactyla

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The patella is the largest sesamoid bone. It is located in the major extensor tendon of the knee joint that it partitions into the quadriceps and patellar tendons, and articulates with the trochlea of the femur forming the patellofemoral joint. The patella is considered mechanically advantageous notably in enabling to keep the tendon further away from the joint, thus lengthening the moment arm of the muscle force, and for the tendon to better resist compression. However, despite the consideration of the functional role of the patella, studies focusing on the structure of this bone are rare, especially in a comparative perspective. In this context, our study proposes to investigate the form/function relationships of the outer and inner structures of this bone. We focused our study on Perissodactyla. While the structure of the patella is indeed functionally adapted to specific locomotion abilities, clear differences should be observed between cursorial horses and graviportal rhinos, with intermediate patterns in tapirs. We performed 3D-geometric morphometrics using anatomical and sliding landmarks in order to analyze in detail the structure of this hemispherical simple-shaped bone, both qualitatively and quantitatively. This enabled to detect anatomical changes in the articulating surface but also in the convex superficial surface. In addition, the resort to 3D-microanatomy revealed differences in cortical thickness but also in the organization of the bone trabecular network (trabecular thickness, orientation, density). The combination of these two approaches offers a more complete understanding of the whole bone adaptation to the functional requirements associated with high body mass support and propulsion and with high-speed running in perissodactyls and, more generally, a better understanding of the functional role of this bone in an evolutionary perspective.

Alternate Phylogenetic Positions of Fossils Affects Body Size Estimates of Snake Origins

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Hypotheses of snake origins remain controversial due to conflicting data sets, distinct anatomical and ecological inferences, and problematic fossils. Two alternate ecological specializations, fossoriality or aquatic swimming, have been proposed to be driving adaptations for the origin of the clade. Although a fossorial habitat has been shown to correlate with a reduction in body size in extant snakes, ancestral body sizes at the origin of snakes have not been investigated. Studies into body size reconstructions in other clades, namely mammals, have shown the importance of including fossil taxa in analyses, as these represent lineages with unique evolutionary histories which can profoundly change ancestral state estimations. To understand the role of fossils in body size evolution in snakes and their implications for competing origin ecologies, we performed ancestral state reconstructions using molecular and morphological phylogenetic topologies of snakes. Alternate placements of fossil taxa affected estimates of body size for the most recent common ancestor of all snakes (living and fossil). For example, inclusion of the Late Cretaceous snake *Dinilysia patagonica* as a stem snake greatly increased estimated body size of the most recent common ancestor of all snakes when compared to estimates resulting from analyses on extant snakes alone. Even when included as a stem alethinophidian, *D. patagonica* still increased estimates of ancestral body size for the snake total clade. These results are not consistent with a hypothesis that the ancestor of snakes was a small scolecophidian-like burrower. This highlights the importance of fossil inclusion and placement when reconstructing evolutionary histories of body size.

Deficiency of Sprouty Proteins in Mice Resemble Ciliopathic Phenotype

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The Sprouty family of proteins is a highly conserved group of intracellular modulators of receptor tyrosine kinase signaling, including the fibroblast growth factor receptor (FGFR) pathway. There are four orthologs (Sprouty1-4) in mammals. During embryonic development and postnatal bone remodeling, tight regulation of FGFR signaling is essential in endochondral ossification and in bone and mineral homeostasis. Sprouty2 was shown to be implicated in endochondral bone formation in Sprouty2-/- mice with reduced postnatal skeletal size and trabecular bone mass. Nevertheless, the underlying mechanism of its action at the molecular level remains to be elucidated. Moreover, long bones of Sprouty4-/- display limb malformations, such as chondroma-like lesions in locations adjacent to growth plate, or fused and/or supernumerary digits on front limbs. Our skeletal and other phenotypic findings on Sprouty2- and 4-deficient mice and Sprouty2/4 double knockouts (DKOs) strikingly resemble the phenotype of model mice bearing mutations in genes associated with primary cilia structure and function. Furthermore, *in vivo* evidence for disruption of primary cilia length was reported in achondroplasia and thanatophoric dysplasia cartilage growth plates with sustained activation of FGF signaling. Moreover, new links between ciliopathies and FGF-related syndromes have been discovered recently. Indeed, our analysis of Sprouty2-/- and Sprouty2/4 DKO embryonic and postnatal growth plates revealed elongation of ciliary axonemes compared to corresponding wildtype tissues and expression of several genes associated with ciliogenesis were downregulated in embryonic Sprouty2-/- tissue. Taken together, we propose that Sprouty proteins deficient mice may be actually ciliopathic in nature and that they represent a valuable model for studying the association of FGF signaling overactivation and cilia dysfunction, not only in skeletogenesis. This study was supported by the MEYS CR (CZ.02.1.01/0.0/0.0/15_003/0000460 and CEITEC 2020: LQ1601).

Complex Morphology of Gnathal Elements in Devonian Placoderms from the Early Devonian of Australia Sheds Light on the Evolution and Development of Teeth

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The evolution and development of teeth is one of the most important events for gnathostomes. However, how and when teeth evolved remain debatable. The extinct Devonian arthrodire placoderms, as a possible sister group of Chinese 'maxillate' placoderms plus crown gnathostomes, provide important information regarding early evolution of jaws and teeth. Synchrotron X-ray tomographic microscopy on several gnathal elements of arthrodire placoderms from Australia permits a detailed description of different types of gnathal elements in basal arthrodires. In displaying numerous denticle rows, gnathal element morphology is very different from the much reduced denticulation in higher brachythoracid arthrodires, even though the latter have been used recently to interpret the origin and early evolution of teeth. The gnathal element ossification centers of basal arthrodires have radiating denticle rows forming dental fields. They resemble those in phlyctaeniid and actinolepid arthrodires rather than advanced brachythoracids, and indicate the primitive arthrodire condition for comparison with the dermal jaw bones of Chinese 'maxillate' placoderms. These have been homologized with the premaxilla, maxilla and dentary of osteichthyans. The CT-data from this study demonstrates much more new morphological information than previously obtained from vertebrate fossils, and clarifies the sequence of character acquisition in the evolution of marginal jaw bones in basal gnathostome groups.

Evolution of the Feeding Morphology in Serrasalmid Fishes (Pacus and Piranhas)

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Serrasalmid fishes (98 species including pacus and piranhas) have largely diversified their diet in terms of food items. Some species prefer to feed on algae, plants, fruits, seeds or nuts whereas others eat flesh, fishes, fins, scales, parts of vertebrates or invertebrates. Despite this high trophic diversity, all species have in common the use of biting to capture food. How does the morphology of the feeding system evolve to trophically diversify in this monophyletic taxon while maintaining a unique feeding mode? To answer this question, we dissected and photographed different elements of the feeding system (cephalic region, adductor mandibulae muscle, lower and upper jaws, and buccal teeth) in 30 serrasalmid species representing a large part of dietary diversity. We quantified shape variation of these elements using landmark-based geometric morphometrics and explored their degree of specialization using phylogenetic comparative methods. Our results reveal two main groupings of species that are mainly consistent with diet (carnivorous *vs* herbivorous) and few intermediate forms (omnivorous?) considering the effect of shared ancestry. Carnivorous species show smaller eyes for a larger adductor mandibulae muscle and a superior mouth position allowing the lengthening of lower and upper jaws. They also have numerous teeth, which are highly triangular and sharp. Herbivorous species display larger variation of the size of the adductor mandibulae muscle, the mouth position and tooth shape. This difference in morphological disparity could be related to the feeding constraints and suggest that herbivorous taxa could exploit more ecological niches than carnivorous species. This study highlights how a set of subtle modifications in the feeding system of serrasalmid fishes has allowed their large trophic diversification.

Pleiotropic Jaw Morphology Links the Evolution of Mechanical Modularity and Feeding Convergence in Lake Malawi Cichlids

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Complexity in how mechanistic variation translates into ecological novelty could be critical to organismal diversification. For instance, when multiple distinct morphologies can generate the same mechanical or functional phenotype this could mitigate tradeoffs and/or provide alternative ways to meet the same ecological challenge. To investigate how this type of complexity shapes diversity in a classic adaptive radiation, we tested several evolutionary consequences of the anterior jaw four-bar linkage for Lake Malawi cichlid trophic diversification. Using a novel phylogenetic framework, we demonstrated that different mechanical outputs of the same four jaw elements are evolutionarily associated with both jaw protrusion distance and jaw protrusion angle. However, these two functional aspects of jaw protrusion have evolved independently. Additionally, although four-bar morphology showed little evidence for attraction to optima, there was substantial evidence of adaptive peaks for emergent four-bar linkage mechanics and jaw protrusion abilities among Malawi feeding guilds. Finally, we highlighted a clear case of two cichlid species that have independently evolved to graze algae in less than two million years and have converged on similar jaw protrusion abilities as well as four-bar linkage mechanics, but have evolved these similarities via non-convergent four-bar morphologies.

Seed Predation: Testing for Convergence in Masticatory Anatomy

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Primate seed predators are often considered functionally extreme due to the mechanical challenges presented by their diet. Numerous primates spanning a diverse phylogeny feed extensively on hard seeds, but whether morphological convergence has occurred is as yet unknown. This study compares the masticatory anatomy of hard and non-hard object feeding primates belonging to the families Atelidae, Cebidae, Pitheciidae, Cercopithecidae and Hominidae. 90 landmarks

(3D) representing key masticatory features were recorded from a sample of 101 primate specimens spanning 11 species. Landmarks placed on occluded crania and mandibles captured masticatory form. An analysis using geometric morphometrics was carried out on the full sample, followed by a distance-based test of convergence on representative males. It was predicted that the masticatory form of the specialist hard object feeding *Cercocebus atys* would converge with pitheciid seed predators, relative to more closely related or sympatric non-hard object feeding species. Results demonstrate that hard object feeding primates do not converge in the way that was predicted. The tougher feeding *Sapajus apella* showed significant convergence with the hard object feeding Pitheciidae; however, *C. atys* did not converge with the other hard object feeding primates. The results may suggest many-to-one-mapping of masticatory form in order to process hard objects, but alternatively they may relate to differences in food processing behavior and/or differences in the mechanical properties of 'hard' seeds. The results also indicate that tough and hard foods appear to place similar demands on the masticatory form. Further analyses will explore the functional differences between these masticatory forms to establish if there are many ways to crack a nut.

Evolution of the Patellar Sesamoid in Marsupials

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The patellar sesamoid plays an important role in knee joint leverage and protection, and has evolved as a mineralization over three times in tetrapod evolution. Our prior work noted complex patterns across family-level clades of metatherian mammals, especially marsupials, with perhaps ancestral ossification, then reduction to a fibrocartilage "patelloid", then re-ossification in some lineages. Here, we re-investigated this question at a species level with finer sampling of literature and specimens, including radiography and computed tomography of museum skeletal and fluid-preserved specimens along with some histological analysis of cadaveric tissue. We tested the hypothesis that a patelloid was ancestral for Marsupialia and repeatedly ossified in different clades; or even lost and regained. We found unusual incidences of bony patellae dispersed throughout the crown clade, including ossification of the patella on one limb but not the other of a single *Macropus rufogriseus* wallaby, and previously unreported patellar ossification (bilaterally) in a specimen of the extinct thylacine *Thylacinus cynocephalus*. Our results offered conditional support for our hypothesis if maximum likelihood evolutionary algorithms were used across metatherian phylogeny, with independently ossified patellae in Caenolestidae, Notoryctidae and Peramelidae. However, parsimony-based algorithms better supported our prior conclusion that a bony rather than fibrocartilage patella/patelloid was ancestral for Metatheria and thus the patelloid evolved later, close to Diprotodontia (and repeatedly in other lineages). Regardless, there is clear evidence for extensive homoplasy in the evolution of the patellar sesamoid in Marsupialia, which may relate to their apomorphic hindlimb development. Future work must be wary of the potential for remarkable individual variation (ontogenetic/other), perhaps due to incomplete evolutionary fixation of patellar ossification in various marsupial lineages.

Sternal Anatomy in Limbed and Snake-like Squamates; Implications for Evolutionary Developmental Mode and Mechanisms in Body Elongation

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The snake-like body form has evolved multiple times within squamates. Many anatomical specializations are associated with transitions from limbed to snake-like morphologies, including axial skeletal elongation, increased vertebral counts, and reduction and/or loss of girdles and limb elements. Despite these trends, there is no consensus as to whether this body form evolution is achieved through common evolutionary developmental innovations. Previous studies have focused on aspects of external morphology, axial osteology, and limb morphology to address evolutionary mode in body forms, but other components of skeletal anatomy have received less attention. To test for potential commonalities in squamate body form evolution, we examined sternal osteology as pairwise comparisons between snake-like squamates and their closest limbed relatives, based on microCT-imaging. We examined patterns of osteological reduction, presence/absence, and the relative positions of sternal anatomy as landmarks for assessing mode of axial skeletal elongation. Comparisons demonstrate a high degree of variation in sternal development, including loss, but a general conservation of topographic position relative to the axial skeleton and skull. Despite variation in morphology, all taxa possessing forelimbs retain distinct sternebrae, with the exception of the fore-limbed amphisbaenian *Bipes*, which has been proposed to have re-developed its girdle and limbs. The relative position of the sternal skeleton in snake-like taxa suggests a fairly conservative mode of body elongation. In all taxa, elongation occurs through postcervical addition of segments and extension of vertebrae. The cervical skeleton, defined by the position of the sternum, is either conserved in relative length, or is shortened relative to limbed taxa. Our results demonstrate the need for comprehensive comparative studies to resolve questions concerning both the evolution and development of anatomical novelty.

Evolutionary Implications of Dentitional Metamorphosis in Caecilian Amphibians: a Revisit

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Caecilians are fossorial pantropical amphibians renowned for their remarkable diversity of reproductive modes and ways of parental investment. The dentition of fetuses or juveniles differs from the adult condition in morphology, position and even in function among caecilian amphibians. Functionally fetal or vernal teeth are used to peel off the mother's skin post-partum or -hatching or to scrape off oviductal epithelium. We studied the dentition of selected caecilian species using

3D-reconstructions obtained from microCT-scans. The analysis included representatives of six out of the ten currently recognized families covering oviparous and viviparous reproductive modes. The dentition was followed throughout ontogeny, from larval to adult stages. In several species tooth number was positively related to body length. Significant differences in tooth numbers on dentigerous bones were especially found on the dentaries of dermatotrophic species such as *Caecilia pachynema*. In other species tooth number did not increase during ontogeny. The updated knowledge on the dentitional metamorphosis of caecilians helps to draw conclusions about specific ecologies and life histories but also aids in the understanding of amphibian evolution.

Cetacean Bone Mechanical Properties Vary among Swimming Modes and Diving Behaviors

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In cetaceans, the dorsoventral displacement of the axial body and bending properties of the vertebral column varies rostrocaudally during swimming. We hypothesized that interspecific variations in swimming modes and diving behaviors would be reflected in the mechanical behavior and in vertebral bone. Our goal was to quantify trabecular bone mechanical properties among cetacean species and among regions of the vertebral column. We categorized ten cetacean species based on functional groups determined by swimming modes (rigid *vs* flexible torso) and diving behavior (shallow *vs* deep). We predicted that stiffness and strength would be greatest in shallow-dwelling, rigid-torso swimmers due to their high performance body morphology, and also in the caudal regions of the vertebral column since the greatest forces translate to the peduncle and fluke during swimming. Delphinid and kogid vertebrae were obtained from necropsies and stored unpreserved and frozen before testing. Vertebrae were dissected from four regions of the vertebral column (thoracic, lumbar, and two caudal) and were cut into 6 mm^3 cubes. Bone cubes were tested in compression along the principal direction of stress, the rostro-caudal orientation, using a strain rate of 2mm/min using an Instron E1000 material tester. Stiffness and yield strength were calculated from stress-strain curves. We found that rigid-torso, shallow-diving cetaceans had the greatest stiffness and strength compared to flexible-torso, deep-diving animals, while deep-diving animals with rigid torsos were intermediate. These data suggest that animals habitually overcoming surface drag and wave turbulence have increased skeletal loading during active swimming, which results in increased bone stiffness and strength, compared to those that incorporate prolonged glides during deep descents in the water column.

Morphogenesis of the Lingual Gustatory Papillae in Donkey (*Equus asinus*, Equidae)

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It is generally known that the gustatory papillae in mammals develop as the first type of lingual papillae during the prenatal period. The appearance of the primordia of fungiform, vallate and foliate papillae and their morphogenesis was studied so far mainly in rodents, carnivores and camel. Our previous anatomical and histological study of the tongue in adult donkey showed the presence of three types of gustatory papillae. The data about the morphogenesis of the lingual papillae in donkey, as in other representatives of Equidae, are poor. Therefore, the aim of the present study is to establish a timeline of formation of lingual gustatory papillae and to characterize changes in the distribution and microstructure of these papillae in the donkey during the prenatal period, lasting ca. 360 days. The study was carried out on the tongue dissected from fetuses (ca. 131st to 320th day p.c.) using LM and SEM analysis. The observation of the fetal tongues allowed to distinguish three developmental stages. At about 131-138 day p.c. primordia of all types of gustatory papillae occur in the lingual mucosa. The primordia of the fungiform papillae slightly protrude over the surface. In the primordia of the vallate papillae the formation of a circumferential furrow starts. No clefts were present in the primordia of the foliate papillae. Taste buds were observed only on the apical surface of the primordia. Between 201-208 day p.c. all types of papillae consist of a connective tissue core and stratified epithelium. Folia of foliate papillae were separated by deep shallow clefts. At 295-320 day p.c. the microstructure of the gustatory papillae resembles that in the adult but the number of taste buds in the vallate and foliate papillae increases approx. five times. Noteworthy is that the taste buds develop both on the apical and lateral surfaces of the papillae. Summing up, the gustatory papillae in the donkey develop in the lingual mucosa in the second part of pregnancy. The taste bud system differentiates one month before birth. The developmental processes continue postnatally.

Embryonic Development of Tongue in Sand Lizard (*Lacerta agilis*, Lacertidae, Reptilia)

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Our current understanding of the morphology and histology of the lizard tongue is mostly focused on the hyolingual apparatus. Problematic issues in these studies are (i) evaluation of microstructures, which are described mostly using nomenclature for mammalian lingual papillae, and (ii) descriptions of mucosal epithelium. The sand lizard tongue possesses typical features of lizards such as two keratinized processes, mucosal folds of the dorsal surface and division of the posterior part of the tongue. Our own histological analysis of the sand lizard tongue showed that lingual papillae are in fact wide connective tissue folds, covered with non-keratinized epithelium without taste buds. The aim of this present work is to characterize the timeline and differentiation of lingual structures of sand lizards from developmental stage 25 to 40.

The results were obtained from LM and SEM observations. The morphology of the triangular tongue with two posterior lateral 'wings' is established between developmental stage 25 - 27. At this stage differentiation of anterior processes starts from the rise of a median furrow on the rounded lingual apex, followed by their rapid elongation from developmental stage 33. The keratinization of the epithelium on the anterior processes starts unusually from the ventral to dorsal surface on developmental stage 34. Histogenesis of the mucosa on the dorsal surface of the tongue starts from stage 28 and is preceded by such phenomena as first undulation and then folding of epithelium, as well as pigmentation starting from the posterior to anterior part of the tongue. The pattern of parallel ridges running transversely to the axis of tongue corresponds to an internal system of alternating connective tissue cores and epithelial bands. The formation of the mucosal folds and lingual, mostly intraepithelial glands, starts at developmental stage 34. The analysis of lingual structures in the sand lizard revealed the readiness to participate in food intake at the moment of hatching; however some developmental processes are continued.

Scar-Free Wound Healing of the Gecko Heart

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Among vertebrates, injuries to the heart are resolved via one of two different mechanisms: scar formation or scar-free tissue restoration. In adult mammals, the primary mode of cardiac wound healing is scar formation, leading to the permanent replacement of contractile muscle cells (cardiomyocytes) with non-contractile fibrous tissue. In contrast, among some teleost fish and salamanders lost or damaged heart muscle can be regenerated, thus restoring function. For reptiles less is known. Here, we investigate wound healing following a cardiac puncture in the lizard *Eublepharis macularius*, the leopard gecko. As for other squamates, the gecko heart has two atria and a single ventricle. The ventricular myocardium is trabeculated (spongy) and, under normal homeostatic conditions, has a large percentage of constitutively proliferative cardiomyocytes. Cardiac punctures to the ventricle are readily tolerated by geckos. To characterize the reparative events post-puncture, we used serial histology and immunostaining for markers of cell proliferation (proliferating cell nuclear antigen), cardiomyocytes (myosin heavy chain), and fibroblasts and endocardial cells (Vimentin). One day post-cardiac puncture (dpc), the wound site is characterized by the formation of a blood clot capping the puncture, and the localized loss of cardiomyocytes. Between 5 and 10 dpc, there is a surge in proliferating cardiomyocytes at the border of the lesion, and an increase in proliferating Vimentin+ cells within the wound itself. By 14 dpc, cardiomyocytes have repopulated the wound site, restoring the original trabeculated architecture of the myocardium. There is no evidence of fibrous tissue replacing cardiac muscle. Taken together, these data demonstrate that the gecko heart is capable of scar-free wound healing. Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grants 400358.

Evolutionary Trends and the Phylogenetic Relevance of Tooth Mineralization Patterns in Sharks (Chondrichthyes; Elasmobranchii)

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The evolution of jaws and teeth in vertebrates is considered a crucial step for their success. This is especially apparent in sharks, which are armed with several series of highly specialized teeth, allowing them to occupy a variety of different ecological niches at the top of aquatic food webs. Shark teeth not only exhibit a high diversity of different morphologies, but also three tooth mineralization patterns are known for this group: orthodonty (teeth have a hollow pulp cavity within the crown, which is encased by a dense layer of dentine (orthodentine)); osteodonty (the crown constitutes of porous, cellular dentine (osteodentine), which fully fills the hollow pulp cavity during the mineralization process); pseudoosteodonty (the hollow pulp cavity is replaced by a dentinal core of osteodentine, which is encased by orthodentine). Although a lot of work was conducted on the tooth histology of fishes, the emergence of several mineralization patterns in sharks as well as the evolutionary trends they are following have never been properly resolved and stay ambiguous to this day. High resolution microCT-images of jaws and teeth from selected species of all eight recent shark orders as well as members of the extinct order †Synechodontiformes reveal that the plesiomorphic condition for sharks is the pseudoosteodont tooth histoype and a change from pseudoosteodonty to orthodonty took place on the transition between orectolobiform and carcharhiniform sharks. The osteodont histotype was only present in the highly derived shark order Lamniformes, representing a synapomorphy for this group, which reopens the discussion of the systematic affiliation of the Jurassic shark †*Palaeocarcharias stromeri* and, therefore, the origin of the order Lamniformes.

Unusual Mandibular Morphologies in Two Undescribed Fossil Crows (Aves: *Corvus*) from the Island of Hawaii

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Three species of crows (genus *Corvus*) are known from the Hawaiian Islands: the extant but highly endangered `Alala (*C. hawaiiensis*) and two Quaternary fossil species, *C. impluviatus* and *C. viriosus.* The fossil record of Hawaiian crows also includes two undescribed species from the Holocene of Hawai`i Island. Both are diagnosable primarily on traits of the mandible, which is consequently the focus of this study. Using CT-scans, I show that the first fossil species has a distinctive bony buttress in the pars caudalis of the mandible. A previous study of a similar buttress in the mandible of New World jays (i.e., *Aphelocoma*) concluded that it functions to stabilize the mandibular articulation during pounding with the beak, to peel open acorns. The Akiapola`au (*Hemignathus wilsoni*), a Hawaiian Honeycreeper, is the only other species of bird previously noted to have such a buttress. The Akiapola`au also uses its mandible for hammering, in this case to access bark-boring beetle larvae. Although it lacks a bony buttress, the extant `Alala has been observed to hammer with the mandible to open large, hard seeds. I conclude that, among birds, the fossil crow from Hawai`i Island represents a third, independent evolution of a mandibular buttress that functions to facilitate vigorous pounding with the mandible. The mandible of the second undescribed crow had an unusually straight tomial crest. To place this in context, I measured the degrees of arc of the tomial crest in many species of *Corvus*. The second undescribed crow, as well as the previously described *C. viriosus*, have straighter tomial crests than almost all other crows except the New Caledonian Crow (*C. moneduloides*), which has the mandible adapted for tool use. The evidence is not clear enough to conclude that this second extinct species was a habitual tool user.

Postcranial Elements of Small Mammals as Indicators of Locomotion and Habitat

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Small mammals (<5kg) are often considered to be highly generalized, and their anatomy uninformative of specialized modes of locomotion. Anatomical correlates of locomotor behavior are easier to determine in larger mammals, but useful information can be obtained from the smaller ones, and may be applied to Mesozoic mammals (almost all <5kg). Bone proportions (e.g., brachial index) can be useful locomotor indicators; but complete skeletons, or even complete long bones, are rare for Mesozoic mammals. However, isolated articular surfaces are often preserved. While taxonomic assignation may be difficult, the taxon-free diversity of locomotor modes in a fossil assemblage may provide information on ancient habitats. We employed 2D-geometric morphometrics on limb bone articular surfaces: informative non-articular features of the ends of long bones (e.g., the olecranon process) are often broken in fossils. We included 82 species of extant small therian mammals (26 marsupials, 56 placentals) of known locomotor mode (arboreal, scansorial, terrestrial), to establish morphological correlates of locomotor behavior applicable across extant and extinct small therians. Canonical Variate Analyses showed varying results for different bones. The humerus and ulna are the best indicators for arboreal taxa, but cannot distinguish scansorial from terrestrial. In contrast, the femur can distinguish scansorial forms from other locomotor modes. The astragalus and calcaneum, although excellent locomotor indicators within mammalian orders, do not show good correlation with locomotor mode across the range of therians. Our results hold promise for the determination of past habitat types from assemblages of small mammal fragmentary postcrania. Note that these results are only applicable to therian mammals: the posture of non-therians is sufficiently different to preclude confident assessment of locomotor mode from a therian reference. Funding: Marie Curie Incoming Fellowship 623328 to CMJ.

Modeling the Mechanical Effects of Fiber Architecture and Muscle Bulging on Swimming and Suction Feeding in Fishes

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For most fishes, survival hinges on the ability of the axial musculature to generate powerful bursts of axial flexion for both swimming and suction feeding. During these behaviors, the axial musculature undergoes non-uniform strain like that of a beam, wherein the muscle tissue closer to the neutral axis of bending undergoes less longitudinal strain than tissue located farther from the neutral axis. Swimming (lateral flexion) and suction feeding (dorsoventral flexion) have different neutral axes of bending, such that non-uniform strain occurs along the mediolateral axis for swimming and the dorsoventral axis for suction feeding. If muscle fibers were oriented parallel to the length of a fish, non-uniform strain would allow only a fraction of the muscle fibers to shorten at the appropriate velocities for generating maximal power. However, prior studies have shown that fishes circumvent non-uniform strain during swimming (i.e., lateral flexion) with a gearing system in the axial musculature formed by oblique fiber orientations. But what effect does this complex fiber architecture have on muscle function during suction feeding which, unlike swimming, uses dorsoventral axial flexion? To answer this question, we developed a 3D-model to explore the effects of 3D-fiber angulation and muscle bulging on muscle strain during swimming and suction feeding. We created 'muscle cube' models with all permutations of dorsoventral (alpha) and mediolateral (phi) muscle fiber angles and simulated a range of dorsoventral and mediolateral bulging conditions. We use the model to determine whether certain combinations of alpha and phi—along with distinctive bulging conditions—can produce uniform strain during both behaviors, and to compare these to the actual architecture of the axial musculature in suction-feeding fishes.

The Ecological Diversification and Evolution of Teleosauroidea (Crocodylomorpha, Thalattosuchia)

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During the Jurassic, a plethora of marine reptiles dominated the oceans, including long-necked plesiosaurs, dolphin-like ichthyosaurs, large-headed pliosaurs and thalattosuchian crocodylomorphs (which included dolphin-like metriorhynchids and the more recognizably crocodile-like teleosauroids). Jurassic ecosystems were characterized by high niche partitioning and spatial variation in dietary ecology (Foffa et al., 2018, Nat. Ecol. Evol. 2: 1548–1555). However, while the ecological diversity of many marine reptile lineages is well understood, the overall ecological diversification of Teleosauroidea has never been investigated, perhaps due to their instable alpha taxonomy and phylogenetic framework. Here, we investigate the ecology and feeding specializations of teleosauroids, using morphological and functional cranio-dental characteristics. We assembled the most comprehensive dataset of nineteen teleosauroid taxa and ran a principal component analysis (PCA) to categorize them into various feeding guilds based on twenty-two dental characteristics, as well as a set of functionally significant mandibular characters. The results were examined against time and our comprehensive thalattosuchian phylogeny (154 taxa, including 26 teleosauroids, and 502 characters) to determine macroevolutionary patterns and significant ecological shifts. Teleosauroids have historically been thought of as “ancient marine gharials” with similar body plans; however, our results show teleosauroids to have been extraordinarily diverse. Multiple taxa fall into the pierce and crushing guilds (with intermediate forms), and there is increased bite efficiency in the shift from longirostry to brevirostry in the subclade Machimosaurini. Teleosauroids also show a range of body forms, from semi-terrestrial (e.g., *Mycterosuchus*) to nearly pelagic (e.g., *Aeolodon*). In addition, machimosaurins (e.g., *Lemmysuchus*, *Machimosaurus*) represent the first known evidence of durophagy in marine crocodylomorphs.

In Silico Models of Heat-Transfer Across the Artiodactyl Carotid Rete

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The central nervous system requires extensive temperature control in order to maintain homeostasis, such as preventing excess water loss. Because of the ecological potential of temperature control, osmoregulatory structures convey many advantages. Artiodactyls possess a unique arterial structure, known as the carotid rete, which functions as a heat exchanger that cools blood entering the brain, which in-turn delays hydrologically expensive heat-stress responses like panting. The carotid rete branches into numerous arteries which are surrounded by the subdural cavernous venous sinus. The blood of the venous sinus is cooled extracranially by the nasal cavity. The coupling of the arterial and venous structures forms a countercurrent heat exchanger where warm blood from the carotid rete is cooled by the venous sinus. Mathematical models of countercurrent heat exchangers dictate that there should be a positive relationship between surface area and heat exchange. Despite this mathematical relationship, previous *in vivo*, field-based studies have found no correlation between carotid rete height or volume and magnitude of cooling. To further explore the relationship between heat transfer and surface area/volume in artiodactyl carotid retia, we employed *in silico* computational fluid dynamic simulation. The effects of factors such as surface area and velocity on heat transfer were explored across these simulations, and we confirmed and quantified the positive relationship between surface area and heat-exchange. By isolating the effect of velocity and volume on heat transfer, future studies can explore the effects of alternative variables on cerebral thermo- and osmoregulation in mammals, such as adrenergic tone and behavioral thermoregulation.

Does the Defensive Role of the Pectoral Girdle Inhibit Mobility during Suction Feeding in Channel Catfish, _Ictalurus punctatus_ (Actinopterygii: Siluriformes)?

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Catfishes have a disproportionately robust pectoral girdle compared to most suction-feeding fishes. The large girdle articulates with defensive pectoral spines and has an expanded ventral surface that buttresses the spines and serves as the attachment site for muscles that flare and lock the spines, defending the fish against gape-limited predators. Despite its robust size and its role in stabilizing the pectoral spines, the pectoral girdle must also be mobile for suction feeding. Prior studies of clariid catfishes have shown pectoral girdle retraction (caudoventral rotation) also retracts and depresses the hyoid through the sternohyoid muscle, causing ventral expansion and producing suction. Catfish rely on this ventral expansion, as they use less neurocranial elevation than other suction feeders. But it remains unknown how the morphology of this robust pectoral girdle impacts its three-dimensional motion during suction feeding. We used XROMM and CT-scans to quantify the size and mobility of the pectoral girdle of channel catfish (*Ictalurus punctatus*) in comparison to two other suction feeders: largemouth bass (*Micropterus salmoides*) and bluegill sunfish (*Lepomis macrochirus*). In comparison to those of bass and sunfish, the pectoral girdle of catfish is longer and wider, relative to body size, and has two fewer joints per side and a highly interdigitated midline symphysis. Even so, catfish retract their girdles further during suction feeding, without the accompanying long-axis rotation that contributes to caudal displacement in sunfish and bass. The mobility of the catfish pectoral girdle, despite its size and fewer joints, highlights the anatomical flexibility that is available to suction-feeding fishes. Although the pectoral girdle is a crucial component of the feeding mechanism, our comparison suggests that it is able to serve other functions without impairing feeding.

Embryology of the Vomeronasal Organ and Associated Structures in Geckos (Squamata: Gekkota)

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The vomeronasal organ (VNO), or Jacobson’s organ, constitutes a part of the vomeronasal system, which is responsible for prey discrimination and response to pheromones. According to the long-standing hypothesis on the phylogeny of squamate reptiles, based on morphological and ecological data, Iguania (visually-oriented animals) is the sister group to Scleroglossa, which includes the rest groups of squamates: Gekkota (olfactory specialists) and Autarchoglossa (vomerolfactory specialists). Molecular studies reject the monophyly of Scleroglossa, suggesting that Iguania is nested deep inside Squamata, with Gekkota recognized as sister group to the rest of the living lizards and snakes. The close relationship of Iguania and vomerolfactory specialists such as snakes, was unexpected. However, little is known about the adaptations of the VNO, choanal groove (which constitutes the remnants of the primitive choana), and lacrimal duct to chemoreception. In adult representatives of Iguania and Gekkota, the choanal groove is confluent with the duct of the vomeronasal organ. Historically, Iguania and Gekkota were even combined into one group, Ascalabota, but it was a non-monophyletic group, formed on the basis of plesiomorphic traits. The purpose of this study was, first, to examine the embryonic development of the VNO and associated structures of two representatives of Gekkota, the mourning gecko *Lepidodactylus lugubris* (Gekkonidae) and the leopard gecko *Eublepharis macularius* (Eublepharidae), using histological studies and 3D-reconstructions based on X-ray microtomography; and, second, to compare the obtained results with those of our previous studies on the grass snake and brown anole (Iguania). Developmental data of embryonic VNO and associated structures of geckos may provide an important contribution to future studies considering the phylogeny of Squamata. The studies were supported by a grant from the National Science Centre (NCN) Poland (2018/28/T/NZ4/00182).

Hypertrophied Snout of the Lake Kronotskoe Littoral-dwelling Charr *Salvelinus malma* (Salmonidae, Teleostei): anatomy and developmental pathways

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The descendants of *S. malma* inhabiting the Lake Kronotskoe (Kamchatka, Russia) represent a spectacular example of adaptive radiation. This sympatric flock consists of eight ecomorphs differing in their biology, ecology and functional morphology. The benthivorous nosed charrs (N1,2,3 morphs) dwell in the littoral zone and consume amphipods (Crustacea) mainly. The most reliable morpho-functional adaptation of these morphs is the sub-terminal mouth position determined by a relatively long snout. The shape and size of the snout differ significantly among the morphs. In the morphologically most advanced one (N3), the snout tip takes a large bulbous shape overhanging the lower jaw. Here, we present data of the comparative histological analysis of the ancestral *S. malma* and N3 morph clarifying the anatomy of a hypertrophied snout and developmental aspects of its formation. We revealed that the adult individuals of the N3 morph have specific changes in the cartilaginous and loose connective tissues. Ethmoid cartilage displays a well-distinguished fibrocartilaginous zone in its rostral part. The active chondrocyte proliferation in this zone provides the expansion of the ethmoid cartilage forward and laterally, which, in turn, shifts the premaxillary bones in the lateral directions. Consequently, these bones lose contact with each other. In the ancestral form, premaxillary bones connect in the midline of the snout. A thick layer of loose connective tissue between the cartilage and skin, forming the upper and front part of the snout, is also typical of the N3 morph only. Thus, the formation of hypertrophied snout is provided by the expansion of the ethmoid cartilage and the overgrowth of loose connective tissue. Such transformations provide a novel mechanism of amphipod grabbing and contribute to the implementation of a specific diversification mode within the lake's littoral zone. This work was supported by RSF Grant № 18-74-10085.

Understanding Sexual Dimorphism in the Bovid Species at Harappan Site of Rakhigarhi, District Hissar, Haryana, India

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The site of Rakhigarhi, situated in Tehsil Narnaul, District Hissar, Haryana on the Northwestern frontiers of India (29°16' N and 76° 10' E) is possibly the largest Harappan metropolis uncovered till date. Series of excavations from 1999 to 2000 had yielded a quantitatively and qualitatively rich faunal deposit from the habitation area. It comprises a diverse population of small to large vertebrates including rodents, carnivores, large to small felids, equids, bovids, cervids, rhinoceros, elephants, suids, birds, fresh water fish, as well as mollusks. However, bovids predominate the assemblage, with nearly 60 % of bones belonging to large bovines. This phenomenon is observed in most of the harappan sites in the Indian subcontinent. The bovids have been exploited not only for their primary product, meat, but also for secondary products, like traction, milk, hide, dung etc. Bones with cut marks and charring indicate their significance for the diet. Cattle dung is still used in the area for plastering wattle and daub houses as was found in the houses of Harappans. Skeletal anomalies on the phalanges resulting from draft exploitation are evident in the assemblage. All of these emphasize the major role played by cattle in the agropastoral economy of Harppans. However, the geographical area under consideration is inhabited by different species of bovids namely cattle (*Bos indicus*), buffalo (*Bubalus bubalis*) and Nilgai (*Boselaphus tragocamelus*).The osteological similarities in the bovids makes species level identification of archaeological remains difficult. Thus, understanding the exploitation pattern and dietary dependence on wild and/or domestic species becomes more doubtful. This work focuses on species level identification of bovids using skeletal markers, morphometry of astragali and phalanges to differentiate among *Bos*, *Bubalus* and *Boselphas* species and tries to shed light on sexual dimorphism in bovids from the Early Harappan levels of Rakhigarhi.

Bone Pedicle Development and its Association to the Tooth Germ in Acrodont Chameleons

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Most lizards and snakes exhibit teeth ankylosed to the underlying bone. In chameleon the teeth are firmly attached to the top of the tooth-bearing bone pedicles (acrodont dentition). The aim of our study was to reveal the developmental processes contributing to the formation of the tooth-bone interface - what are the differences between labial and lingual parts of the bony pedicles? When is the asymmetry in bone formation lost? How is the bone translocated under the teeth? Bone pedicle initiation was analyzed by microCT in pre-hatching animals to reveal possible asymmetries in their initiation at the labial and lingual side of the lower jaw, the relation of the tooth germ to pedicle formation along the jaw, and the rearrangement of the spatial relationships between cervical loop and underlying bone. Native and iodine stained samples of several stages of chameleon embryonic jaws were scanned with GE phoenix micro CT-device, which allowed analysis of the samples in both 2D-slices and 3D-model in VG studio MAX software. TRAP-analysis was performed to detect osteoclast distribution during pedicle formations. TEM was used to analyze submicroscopic changes in cells in the area between tooth and bony pedicles. We found that chameleon teeth grew asymmetrically with higher progress on the labial part of the cervical loop at early stages. The early tooth germ at cap stage developed at a large distance from the ossification center of the mandible, and tooth and underlying bone seem to develop independently. Later in development, the cervical loop was re-oriented towards the bone ridge to meet the underlying bone. In conclusion, the acrodont dentition resembles a pleurodont dentition during development with distinct asymmetries in the cervical loop as well as early bone morphology. The project was supported by the Czech Science Foundation (project No. 17-14886S) and by CEITEC 2020 (LQ1601) with financial support from the National Sustainability Programme II and CEITEC NRI (MEYS CR, 2016–2019).

Extreme Gigantism of the Enigmatic Tethythere Desmostylia (Mammalia: Afrotheria) from the Early to Middle Miocene of the Western North Pacific

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The enigmatic extinct tethythere paleoparadoxiids (Desmostylia: Paleoparadoxiidae) are known from the early and middle Miocene of the North Pacific realms. They consist of at least three genera and four species, and some are also known from the Japanese Islands. Among them, three different sized paleoparadoxiids have been reported from the lower to middle Miocene marine deposits in Sado Island, Niigata Prefecture, Japan, and they show interesting trends of their morphological and paleoecological evolution. Specimen 1 (comprising a pelvis, femur and tibia) and specimen 2 (molar tooth) were collected from the late Early Miocene shallow marine Orito Formation (ca. 17.0-16.7 Ma). Specimen 1 was recovered from the lower part of the Formation, while specimen 2 was collected from the upper part of the same Formation. Specimen 3 (consisting of vertebrae, ribs and pelvis) was found in the Middle to Late Miocene bathyal Tsurushi Formation (12.3-9.9 Ma). These three specimens show distinctive differences in body size. Among them, specimen 2 is much larger than specimen 1. Since the deposition of the Orito Formation is less than one million years, this indicates that the body size of the paleoparadoxiids had increased rapidly into giants in the late Early Miocene of the western North Pacific. Specimen 3 from the overlying Tsurushi Formation is much larger than both specimens 1 and 2 from the underlying Orito Formation. The estimated body length of specimen 3 reaches approximately five to six meters. However, the relative size increase of the pelvis is not greater than that of the ribs. In this regard, the gigantism especially of the rib bones may be analogous to that of the North Pacific sirenians like the Stellar's sea cow lineage during the late Miocene. In addition, the paleoparadoxiids show not only the extreme gigantism of their body size but also the expansion of their habitat to open ocean in the middle Miocene of the western North Pacific.

Comparative Morphology of the Forelimb and Pectoral Girdle in Forward-burrowing Frogs

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Anuran locomotor strategies are diverse and include saltation, swimming, walking, climbing, and burrowing. Burrowing has many benefits for frogs: predator avoidance, exploitation of novel food stores, and access to a moist and cool environment. This behavioral strategy is widely convergent across anuran phylogeny. Within burrowing frogs, there are two main burrowing strategies: head-first burrowing and feet-first burrowing. The majority (95%) of burrowing anurans dig feet-first, such as in the spadefoot toads (*Scaphiopus*). While front-first burrowing is less common, it has evolved independently at least seven times across Anura. These forward-burrowers tend to be more specialized for life underground. Some of their adaptations include a reinforced rostrum, ossified sternum, enlarged forelimb retractor muscles, and robust forelimb and pectoral girdle bones. Using CT-data generated through the oVert Thematic Collections Network, this project (1) quantifies shape variation in the humerus, coracoid, and scapula of burrowing taxa with 3D-morphometrics, (2) compares the shape of burrower humeri to that of non-burrowers across all 55 frog families, (3) visualizes the muscular anatomy of the pectoral girdle with DiceCT-techniques, and (4) identifies potential front-first burrowing species based on their pectoral anatomy. This work provides a framework for predicting locomotor modes in taxa for which the natural history is poorly known. This is of particular importance for fossorial taxa, which have historically been understudied due to their cryptic nature.

The Role of Thyroid Hormone in Proper Shape and Size of Skeletal Elements during Ontogeny

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Thyroid hormone plays a key role in proper skeletal development in vertebrates. Previous data using thyroid-ablated zebrafish has shown that a great number of bones are affected in size, shape, and mineralization. As such, zebrafish are an excellent model system with which to investigate the developmental consequences of thyroid disruption. Disruption of thyroid hormone in zebrafish leads to several morphological changes in the adult skeleton. Some of the most affected elements include the lower jaw, hyomandibula, pharyngeal jaws, and tripus. In addition to being significantly impacted by thyroid disruption, these bones are all functionally important. The lower jaw plays a role in food capture, the hyomandibula supports the jaw and connects it to the neurocranium, the pharyngeal jaws process food, and the tripus is part of the Weberian apparatus which connects the swim bladder to the inner ear for hearing. Given that these bones are significantly impacted by thyroid disruption, an ontogenetic sequence of zebrafish was cleared and stained and investigated to document changes to timing, ossification, and shape of these bones from larval to adult stages. Overall thyroid disruption led to delayed growth and ossification in hypothyroid zebrafish, and accelerated growth and ossification in the hyperthyroid condition. Furthermore, thyroid disruption led to changes in the shape of bones in both hypo- and hyperthyroid zebrafish. By determining ontogenetic changes in morphogenesis and ossification of these bones we can better direct future studies which will investigate both the molecular pathways that thyroid disruption affects as well as the functional impact of altering the morphology of these bones.

The Role of Thyroid Hormone in Phenotypic Effects on Cypriniform Cranial Morphology

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With over 4000 described species Cypriniformes is a diverse group of freshwater fishes showing nearly unparalleled diversity in trophic anatomy. Specifically, this group is characterized by several feeding novelties which include pharyngeal jaws comprised of hypertrophied fifth ceratobranchials as well as kinethmoid-mediated premaxillary protrusion. The hypertrophied 5th ceratobranchials have teeth ankylosed to them and since upper pharyngeal jaws have been lost, these fishes process food against the basioccipital pad at the base of the skull. Here, we show that thyroid disruption has profound effects on the morphology of the pharyngeal jaws, phenocopying some of the natural variation seen within cypriniform pharyngeal jaws. In contrast to the euthyroid condition, the pharyngeal jaws of hypothyroid zebrafish have significantly more teeth, the posterior and anterior arms are the same length, and the supporting struts are thinner and more disorganized. Alternatively, the pharyngeal jaws of hyperthyroid zebrafish have significantly fewer teeth, and pronounced differences associated with skeletal architecture of these jaws. Kinthemoid-mediated premaxillary prostrusion was also strongly affected by thyroid hormone. The kinethmoid, a sesamoid bone that sits ventral to the ascending process of the premaxilla, has been shown to play a vital role in cypriniform jaw protrusion. In the hypothyroid zebrafish, the kinethmoid failed to ossify properly and lacked the characteristic lateral wings and dorsal process. In the hyperthyroid zebrafish, the kinethmoid is hyperossified and misshapen. Thyroid hormone therefore appeared to regulate the proper development of these feeding novelties, and evolutionary modulation of thyroid hormone may give rise to some of the trophic diversity observed within Cypriniformes. Understanding how the modulation of thyroid hormone changes these bones, and thus their ability to function, may lend insight into how they may have evolved.

Bats to Belugas: Functional Anatomy of Biosonar in Air and Water

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During the explosive period of mammalian radiation, two groups, Microchiroptera and Odontoceti, emerged with highly evolved adaptations for ultrasonic hearing and echolocation in radically different media - air *vs* water. In the last 50 million years, these groups proliferated into diverse species, all of which possess highly sophisticated biosonar capabilities. This paper addresses media related functional commonalities and differences of biosonar receptors of bats *vs* dolphins, comparing the auditory peripheries of these groups; i.e., structural variations in the outer, middle, and inner ears, highlighting convergences in the cytoarchitecture and morphometry of their inner, middle, and outer ear structures. Data presented are taken from behavioral, electrophysiological, microscopical, ultrahigh resolution imaging, and finite element simulation studies. Inner ear anatomy is fundamentally similar across the groups although differences exist in both neural densities and distributions as well as basilar membrane dimensions and cochlear spiral configurations. Specialist ears are present in both groups, suggesting at least one odontocete has cochlear specializations consistent with those found in some CF-FM bats (bats producing constant frequency (CF) and frequency modulated (FM) vocalizations), including specialized basilar membrane regions and high frequency neural foci. Cochlear specializations in both groups are primarily linked to peak spectra of their echolocation signals, expanded frequency representation, and in some cases, possibly enhanced tuning in adjacent ear segments derived from standing wave phenomena. Differences that are consistent with processing of aerial *vs* aquatic borne sound, such as the fatty tissue pinnal analogues in odontocetes, are found primarily in the outer and middle ear elements. Other differences among species within each group are correlated with signal type, prey, and/or habitat complexity. Funding sources: Hanse Wissenschaftskollegg ICBM Fellowship; Helmholtz International Fellow research program; Joint Industry Programme on Sound and Marine Life.

Allometric Variation of Skull and Mandibula Shape in *Nyctalus noctula* (Schreber, 1774) (Chiroptera: Vespertilionidae)

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Intraspecific variation of skeletal structures can be a result of genetic or environmental factors. It may reflect either phylogenetic divergence or phenotypic plasticity. *Nyctalus noctula* is one of the most widespread species of bats in Europe that prefers forest habitats for breeding and hibernates in urban areas. It is a long-distance migratory species, capable for long, up to 1600 km migrations. *N. noctula* is thought to be genetically uniform (Petit et al. 1999, Evolution 53: 1247-1258). The aim of our study was to estimate variation in the shape and size of *N. noctula* skull and mandibula. We used the geometric morphometrics approach with several projections of each skull and mandibula to study intraspecies allometric variation. In the results we describe the cranial morphometric differences that are associated with the size of the *N. noctula* skull and mandibula and demonstrate which cranial structures change most of all due to the size increase. We also estimate between-sex differences and describe associated shapes. Estimating *N. noctula* intraspecific and between-groups cranial variation with the methods of geometric morphometry complements the few data available about cranial variation of this widespread species. This study provides evidence for microevolution processes in *N. noctula* populations.

PORCN Inhibition Stimulates Chondrocyte Differentiation

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Porcupine (PORCN) is an endoplasmic reticulum protein belonging to the membrane bound O–acyl transferase superfamily. This molecule is necessary for the attachment of long chain fatty acids to WNT proteins. PORCN is expressed in most tissues of the body and animals with loss of function in PORCN exhibit embryonic lethality at early developmental stages with extensive gastrulation defects. Several dominant mutations in PORCN were described in human patients, who demonstrated significant skeletal abnormalities. Recently, a powerful PORCN inhibitor C59 has become commercially available and has been successfully used to inhibit WNT pathway in several cancer lines. C59 negatively affects WNT signaling by inhibition of WNT palmitoylation, which is necessary to acetylate WNT ligands before their secretion and binding to a carrier protein. Here, we analyzed the possible effect of this inhibitor on skeletogenesis with focus on endochondral bone formation. We observed, enhanced growth of mesenchymal condensations and also increased number of cartilage nodules in primary micromass cultures established from the early limb bud, which were treated by increasing concentrations of C59. This trend was also confirmed by analysis of peanut agglutinin expression visualizing early mesenchymal condensations. Also the amount of extracellular matrix produced by differentiated chondrocytes was enhanced as was shown by Alcian Blue staining on six day cultures. Moreover, *in vitro* cultures of embryonic tibias treated by C59 displayed a massive increase of cartilaginous mass. Histological analysis revealed enlargement of the hypertrophic cartilage zone. The direct effect of C59 on chondrogenesis has not been determined yet. As this inhibitor can influence both canonical and non-canonical WNT signaling, we next plan to analyze changes in activation of WNT members during chondrogenesis using molecular approaches. This study was supported by the MEYS CR (CZ.02.1.01/0.0/0.0/15_003/0000460).

Osteoderms of *Heloderma suspectum* – A New Nano-Micro Hierarchical Biomineralized Structure in Vertebrates

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Helodermatidae is a family of venomous lizards that has evolved osteoderms in the skin. Since they were first reported, osteoderms have generally been described as bone-like structures, and this concept has never been thoroughly challenged. Here, the nano/micro characteristics of the osteoderms of *Heloderma suspectum* are evaluated and compared to bone and tooth samples from the same animal. This characterization study was done using advanced physical-chemical analyses, such as electron microscopy with focused ion beam (FIB). At the micro scale, SEM results show that the osteoderms can be divided into three regions: a highly mineralized dense material present in the upper region of the osteoderm; a bone-like material that runs through the osteoderm, apparently surrounding vasculature; and a mineralized region, with collagen fibers organized in a three-dimensional mesh. At the nano scale, TEM of samples prepared by FIB demonstrated that each of the three different regions is unique, with different nanostructures and crystallinity, as demonstrated by x-ray diffractometry. Comparison with samples of bone and teeth taken from the same animal reveal that the osteoderm is indeed a unique mineralized tissue and not a bone-like tissue. These results are an indication that in vertebrates, natural non-pathological hard tissues are more diverse than suspected, suggesting the existence of completely novel cellular and biochemical biomineralization systems. Further preliminary results indicate that the three structures described here are the fundamental components of osteoderms in lizards, with variations in the shape and proportion of these three structures between species. Finally, beyond the biological, evolutionary and ecological significance of these hard tissues in vertebrates, the hitherto unknown nano/micro structures described here might prove valuable in future translational applications, including the creation of bioinspired materials with special properties.

Divergent Trends of Cranial Modularity and Integration in a Highly Homoplastic Clade of Squamate Reptiles

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Whereas studies on integration and modularity have been frequently performed on mammals, many other vertebrate clades remained poorly studied. Here, we focus on lacertid lizards, an Old-World clade of squamate reptiles which can be divided into an extremely homoplastic Palearctic clade and its morphologically well differentiated African sister group. To test whether both groups show different patterns of cranial modular evolution and how this relates to their ecology and phylogeny, we generated 3D-microcomputed tomography models of 250 lacertid lizard skulls representing 83 species from 39 genera, covering almost the entire genus-level diversity of the family, and subjected these data to a 3D-geometric morphometric analysis. We also included linear body measurements and ecological traits and used a newly generated phylogenomic dataset for our phylogenetic comparative analyses. Results show that the skulls of the African taxa display a much higher degree of variation, whereas the Palearctic species are distinctively more similar to each other. However, the Palearctic taxa show a significantly higher degree of modularity and are less integrated than the African species, which is surprising given the overall cranial similarity across the Palearctic clade. Whereas some modules, such as the posterior skull roof, are better predicted by phylogeny than ecology, other modules like snout and facial region show a stronger ecological signal. Overall the Palearctic clade possesses cranial modules that are strongly independent from each other and appear to be primarily determined by ecology, which is likely responsible for the clade's high amount of homoplasies. Our results suggest that different selective pressures during the evolution of a clade may result in strongly divergent patterns of modular organization and phenotypic expression even at relatively low taxonomic levels.

Using Ossification Patterns and Timing to Determine the Homology of the Unique Human Pisiform

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The pisiform and calcaneus are paralogous bones of the wrist and ankle. Both are elongated and typically form from two ossification centers with an associated growth plate in mammals. While the human calcaneus retains two ossification centers and a growth plate, the truncated human pisiform develops from a single ossification center without a growth plate. Pisiforms are highly evolvable across mammals; however, extremely short pisiforms are rare. This raises the question of whether the short human pisiform is homologous to the primary ossification centers or epiphyses in other species. To address this question, we performed an ontogenetic study of pisiform and calcaneus ossification patterns and timing, with respect to dental eruption stage, in macaques, apes, and humans (n=907). Timing of pisiform primary and secondary center ossification and fusion typically corresponds to that of the calcaneus in non-human primates, while the single human pisiform ossification corresponds to the late forming calcaneal epiphysis. The human pisiform ossifies at the same dental stages as pisiform and calcaneal epiphyses in other hominoids. Additionally, the human pisiform ossifies irregularly, much like the epiphyses of other species, and it lacks the characteristic articular surface for the triquetral seen during early ossification of the pisiform primary centers in non-human primates and mice. These data indicate that the human pisiform is homologous to the pisiform epiphysis of other species, and that humans have lost a primary ossification center and associated growth plate. This represents a substantial morphological and developmental change not only among primates, but among mammals. This project was funded by the National Science Foundation Doctoral Dissertation Improvement Grant (NSF BCS-1540418) and by the Hill Fellowship, Department of Anthropology, Pennsylvania State University.

Histovariability in Long Bones of Triassic Diapsida

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Modern amphibians and reptiles have usually slow growth rates and grow with lamellar-zonal bone tissue type whereas most modern mammals and all birds have fast growth rates and their bone tissue type can be summarized as fibro-lamellar. The relative uniform and predictable pattern in modern groups is opposite to what many Triassic diapsids, such as members of lepidosauromorphs, archosauromophs, and marine reptiles, display. Each of these groups shows a variety of combinations of bone tissues and vascularity patterns, by far exceeding what is observed in any modern tetrapod group. One reason for the histological diversity among Triassic diapsids might be related to the origin of many new groups after the Permo-Triassic extinction event. In addition, histological features largely influence life history traits such as growth rate, longevity, and age at sexual maturity, and the observed variability in histology is also related to the expression of different life history strategies. Triassic environments might have been less stable and demand histological flexibility, which in fact goes together with a flexibility in life history. However, the question remains why histological flexibility and variability seem to be lost in modern reptile groups.

Anatomy of the Braincase of the Early Permian *Diadectes absitus* (Diadectomorpha) from Germany Based on High-resolution X-ray Microcomputed Tomography

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The group Diadectidae (Diadectomorpha) includes several genera of Permo-Carboniferous tetrapods from Europe and North America. The members of this group are supposed to be the first clade of early tetrapods to develop a high-fiber herbivory. Although the genus *Diadectes* was described more than hundred years ago, its cranial anatomy, especially the braincase, is poorly known. The main reason for this is that in all specimens of *Diadectes*, in which the braincase is at least partially preserved, the individual bones composing the braincase are almost completely fused together. Further, the more-or-less preserved braincases of *Diadectes* are not sufficiently visible from the outside to enable their study. Here, we present the anatomy of the braincase of the subadult specimen of *Diadectes absitus* from early Permian sediments of Germany based on high-resolution X-ray microcomputed tomography. The individual bones of the braincase (opisthotic, prootic, supraoccipital, basioccipital, exoccipital, basisphenoid, sphenethmoid) and parasphenoid are not co-ossified. This allowed for the first time to segment and describe every bone individually. The supraocciptal, opisthotic and prootic contain a well preserved endosseous labyrinth. It was possible, for the first time, to produce virtual 3D-reconstructions not only of the individual bones of the braincase, but also of the cochlear recess, vestibule and three semicircular canals. It was also possible to identify a shallow subarcuate fossa on the ventral surface of the supraoccipital. A typical feature of the braincase of *Diadectes* is the presence of the otic tube connecting the fenestra ovalis with the vestibule. In *D. absitus*, the anatomy and topology of the otic tube are well identifiable. This project was supported by the VEGA grant agency, Grant number 1/0228/19.

Synchrotron-based 3D-Mapping of Molar Morphogenesis, Jaw Growth and Retromolar Space Creation in a Mouse Model

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The processes that integrate the morphogenesis of vertebrate teeth and jaws remain unclear, including the extent to which surrounding jaw tissue constrains the developing tooth organ including its onset time. We sought to compare retromolar space with molar onset and length. We hypothesized that first (M1), second (M2) and third (M3) molars would initiate only as retromolar space lengthened via jaw growth. We aimed to directly visualize in 3D earliest molar onset to crown completion, and to measure molar, total jaw (TJL) and retromolar (RML) lengths. At the Canadian Light Source synchrotron, we micro-computed tomography (μCT) scanned (8.75μm resolution) a cross-sectional series of PFA-fixed, silver-stained wild-type (C57BL/6J) mice aged embryonic day (E) 10 to postnatal day (P) 32 ($n \leq 3$ specimens/stage). Using Amira software (FEI), we visualized these μCT-scan sets in 3D and, using sagittal, coronal and transverse planes, measured upper and lower molar crypt and crown mesio-distal lengths, TJL and RML. Measurement data were analyzed in Excel (Microsoft). From E14 to P32, in upper and lower jaws, for every stage/age there was space distal to the last-initiated molar. TJL rapidly grew from E12-E18 (spanning M1, M2 onset), slowed from P0/birth-P18 (spanning M3 onset), spiked at P21, and stabilized from P23-P32. Upper/lower molars followed a trend of M1>M2>M3, with lower molars closer to M1>M2≥M3. Until P3, RML≈M1 length in lower and upper jaws. After P6, lower RML>M1 length, while upper RML≤M3 length. In conclusion, space immediately distal to the last-initiated molar was available throughout the period of M1-M3 onset and development. Spatial relationships were comparable between upper and lower molars/jaws; however, upper RML was shorter by ~20%. Jaw space does not appear to constrain molar onset; rather conditions within the dental lamina likely exert greater influence on onset time. FUNDING: NSERC, CFI, CIHR-THRUST, College of Medicine USask.

Developmental Mechanisms Underlying Enlargement of the Telencephalon Differ in their Potential to Generate Large Neuronal Populations: a Case of Galliform and Anseriform Birds

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Galliform birds (landfowl) and anseriform birds (waterfowl) together make up the Galloanserae, the sister group of Neoaves and the most basal clade of Neognathae. However, to date no quantitative data on cellular composition of their brains have been available. Here, we used the isotropic fractionator to determine numbers of neurons and non-neuronal cells in specific brain regions of 15 species of galliform birds and 23 species of anseriform birds. While galliform birds feature low encephalization, a proportionally small telencephalon and generally lower neuronal densities, anseriform birds have large brains characterized by anexpanded telencephalon. Nevertheless, their neuronal densities resemble those of galliform birds, being much lower than in the landbirds, such as parrots and songbirds, other bird groups with expanded telencephalon. Galliform birds have small telencephalic (24–37 % of brain neurons) and dominant cerebellar (49–74 % of brain neurons) neuronal fractions, while the telencephalon of anseriform birds, despite being significantly enlarged, typically contains slightly less than 50% of brain neurons. The total number of neurons and the number of telencephalic neurons for a given brain size is significantly lower in fowl birds than in songbirds and parrots. This suggests that different developmental mechanisms leading to the expansion of the telencephalon differ markedly in their potential to generate large neuronal populations. Anseriform birds are precocial and their telencephalon grows in size early in embryonic development, whereas in altricial parrots and songbirds, telencephalic expansion is associated with protracted neurogenesis and delayed neuronal maturation. Extensive post-hatching neurogenesis is thus evidently much more efficient in generating large neuronal populations.

Did the Cheek Tooth Size of Japanese Wolves Change during 40,000 Years?

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The Japanese wolf distributed on the the Japanese Islands of Honshu, Kyushu, and Shikoku is generally recognized as a subspecies of the Gray wolf that is distributed on the Northern Hemisphere. Although the Japanese wolf became extinct in the 1900s, their remains including skulls and teeth indicated that the Japanese wolf was smaller than the continental subspecies. On the other hand, the middle to late Pleistocene wolves from the Honshu Island are extremely large, and it is thought that the Japanese wolf had gradually reduced in size after the Pleistocene, or that the Pleistocene wolves on the Honshu Island belonged to a population different from the Japanese wolf. In this study, we measured the precise age of the Pleistocene and Holocene wolves from cave deposits and archaeological sites by 14C-dating method, and we determined the size range of the lower first molars (carnassial) of those wolves based on the time interval by absolute ages. As a result, although the current Japanese wolves (i.e., Japanese wolves after the Pleistocene) were smaller than wolves from the Pleistocene deposits, the tooth size of the former was discontinuously smaller than that of the latter. To our surprise, the size range of the lower carnassial of the current Japanese wolf is almost stable within a range of 29 – 24 mm in mesiodistal diameter in contrast to the Pleistocene wolf which has a size range of 35 – 29 mm. This suggests that the Pleistocene wolf on the Honshu Island was abruptly reduced in size after the extinction of larger prey such as bison and/or giant deer from the Japanese Islands and became the current Japanese wolf. Alternatively, it also became extinct with other large mammals and was replaced by the current Japanese wolf in an unknown process. In any case, the current Japanese wolf did not undergo a gradual reduction in size during the Holocene until its extinction in the 1900s.

Comparative Anatomy of the Shoulder Girdle Muscles in Domestic Fowls

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Many previous studies have described the anatomy of the musculature of the domestic fowl, a commonly used animal for developmental experiments. However, some differences in terminology existed among authors. This made it difficult to discuss exactly the muscle homologies between fowl and mammals. In this study, the innervations of the shoulder girdle muscles in three domestic fowls (*Gallus gallus domesticus*) were elucidated and the morphological significance of each muscle was reconsidered. On the basis of these findings, the homology of the shoulder girdle muscles between fowl and other tetrapods is discussed. The terminology is conform with Nomina Anatomica Avium (1993). The M. supracoracoideus is developed in fowl. However, different from reptiles, it originates from the sternum, furcula and costae, and passes cranial to the coracoid to end onto the humerus. The three muscles, described previously as the coracobrachialis muscle group, have different innervations. The M. coracobrachialis cranialis, being separated into two muscles, should be grouped with the deltoid muscles. The M. coracobrachialis caudalis could be thought to belong to the pectoral muscle group. The M. subscapularis in fowl, arising from the inner side of the scapula, could be homologous with the M. subscapularis in mammals. In previous descriptions, the M. scapulohumeralis cranialis has been considered homologous with the M. teres major in mammals, and the M. scapulohumeralis caudalis with the M. teres minor. However, the innervation observed in this study does not support these homologies. I have shown in a previous report that the M. subscapularis in mammals is derived from the M. scapulohumeralis and latissimus dorsi in urodeles and reptiles and the M. teres major from the M. latissimus dorsi in reptiles. In the present study, the morphological relationship between the M. scapulohumeralis cranialis/caudalis in domestic fowl and the M. subscapularis, teres major and latissimus dorsi in mammals, is also discussed.

Evolution of Function in the Feeding Mechanisms of Piranha and Pacu

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The serrasalmids, pacu, piranhas, and their allies, are ubiquitous across South American river systems. These fishes feed on a variety of prey, from seeds to insects, fruit to scales and flesh, despite having an immobile, fused skull. Serrasalmids are also one of the primary seed-dispersing fishes in the varzea, the flooded lowland forests of the Amazon. We were interested in how observed dietary diversity can stem from such a simple feeding apparatus. We used micro-computed tomography scanning (μCT) to image how cranial anatomy varies across the phylogeny of serrasalmid fishes and evaluated mechanical trade-offs between tooth morphology and jaw lever systems, and how these traits correlate with dietary mode. We reconstructed herbivory as the ancestral dietary mode for serrasalmids, from which omnivory, phytophagy, lepidophagy, pterygophagy, and outright carnivory have evolved. We find that piscivorous and carnivorous piranha have greater jaw leverage than herbivores despite longer jaws and muscle in-levers, falciform tooth shapes, and broader muscle attachment areas. Contrastingly, scale-feeding piranhas have long jaws with low mechanical advantage for faster jaw-closing, small muscle attachment areas and squat multi-cusped teeth. Pacu have short jaws with long, tendinous muscle insertions, and lower jaw leverage than most carnivores. Clear differences among herbivores centered around tooth morphology: robust incisiform and molariform teeth were typical of most herbivores, with obligate phytophages typically possessing only incisiform dentitions. Reconfigurations and recombinations of tooth shapes, muscle attachments, and jaw leverage suggest these are interchangeable modules that result in considerable breadth of dietary mode and prey materials.

Embryonic Development of Pancreatic Acini in the Grass Snake *Natrix natrix* (Squamata: Natricidae)

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Pancreatic acinar cells constitute the exocrine part of the pancreas of which the role is producing and secreting digestive enzymes. Acinar cells are organized into lobules called acini that connect to the smallest pancreatic intercalated ducts. In the earliest embryonic period acinar cells are formed from the "trunk" and "tip" parts of the pancreatic anlage. This process is poorly known in reptiles. For this reason we studied structure and ultrastructure of the differentiating pancreatic acini in the grass snake *Natrix natrix*. The first pancreatic acini in *Natrix* started to form halfway embryonic development. Acini were formed in two ways to form mature and immature acini. In the first one, zymogen granules in acinar cells were formed before lobular structure formation. In the second one, acinar cells started synthesis of granules only after they were organized into an acinus. Granules in acinar cells were classified into three types and were related to their degree of maturity. During embryonic development the regions of acinus formation were surrounded by abundant blood vessels. Within certain acini centroacinar cells were present, which were assumed to be a type of ductal cells similar as in other vertebrates. The lumen of the pancreatic acini differentiated in the process of hollowing. In the walls of the acini, similar as in other vertebrates, single endocrine cells were present. Immunogold studies showed the expression of amylase in acinar granules only at time of hatching, which could indicate the preparation of the animal for life outside the egg. This research was carried out with approvals of the Local Ethics Commission in Katowice (87/2015) and the Regional Directorate for Environmental Protection in Katowice (WPN.6401.257.2015.DC). Research was founded by National Science Centre (NCN) in Poland, DEC-2016/23/N/NZ4/00887.

***Cryptoclidus eurymerus* Foreflipper and Hindflipper Muscle Reconstructions and Finite Element Analyses of Humerus and Femur Inform on Muscle Forces, Underwater Flight, and Flipper Twisting**

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Plesiosaurs are secondarily marine Diapsida of the subclade Sauropterygia that, uniquely among Tetrapoda, evolved four cambered hydrofoil flippers. This locomotory design proved to be very successful and experienced only minor changes during 135 Ma of evolution. The mode of plesiosaur locomotion is disputed until today. Tetrapod long bones are loaded by a complex interplay of compression, bending, and torsion. Yet, finite element (FE) analyses of several load cases delineating a limb movement cycle show that their superposition leads to bones that are mostly loaded by compressive stress. Thereby bony material is reduced to a minimum which leads to lightweight structures. So by aiming at a homogeneous compressive stress distribution in a FE analysis of a bone, it is possible to test muscle reconstructions, i.e., hypotheses of muscle attachment areas and muscle courses mechanically. This concept was transferred to FE analyses of a humerus and femur of *Cryptoclidus eurymerus* to learn more about plesiosaur locomotion. Plesiosaur fore- and hind flipper muscles were reconstructed with the extant phylogenetic bracket. For all muscles that attach to or span humerus and femur, lines of action and muscle functions were determined by spanning threads into casts of a *Cryptoclidus* fore- and hind flipper skeleton. Muscle attachments and lines of action were entered into FE models of humerus and femur which were built from microCT-scans. Muscle forces were approximated iteratively by computing the compressive stress distribution for load cases upstroke and down stroke. Highest muscle forces were found in muscles with mainly a flipper elevation or depression function. Unexpectedly high extensor and flexor muscle forces in the fore- and hind flipper are in agreement with the reconstruction of a myological mechanism for flipper twisting which proved to be hydrodynamically neccessary for plesiosaur underwater flight. We acknowledge funding by the DFG (WI1389/8-1).

Genetic Characteristics of Different Dog (*Canis lupus familiaris*) Breeds with Novel ISSR-HRM Markers

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Presently, there are more than 400-recorded breeds of domestic dogs (*Canis lupus familiaris*) which show a wide range of morphologies such as, skull morphology, tail length and skin color. The current study aimed to use 10 Inter-simple sequence repeat (ISSR) markers for identifying the genetic characteristics of 40 different domestic dog breeds by using real-time polymerase chain reaction (PCR) coupled with High resolution melting analysis (HRM). The results showed that using one ISSR primer can at most identify 31 dog breeds out of 40 and at minimum 17 dog breeds out of 40 which can be calculated into a range of 42.5-77.5%. In addition, when 2 ISSR primers are combined, the HRM derivative melting curves were able to separate 80-90% from 40 different dog breeds. Moreover, we found that HRM derivative melting curves could identify 40 different dog breeds with a 100% success rate with 3 combined ISSR primers. Analysis of genetic characteristics of different dog breeds using derivative melting curves of HRM analysis allowed us to identify each dog breed with an accuracy of 100% when using 3 combined ISSR markers regardless of the morphology of each breed. Results of this study may serve as a baseline information for further studies about genetic

variation between different dog breeds and provide an easier and more accurate method for identifying unknown dog breeds at the molecular level.

Drivers of Taxonomic and Functional Diversity in Extinct Non-Teleostean Neopterygians (Osteichthyes, Actinopterygii)

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Durophagy became an increasingly important method of feeding for neopterygian fishes during the Mesozoic, especially in Ginglymodi (Middle Triassic – recent), Dapediiformes (Late Triassic – Middle Jurassic) and Pycnodontiformes (Late Triassic – Palaeogene) that were the foremost Mesozoic non-teleostean fishes in terms of species richness and abundance. Taxonomic diversity patterns, however, are strongly different with dapediiforms vanishing during the Middle Jurassic, while ginglymodians and pycnodontiforms survived the end-Triassic, the end-Jurassic and the end-Cretaceous mass extinctions, and also persisted through several episodes of environmental and climatic perturbations. Taxonomic diversity (species richness) increases correlate with extinctions (dapediiforms) or environmental shifts (ginglymodians) resulting in pycnodontiform fishes becoming the most diverse marine non-teleostean neopterygians in the Late Cretaceous. However, the importance of functional characteristics for shaping taxonomic diversity in these three Mesozoic fish groups and the underlying mechanisms (e.g., selection, competition, global warming) has not been analyzed so far. Here, we used the lower jaw as functional proxy for feeding adaptations, because morphological variations in this system have biomechanical consequences linking structure and performance, and geometric morphometrics to identify morphospace occupation of taxa through time. The results show that competition for food resources is the major driver for taxonomic and functional diversity patterns in these three non-teleostean clades resulting in niche partitioning to reduce competition but also in displacement and their final extinction. Latitudinal distributions or climatic changes, that are generally assumed to regulate taxonomic and functional marine diversity patterns today and in the past, seemingly are not the underlying mechanisms of functional diversity patterns in the neopterygians studied here.

En Garde! The Poachers' Body Armor is no Show-off but a Heavy Defensive Trait

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Many vertebrates are armored over part or all of their body. The armor can serve several functional roles including defense/protection, offense, visual display, and communication of capability. Different roles imply different tradeoffs, for example defensive armor often trades resistance to attack for maneuverability. The poachers (Agonidae), 47 species of Scorpaeniform fishes, are a useful system for understanding the evolution and function of armor due to their high variety in extent of armoring. We report on an assessment of the amount of mineral in the armor compared to endoskeleton in a diversity of poachers, and an assessment of the damage type in armor across a growth series of one species of poacher. Using publically available CT-scan data from 27 species from 16 of 21 genera of poachers we compared the armor to skeletal mineralization for a body region starting at the posterior end of the (first) dorsal fin going two times the body depth. The average material density (a measure of mineralization) of the armor in comparison to the skeleton ranged from 0.77 to 1.17, but the more impressive data is in the total mineralization (volume average density). In some small, smooth scaled species, like *Aspidophoroides olrikii*, there was 10 times the material expenditure in the armor as in the endoskeleton. With 34 *Agonopsis vulsa* we carefully categorized the extent and type of damage to each of 35+ scales in the eight rows along the body. The ventral rows begin to show abrasive damage along the entire length of the fish. Impact damage to head and tail scales gets more severe and occurs at higher rates with age, suggesting the armor is not just for show.

Relationship between Stomach Contents and Dental Microwear Texture of Extant Wild Ruminants in Japan

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Dental microwear texture analysis, which quantitatively analyzes microscopic use wear on tooth surface, has been applied to various extant and extinct vertebrates to elucidate their diets and foraging ecology. Comparative studies of herbivorous mammals, especially ruminants, revealed that animals which depend on grasses (grazers) had rougher tooth surfaces than those which selectively feed on dicots (browsers). Recent studies of feeding experiments in laboratory reared animals supported the results of the interspecific comparisons that higher forage phytolith content was associated with rougher tooth surface. It has been pointed out that if the animals eat irregular items just before their death, the microwear will not reflect their "average" diet: a phenomenon called "Last Supper effect". In order to reveal the effect of the last meal, we investigated extant wild ruminants in Japan, sika deer (*Cervus nippon*) and Japanese serow (*Capricornis crispus*), which were culled and their stomach contents were analyzed. We collected 3D-surface texture data from the occlusal surface of lower molars by a confocal laser microscope. From the surface data, we calculated surface roughness parameters defined by ISO 25178. In sika deer, we did not find significant correlation between roughness parameters and stomach contents, a finding already reported for roe deer (*Capreolus caprelous*). However, we found significant correlations for Japanese serow: individual serows which consumed more grass showed rougher tooth surface. The difference between serow and deer would be explainable by their difference in territoriality and degree of selective feeding. We need further data of wild-shot animals where stomach contents are analyzed to clarify whether the relationship between stomach content and microwear texture is variable depending on foraging ecology.

Dental Microwear Texture Analyses of Placodontids (Diapsida: Sauropterygia)

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Placodontids are Triassic aquatic reptiles that were found in marine deposits of Europe and South China. They are characterized by large plate-like palatal teeth that covered most of their palatine and have been regarded as durophagous, feeding on hard-shelled invertebrates. However, some researchers consider placodontids as a soft sea-plants eater due to the morphological similarity of their jaw with extant dugon. In order to elucidate the diet of placodontids, we observed dental microwear of teeth of *Cyamodus* and *Placodus* and conducted tooth surface texture analysis. Three-dimensional surface data were obtained by a confocal laser microscope, and surface roughness parameters defined by ISO 25178 were calculated. Further, for comparison, tooth surface texture was analyzed for various modern durophagous fishes: eagle rays (*Aetobatus narinari* and *Aetomylaeus vespertilio*), guitar fish (*Rhina ancylostoma* and *Rhynchobatus djiddensis*), Japanese bullhead shark (*Heterodontus japonicas*), humphead wrasse (*Cheilinus undulates*), and Singapore parrotfish (*Scarus prasiognathos*). Observation of two-dimensional images indicates that the surface of the anterior teeth of placodontids exhibited more pits and scratches compared to that of the posterior teeth. The surface of posterior teeth were bumpier than that of anterior teeth. Among modern fishes, eagle rays showed flat dental surfaces, which was reflected in some ISO 25178 parameters (e.g., Sq: root mean square height, Sdr: developed interfacial area ratio). Other fishes exhibited undulated and rough tooth surfaces, which resulted in high values for these parameters. The values of placodontids fell between these two groups. Differences in these values may reflect differences in feeding habitats (sandy bottom *vs* reef) and/or gross morphology of the tooth (with or without denticles). These results implies that usage of teeth differs in placodontids depending on the tooth positions and that they did not feed on sandy sea-bottoms as modern eagle rays do.

Myogenesis at the Head/Trunk Interface and Acquisition of Gnathostome-specific Musculature

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Vertebrate skeletal muscles have their developmental origins in somites and unsegmented mesoderm of the head. Around the border between head and trunk, these tissues generate myogenic precursors that differentiate into a variety of complex and functionally specialized muscles, such as muscles in the limb, shoulder girdles, diaphragm and the tongue. Precursors of each muscle undergo migration/extension toward the site of differentiation where they form mature myofilaments at remarkably varied timings. In order to clarify the evolutionary mechanisms underlying the formation of complex muscles associated with other tissues, such as cartilages and tendons, we have examined the expression of developmental genes and protein markers in cyclostome lampreys, shark, and other gnathostome species. In lamprey embryos, precursors forming a coherent hypobranchial muscle at the ventrolateral side of the pharynx emerge from the ventral edges of the anterior somites. Lamprey hypobranchial muscles developmentally correspond to the gnathostome tongue muscles, undergo differentiation much later than other somitic muscles, and remain lateral to the pharynx. On the other hand, sharks possess paired fins and compartmentalized hypobranchial muscles, the most anterior part of which fuses at the midline, similar to other gnathostome species. Comparison of the tissue structure and the expression of developmental regulatory genes has illustrated the temporal order of differentiation of various muscles in each species. Our analyses provide new insights for cellular and molecular characteristics of tongue and other musculature as well as for their contribution to the complexity of the vertebrate body plan.

Cellular Composition of Reptilian Brains

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Reptiles account for almost one third of extant amniotes, but little quantitative data is available on reptile brains, although needed to shed light on amniote brain evolution, especially given the recent discovery of wildly different neuronal scaling rules in birds and mammals. We collected brains of 125 species of squamates and turtles and, using the isotropic fractionator, we estimated the total numbers of neurons and glial cells in whole brains and six brain parts, including the olfactory bulbs, cerebral hemispheres, diencephalon, optic tectum, cerebellum, and brain stem, in 55 species so far. We found that at a comparable size, reptile brains contain 3.5-14 times fewer neurons than those of other amniotes, while the number of other cells is comparable to mammals and only 2-3 times lower than in birds. It is therefore likely that birds and mammals independently increased their neuronal densities. Reptiles seem to be constrained by the metabolic cost of brain tissue, which scales linearly with the number of neurons. The telencephalon harbors 21-45% of brain neurons, which is similar to gallinaceous birds and pigeons (23-32 %), but higher on average than in mammalian cortex (10-32%). While this is not directly comparable, low percentage of brain neurons in the telencephalon seems to be a derived characteristic of mammalian brains, connected to the expansion of the cerebellum. Cerebellar neurons outnumber telencephalic neurons only in some turtles and crocodiles. Since this condition is also found in basal birds, it points to an evolutionary trend of increasing cerebellar neuronal fraction in Archelosauria. Neuronal distribution furthermore reflects sensory specializations of different species, and the complete dataset will allow for testing of specific evolutionary hypotheses.

Embryonic Development of Photoreceptor and Müller Cells in Brown Anole *Anolis sagrei* (Reptilia, Dactyloidae)

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The brown anole (*Anolis sagrei*) has a diurnal activity. It is known to possess an excellent, high-acuity visual system. The retina of this species contains double cones with an oil droplet and single cones. The aim of this study is to characterize timeline and way of structural and ultrastructural differentiation of the brown anole retina. Particular attention was paid to the formation of photoreceptor and Müller cells of this species from the 8th developmental stage to hatching. Embryos of brown anole were isolated at regular intervals, starting at egg laying and finishing at hatching of the first individuals. The age of the embryos was calculated using the table of species development. Our results indicated that at developmental stage 8 the prospective retina made contact with the presumptive retinal pigment epithelium, but the largest part was composed of a pseudo-stratified columnar epithelium with no apparent morphological signs of differentiated neurons. From developmental stages 10 to 12 photoreceptor cells were still undifferentiated. They started to differentiate from developmental stage 14, when cilia of the presumptive outer segment, ellipsoid and small oil droplets of the inner segment were seen for the first time. From developmental stage 17 onward, double cones occurred for the first time. They differentiated until hatching. Differentiation of the ellipsoid was associated with agglomerates of mitochondria formation that underwent various modifications. Müller cells observed from developmental stage 14 onward were identified by their dark cytoplasm, intermediate filaments and glycogen particles. Our findings indicate that final differentiation of the retina in the brown anole occurs after hatching.

Phalangeal Morphology Refines Meristic Patterns of Limb Diversity in Salamanders and Newts (Lissamphibia: Caudata)

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The evolutionary history of Tetrapoda comprises several independent events of limb reduction, and digit loss has been reported both in fore and hindlimbs of all major tetrapod lineages. Among such morphological transitions, those involving digit loss in living representatives of Caudata are particularly interesting given the peculiar mode of digit development in this lineage. Despite the different degrees of variation in digit number and phalangeal formulae observed in Caudata, their evolutionary trajectories and associated anatomical patterns remain obscure. Here, we performed phylogenetic reconstructions of the variation in digit number and phalangeal elements in fore and hind limbs among all major lineages of extant salamanders and newts and subsequently described the osteological anatomy of phalanges. We accessed digit number and phalangeal formulae from literature and mapped their evolutionary trajectory using ancestral reconstructions. Osteological descriptions from cleared and stained specimens available at the UC-Berkeley collection were used to refine our evaluation of morphological transitions in the Caudata autopodium. We verified that diversity in digit number and phalangeal formulae is more expressive in hind limbs and relatively conserved in the forelimbs. Thus, we identified 20 phalangeal formulae in the Caudata hind limbs and 9 in the fore limbs. Patterns of digit number differed from ancestral condition for only 1.3% of the sampled species in forelimbs (4 digits) and 11% of species in hind limbs (5 digits). Some species having the same number of digits in the autopodium significantly differed in the osteological anatomy of phalangeal elements. While proximal and intermediary phalanges usually have similar shape, distal phalanges seem to be morphologically dissimilar. These results highlight an interesting scenario where a striking anatomical diversity in phalangeal elements evolved among species characterized by similar meristic patterns in their autopodia.

Convergent Loss of the Functional Vomeronasal System and Associated Gene Loss in Mammals

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The vomeronasal organ (VNO) or Jacobson's organ is a chemosensory system involved in the reception of pheromones playing a major role in sociosexual behavior and relationships in mammals. It is located ventrolaterally to the nasal septum in the anterior nasal cavity forming a paired tubular structure. The VNO is connected via the vomeronasal nerve to the accessory olfactory bulb (AOB). The reduction or loss of the VNO is often associated with a reduction or loss of the AOB resulting in a non-functional vomeronasal system (VNS). Although it is present in most mammals it was lost secondarily in some species. To gain insights into the evolution of the VNS, we collected data of the absence or presence of the vomeronasal organ and the AOB for 86 species covering all mammalian orders. The VNO was lost independently in most aquatic species like cetaceans and the manatee but also in higher primates and some chiropterans. Relaxed selection pressure on the VNS may not only explain the reduction of the VNO and AOB but may also be reflected in the genomes of the corresponding species and can result in the inactivation (gene loss) of VNS specific protein-coding genes. To detect the convergent loss of VNO specific protein-coding genes, we applied a computational Forward Genomics approach which links convergent gene loss to the convergent loss of a phenotype. We could confirm the VNO specific loss of Trpc2, extend previous findings and present additional gene losses that may be associated with the reduction of the VNS. The example of the vomeronasal system shows that Forward Genomics is a useful tool to detect gene losses linked to the loss of phenotypic traits.

Two-cusp Addition Events Underlie the Evolution — but not the Development — of Molars in Arvicolinae (Cricetidae: Rodentia)

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Patterns of pervasive phenotypic convergence have been of longstanding interest for the study of adaptation and its mechanisms. Notably, the diversification of several mammal groups is attributed to the repeated independent evolution of increasingly complex teeth through the addition of cusps — the positive reliefs of the occlusal surface — during development. With phylogenetic comparative methods, we investigate the evolution of highly multicuspid molars in fossil and living Arvicolinae (voles, lemmings, muskrats). Then, through observation and experimentation on molar development in an extant vole (*Myodes glareolus*), we test whether mechanisms of odontogenesis can explain the observed macroevolutionary pattern. We reconstruct the evolution towards higher cusp numbers (a proxy for higher tooth complexity) as a phenomenon convergent in the lower first molars of 27 independent Arvicolinae lineages. Molar complexity decreases also occurred, though far more rarely. This pattern of increases and decreases is best explained through a two-cusp stepwise model. However, *in vivo* observations of the development of lower first molars in *Myodes glareolus* reveal a different mechanism: a burst of cusps developing rapidly characterizes early vole tooth growth, compared to a slower dynamic in the simpler teeth of mice. The size of the developing tooth bud — and especially the extent of its anterior region — appears to be determining for final tooth complexity, as *in vitro* experiments show that longer buds develop more cusps. A similar relation exists at the macroevolutionary level, with a strong phylogenetic component. Therefore, we propose that increasing molar size during odontogenesis was a potential driver of the evolution of increasingly complex teeth in Arvicolinae. Nevertheless, this two-cusp stepwise macroevolutionary pattern has no direct equivalent at the developmental scale. Ontogeny does not recapitulate phylogeny in the molars of arvicolines.

Conservation and Transformation of the Shoulder Musculoskeletal System in the Evolution of Mammalian Limb Posture

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The evolution of upright limb posture preceded the explosive ecological radiation of therian mammals, sparking interest in understanding the anatomical and functional differences that separate sprawling and upright posture. While the locomotor kinematics of sprawling and upright animals have been well-studied, the underlying differences in musculoskeletal anatomy related to function are less well explored. We set out to characterize the shoulder musculoskeletal system of an extant sprawling lizard (Argentine black and white tegu) and an extant upright therian (Virginia opossum) in a comparative context, combining traditional physical dissection with non-destructive digital dissection of contrast-enhanced CT-scans. We identified 3D-attachment sites (origin-insertion) for muscles crossing the shoulder joint, and measured muscle architectural parameters (muscle mass, fascicle length, pennation, and physiological cross-sectional area). Our data demonstrate broad-scale conservation in muscle organization and size-corrected architecture between two animals that span the sprawling-to-upright continuum. These results point to skeletal geometry rather than muscle anatomy as the primary driver of functional transformation in mammalian shoulder evolution. Morphological change in the pectoral skeleton likely reoriented muscles relative to joints, thereby shifting their functional roles during the acquisition of upright posture. The apparent importance of hard-tissue over soft-tissue morphology gives confidence in reconstructing forelimb musculoskeletal function in fossil synapsid intermediates, and provides an opportunity to test functional hypotheses across the “reptile-to-mammal” transition.

Demography, Morphology, and Nonlinear Selection on Bite Force in Male *Anolis carolinensis* Lizards

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Both, animal whole-organism performance capacities and the morphologies that enable them, are shaped by natural and sexual selection. These performance capacities in turn can affect individual fitness. However, detecting the signal of selection in natural populations is often a challenge, particularly for traits that are subject to stabilizing or disruptive selection. Not only can the form and intensity of selection fluctuate over time, but the signature of nonlinear selection can be especially difficult to detect within small populations that are subject to shifting population dynamics. We develop a simple mathematical model to simulate the effects of nonlinear selection on performance trait distributions and use it to predict the sensitivity of such effects to changes in population demography. We then test those predictions against the results of two different selection studies on *Anolis carolinensis* lizards in southeast Louisiana. More specifically, we test the hypothesis that nonlinear selection on bite force in adult *A. carolinensis* males has driven the evolution of two age-dependent male morphs, but is effective only in populations that exceed a particular size threshold.

Quantifying Three-Dimensional Shape Variation in the Carnivoran Calcaneum Using Spherical Harmonics

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The calcaneum (heel bone) plays a critical role in posture and locomotion in mammals, due to its importance for ankle joint mobility and influence on associated muscle lever arms. This bone is also potentially useful for inferring ecomorphology in extinct taxa because of its high preservation potential in the fossil record. Ecomorphological and two-dimensional geometric morphometric analyses have been used in the past to understand the relationship between calcaneal morphology and locomotor behavior in the mammalian order Carnivora, and have found support for a form-function relationship that is mediated by phylogenetic signal. However, it remains to be seen if the calcaneum can be used to successfully separate distinct locomotor modes based on its overall 3-dimensional shape. In this study, we use spherical harmonics (SPHARM), a homology-free 3D-morphometric method, to quantify calcaneal shape variation in over 100 species from 12 families of Carnivora, spanning digitigrade, semi-digitigrade, and plantigrade foot postures in taxa with cursorial, arboreal, ambulatory, scansorial, semi-fossorial, and semi-aquatic habits. Surface scans were created using a structured light scanner, then smoothed and registered using six landmarks before calculation of spherical harmonic coefficients. Finally, specimens were ordinated using principal component analysis. While our results reveal some phylogenetic and functional signal, we find a wide range of calcaneal shapes in carnivorans that is independent of clade membership, foot posture or locomotor mode. The high degree of morphological diversity suggests that 2D-approaches for characterizing ecomorphological variation may fail to adequately describe the gross morphology of 3D-structures.

Is the Enamel Knot Present in Reptiles?

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In mammals, odontogenesis is regulated by transient signaling centers known as enamel knots (EKs). However, the developmental mechanisms contributing to the formation of superficial tooth structures in reptiles are not fully understood. The aim of our study is therefore to elucidate whether signaling centers similar to enamel knots appear also during reptilian tooth development. Here, we have selected the veiled chameleon as a model species with several unique features including: heterogeneous tooth shape along the jaw, a monophyodont dentition and teeth that are firmly ankylosed to the underlying bone. The crown of the chameleon tooth possesses one central and two lateral cusps with the central cusp further split into two ridges. In early embryos, a morphological structure resembling the mammalian enamel knot was observed which expressed SHH. This structure housed large numbers of apoptotic bodies and no PCNA-positive cells, similar to the mammalian EK. Based on these findings, we propose that this structure may act as an organizer of tooth formation in the chameleon tooth. Later in development, a deep ridge appears at the tip of the developing central cusp. An associated cluster of cells was observed forming in the center of the developing enamel organ, resembling a mammalian secondary enamel knot. 3D-analysis of the shape of the nuclei in this cluster of cells revealed a distinct arrangement of the cells in this region, associated with ultrastructural changes that would lead to asymmetrical enamel deposition. We suggest that such asymmetric deposition would then initiate the formation of two enamel ridges separated by a groove with low production of enamel, thereby creating the final ridge pattern. Whether there is a link between the early cluster of SHH-cells and the later cells contributing to the ridge is recently under investigation. This study was supported by the Czech Science Foundation (17-14886S) and by the MEYS CR (CZ.02.1.01/0.0/0.0/15_003/0000460) and under project CEITEC 2020 (LQ1601).

Midfacial Convergence is Required for Nasal Septum Development

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The nasal placodes are laterally positioned and shift medially during early facial development, resulting in the two nostrils separated by a single nasal septum cartilage. The mechanisms of nasal septum development and midfacial convergence are understudied owing to a paucity of animal models, and the very low prevalence of anomalies associated with it. To explore the embryological manifestations of midfacial convergence, we recovered the *Unicorn* mouse line. The *Unicorn* line is an ENU-mutagenized line that was recovered in a forward genetic screen. We have outbred the line and captured the phenotype for 10 generations. *Unicorn* mutants develop two normal nostrils that are supported by a bifid nasal septum that is surrounded by completely normal bones and cartilages in contrast to a single central rod of cartilage in control littermates. We observed that the *Unicorn* embryo medial nasal prominences (MNPs) were displaced laterally by E10.5. The *Unicorn* MNP medial edge epithelium loses its epithelial markers and gains mesenchymal markers with no significant differences in apoptotic or proliferative markers. We followed morphogenetic movements in the nasal septum chondrocytes by using *Collagen2-creERT;Tdtomato* embryos. We observed that the nasal septum begins developing as two independent rods of *Collagen2-Cre* positive cells approximating the midline of the MNPs as early as embryonic day (E) 10.5. By E11.5, the *Collagen2-Cre* positive rods begin fusing together in the superior to inferior direction resulting in a single nasal septum. Our data suggests that midline convergence of MNPs is dependent upon an epithelial to mesenchymal transformation of the medial edge epithelium and is influenced by frontonasal ectodermal zone signaling. The presumptive nasal septum begins as a paired organ in the MNP mesenchyme that converges into a single midline organ during midfacial fusion.

Let it Grow: Ontogenetic Sequence of the Skull of Minke Whales and Implications for the Teeth-to-Baleen Transition in Mysticeti (Cetacea)

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Baleen whales (Mysticeti) have an extraordinary fossil record documenting the transition from toothed raptorial taxa to modern species that employ baleen plates for filter feeding. However, while adults bear baleen plates, tooth germs still develop unerupted in utero. Ontogenetic data, combined with present knowledge of modern and fossil mysticete skull anatomy, provide a better understanding of the mechanisms of this unique macroevolutionary transition. Though, currently little information is available on prenatal development of baleen whales, especially regarding tooth resorption and baleen development. Here, I present the first comprehensive description of a virtually complete ontogenetic sequence of minke whales (*Balaenoptera acutorostrata* and *B. bonaerensis*), concentrating on the skull internal anatomy and tooth germ development, resorption, and baleen growth. The anatomy was analyzed using traditional and iodine-enhanced computed tomography (CT and diceCT) scanning of 10 specimens of both minke whale species, spanning from the earliest fetal stages to full term. Using these non-invasive methods allowed reconstruction of virtual 3D-models of the specimens and geometric morphometric (GM) analyses, in addition to providing traditional qualitative descriptions. Tooth germs appear to resorb completely just before eruption of the baleen from the gums, and they are still present for a brief period along with baleen rudiments. GM-analyses show that the rostrum progressively grows in length relative to the braincase, and that the supraoccipital shield elongates anteriorly during gestation. Both changes contribute to a defining feature of cetaceans, the telescoped skull. These data aid in the interpretation of fossil morphologies that exhibit intermediate traits between modern filter feeders and raptorial feeders, but caution is needed when comparing prenatal extant specimens to adult fossils.

High Resolution Morphology of Miniature Teleost Teeth

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Miniaturization of organs has important evolutionary consequences. The size of an organ can decrease by diminishing the size of the cells, the volume of the extracellular matrix, or by reducing cell number. Hence the question arises, how many cells are needed to grow to a complete functional organ? Teleosts offer excellent models to study miniaturization, as many species qualify as miniaturized, sensu Hanken & Wake (1993; Ann. Rev. Ecol. Syst. 24: 501-519). The first-generation teeth in teleosts are mostly of very small size. The aim of this study was to select both a species and specific tooth anlage, presenting a minimal number of odontoblasts (dentin-producing cells) in the dental papilla. To ascertain the exact number of cells, and their spatial relationship to the matrix and surrounding cells, 3D-reconstructions are required. Due to the small size of cells and the teeth and difficulties to determine the exact position of cell membranes even semi-thin sections of 1 μm are insufficient for a 3D-reconstruction. Thus, we used 3D-reconstruction based on transmission electron microscope (TEM) images. We could demonstrate that a fully developed first-generation tooth in medaka (*Oryzias latipes*) contains just one odontoblast. The dentin margin coincides exactly with the cell's proximal boundary. The odontoblast is capped at its proximal side by another, more flattened cell, whose function still needs to be determined. This cell may serve as a "reserve" and take over the function of the single odontoblast in case of failure or death of the latter. 3D-reconstructions based on TEM-photographs of miniature teleost teeth demonstrate the possibility of extreme miniaturization of a functional organ to one cell.

Marker Tracking with DeepLabCut Enables High-Throughput XROMM

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Bottlenecks in digitization can constrain the scope of video-based kinematic studies. In the case of XROMM, the need for highly accurate marker tracking imposes a methodological barrier to automation. DeepLabCut is a new, open-source toolbox based on transfer learning with deep neural networks (Mathis et al., 2018, Nat. Neurosci. 21: 1281–1289). It has been characterized by its robust performance in marker-less tracking across taxa. Here, we integrate DeepLabCut with the existing XMALab marker tracking workflow to dramatically increase XROMM data processing throughput with minimal concessions in error. We first tracked a 2000 frame biplanar sequence of a Rhesus macaque (*Macaca mulatta*) feeding in XMALab. We then extracted the 2D-points from every tenth frame to generate a training set of 200 frames (24 markers per frame) for each camera. DeepLabCut trained independent neural networks for both cameras over 200,000 iterations. To compare performance, we processed a new trial from the same dataset using the resultant networks as well as in XMALab. DeepLabCut processed the new trial in four minutes, whereas it took intermediate and expert users approximately 16 and 8 hours to track the trial in XMALab, respectively. The average reprojection error across all 24 points was higher in the DeepLabCut processed trial (1.57 ± 0.45 pixels) as compared to the version tracked in XMALab (0.55 ± 0.25 pixels). However, 20 minutes of manual refinement in XMALab halved the average reprojection error of the DeepLabCut trial to 0.85 ± 0.37 pixels. Thus, if 20 minutes of correction in XMALab are allowed per trial, DeepLabCut can reduce data processing time by 25-50x, or 1,000 hours for a 100-trial dataset. Optimal training parameters likely vary across datasets and may result in better performance than what is documented here. These findings indicate that DeepLabCut is well suited to ameliorate the data processing bottleneck in XROMM studies and facilitate an expansion of sample sizes. Funded by NIH R01DE02736.

Morphological Convergence Obscures Functional Disparity in Sabre-toothed Carnivores

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Sabre-toothed vertebrates are among the most iconic vertebrate fossils. Due to their unusual appearance, taxa such as *Smilodon* have received considerable academic interest. However, sabre-tooths were much more diverse and abundant than individual, well-known species would suggest. Sabre-tooth morphologies have evolved independently at least seven times over the course of 250 million years in Permian mammal-like gorgonopsians, in the marsupial sabre-tooth *Thylacosmilus*, and five different lineages of carnivorous mammals. It is generally assumed that the cranial function of all sabre-toothed vertebrates was largely comparable. However, this assumption has not been tested in detail from a biomechanical perspective, and it is further unknown if the same evolutionary trends led to the convergent emergence of sabre-toothed morphologies in different clades. Using digital visualization, biomechanical analyses and evolutionary modelling, functional performance measures were compared across seven sabre-tooth groups (absolute/effective jaw gape, bite force, mandibular stability). The results demonstrate that these performance measures varied considerably between different groups and between different species. Evolutionary pathways leading to the sabre-toothed morphology were further found to be significantly different between groups. This demonstrates that functional diversity was widespread among sabre-toothed vertebrates but obscured by superficial morphological similarity, and is likely related to differences in ecological niche occupation.

Ecomorphology and Evolution of Carnivoran Body Plans

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Body shape diversity is one of the most prominent features of phenotypic variation in vertebrates and can lead to increased diversification, niche specialization, and innovations within a clade. Biologists, however, still lack a full understanding of the underlying morphological components that contribute to body shape diversity, particularly in endothermic vertebrates such as mammals. Consequently, little is known about the morphology, ecology, and evolution of mammalian body shapes as well as the underlying traits that contribute to different body plans. In this study, I generated the first quantitative database of mammalian body shapes using osteological specimens within the mammalian order Carnivora. I then test hypotheses pertaining to the relationships between the cranial, axial, and appendicular morphologies and examine how these relationships contribute to the evolution of body plans found across carnivorans. This work fills a critical gap in our understanding of vertebrate evolution by elucidating the evolutionary similarities and dissimilarities across vertebrate body plans and the underlying processes that drive their phenotypic diversity.

Exploration of Cranial Covariation Patterns within a Developmental Series of *Dasypus novemcinctus* (Cingulata, Mammalia)

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Studies of morphological integration and modularity assume that biological structures can be subdivided into various sets of covarying traits (modules), each set varying relatively independently from the other. Many studies have provided evidence for modularity within the skull of amniotes, with modules usually corresponding to continuous and non-overlapping cranial regions. While most modularity methods use covariance or correlation matrices derived from landmark coordinates, few recent studies analyzed these correlations between pairs of landmarks or distances. In this study, we explore cranial covariation patterns based on a set of 131 anatomical landmarks in a pre- and postnatal developmental series of nine-banded armadillos (*Dasypus novemcinctus*), including 166 specimens. Fetuses were used to propose *a priori* hypotheses of modularity based on their ossification sequence. The remaining dataset was analyzed using three subsamples: (1) all specimens; (2) adults only; (3) adults from specific geographical areas only. This division enabled us to estimate how integration patterns relate to ontogeny, allometry, and phylogeny. Modularity was then analyzed in each of these subsamples both with and without *a priori* definition of modules. Following recent recommendations, we applied Procrustes superimpositions at various levels (i.e., within a configuration or separate blocks) to minimize the presence of spurious correlations. Then each modular region was examined separately with PC analysis and with examination of correlations between pairs of standardized linear distances. Based on this approach zooming into potential modules, we show and discuss various cranial covariation patterns and point out that some regions indeed display patches of strongly correlated landmarks while others seem very weakly integrated. This study aims at promoting accurate analyses of the complexity of covariation patterns for a better understanding of cranial evolution.

Real and Hypothetical Evolutionary Pathways for Axial Skeletal Evolution in Twin-Tail Goldfish

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The twin-tail of the ornamental domesticate goldfish is known as one of the examples of drastic morphological change in the axial skeleton. Our previous study revealed that this peculiar morphology is derived from a stop codon mutation in one of two duplicated *chordin* genes. However, it is uncertain whether the *chordin* mutation is the most evolutionary optimized mutation for the formation of the twin-tail morphology in goldfish or a contingently selected mutation by the early middle age Chinese breeders. To address this uncertainty, we reproduced twin-tail morphology in single tail goldfish progeny with morpholino induced knockdown of the *szl* gene and CRISPR/Cas9 mediated mutagenesis on the *chordin* locus. We also succeeded in investigating viability and expressivity of the twin-tail morphology in these morphant and CRISPR/Cas9 mediated mutants. Based on these results, we discuss how artificial selective pressures and/or stochastic events are significant for the drastic change of morphological features during a short time period of domestication.

From Bipeds to Quadrupeds: Investigating the Morphological Evolution Occurring in Limb Bones during the Prosauropod/Sauropod Transition

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Sauropodomorph dinosaurs include the largest terrestrial animals that ever lived on Earth. Their evolutionary history is strongly linked with increase of body size and mass, from small exclusively bipedal early representatives to gigantic exclusively quadrupedal organisms. This shift involves important changes in limb morphology and proportions, from a forelimb with grasping abilities to a columnar element exclusively dedicated to locomotion and weight bearing. However, the transition between these two morphological extremes remains unclear: while the acquisition of high body size and mass has long been associated with the acquisition of sauropod quadrupedal morphoanatomical features (such as columnar limbs), several studies on recently described material and on osteohistological proxies challenge this assertion, with possibly earlier acquisitions of quadrupedality and gigantism. Regarding these conflicting conclusions, we propose here to focus on the morphological modifications of limb bones occurring during this evolutionary episode. By means of 3D-geometric morphometrics, we investigate this problematic by disentangling the different morphological patterns occurring during this evolutionary shift thanks to a large sampling of sauropodomorph taxa containing exclusive bipeds, facultative bipeds and exclusive quadrupeds. By taking into account proxies of body size and mass of the organisms, we highlight the morphological characteristics correlated to these parameters. The comparison of these results with the published literature permits an assessment regarding how the transition occurs (i.e., one or multiple acquisitions of quadrupedal/gigantism patterns), as well as the morphofunctional consequences of such modifications in forelimb and hindlimb toward an exclusively quadruped pattern.

A Giant Soft-shelled Egg from the Late Cretaceous of Antarctica, and the Evolution of Squamate Eggshells

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Lepidosaur eggs are covered by a thin shell, which differs in structure from more mineralized eggshells found in Testudines and Archosauria. The few quantitative studies of eggs in lepidosaur subclades have recovered a significant relationship between egg-related traits and body size. However, the relationships among such parameters across Lepidosauria have not been systematically estimated. Soft-shelled eggs are also rarely preserved in the fossil record, and their evolution remains poorly understood. Here, we describe the largest known soft-shelled egg (~29 cm in length), which was recovered from a nearshore marine Late Maastrichtian formation of Seymour Island. The fossil preserves evidence of a shell curved in soft folds, consistent with deformation resembling deflation, indicating it may have hatched prior to burial. Histological thin-sections of the shell show a fibered, multilayered structure, very similar to that of soft eggshells of most extant squamates, and lacking the calcareous shell unit layer found in some of them (e.g., gekkonids). Phylogenetically-informed regressions for a sample of over 250 extant lepidosaur species yielded significant relationships among egg volume, eggshell thickness, body mass, and snout-vent length (SVL). However, only egg volume was identified as a good predictor of SVL. An SVL value of 7.5 meters was recovered for the animal to which the fossil egg belonged. The remains of a large mosasaur (*Kaikaifilu hervei*; body length estimate ~10 m) were found in proximity to the egg. These results are consistent with the possible association of the egg with a mosasaur, a finding congruent with the description of the Antarctic Peninsula as a breeding area for these marine reptiles. If this new egg belonged to a mosasaur, it would be consistent with the presence of an ovoviviparous/oviparous reproduction strategy in this group. Previous evidence for viviparity in this clade, however, is not incompatible with this result; both strategies could have co-existed among mosasaurs. This work is supported by the Anillo ACT172099 grant (DDR).

Scaling Patterns of Metacarpus Dimensions and Body Size in Non-Avian Dinosaurs

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Many current hypotheses on the locomotor biomechanics of terrestrial tetrapods (living and extinct) include assumptions based on the scaling relationships between the stylopodium-zeugopodium and body size. Less attention has been given to the autopodium, even though this is the part of the body that is usually in direct contact with the environment and potentially under more diverse selection pressures. Whilst the pes is associated primarily with locomotion, the manus can have a wider range of functions, especially in bipedal taxa. Non-avian dinosaurs provide an excellent opportunity to study manus scaling, due to their wide range of body sizes, ecologies and behaviors. In addition, their ancestral bipedal Bauplan allowed diverse manus morphologies to evolve, but multiple independent reversions to quadrupedality also imposed some shared mechanical constraints. Here, we present the first study to compile an extensive dataset of metacarpus measurements across non-avian dinosaurs and use these to assess scaling

patterns of the manus (via proxies of metacarpal dimensions) against overall body size (based on femur length). Our database includes seven measurements for each metacarpal, from more than 50 taxa, representing all major non-avian dinosaur lineages including basal and derived sauropodomorphs, theropods, thyreophorans, ceratopsians and ornithopods. Data were analysed using phytools in R and Past. Across non-avian dinosaurs the metacarpus scales with negative allometry, with no significant differences between metacarpals, major clades, hand function, or locomotive stance. Multivariate analyses, however, show some degree of clustering between clades, as well as identifying some extreme cases, such as tyrannosaurids. Each major clade occupies distinct areas of morphospace, with overlap between basal sauropodomorphs, ceratopsians and thyreophorans, while sauropods and basal ornithischians represent the two extremes of the major axes of variation.

Terrestrial-Style Feeding Kinematics in a Derived Tetrapodomorph Fish, *Tiktaalik roseae*

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Evolution of the tongue-based feeding mechanism was a key innovation that enabled early tetrapods to successfully feed on land. However, it is uncertain whether aquatic tetrapodomorph fishes had the soft-tissue morphology or neuromuscular control necessary for a tongue-based feeding system. The transitional taxon, *Tiktaalik roseae*, presents a unique opportunity to study this transition in a tetrapodomorph fish, due to its unique mixture of conserved and derived features, including a robust gill skeleton, enlarged basihyal toothplate, elongate jaws, and dorsoventrally compressed skull. Here, we present a reconstruction of the feeding mechanism of *Tiktaalik* based on micro-computed tomography (μCT) data, linkage modeling, and comparisons to modern analogs. The feeding morphology of *Tiktaalik* suggests an aquatic feeding system that utilized suction-based, intraoral transit – with a sternohyoideus based jaw-opening mechanism that linked movements of a robust gill skeleton to a loose and retractable pectoral girdle, and with a sliding palate and dermal cheek that allowed for suspensorial abduction. However, modern alligator gars (*Atractosteus spatula*) demonstrate that these same features can be used in a convergently evolved, biting-based, aquatic feeding system, with a prey strike that decouples jaw and hyoid movements despite maintaining the same plesiomorphic jaw opening mechanism found in *Tiktaalik*. Superimposing *Atractosteus* feeding kinematics onto a linkage model of the *Tiktaalik* feeding system shows that these movements are surprisingly similar to kinematics of aquatic cryptobranchid salamanders and terrestrial feeding salamanders that use a tongue-based feeding system. Thus, our analysis shows that terrestrial-style feeding kinematics were possible in a tetrapodomorph fish feeding in water, likely evolved with a similar hydrodynamic function as seen in gars, and may have predated evolution of the tongue itself.

The Ontogeny of Muscle Architecture in *Microcebus murinus* (Primates:Lemuroidea)

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Studies of the fiber architecture of the mandibular adductors – responsible for the production of bite force – have found correlates of specific diets (e.g., food size and mechanical properties in primates and felids) and modes of foraging (e.g., tree gouging in marmosets). Despite the well-elucidated functional implications of this architecture, little is known about the ontogeny of these properties. To characterize age-related myological changes, we studied the masticatory muscles in a large (n=33) intraspecific sample of a small, Malagasy primate, *Microcebus murinus*. We isolated each mandibular adductor and recorded its mass, linear dimensions, and then chemically dissected each muscle to study its fiber architecture – fascicle length and physiological cross-sectional area (PCSA) which relate to stretch (gape) and force capabilities, respectively. We observed that PCSA and muscle mass scaled with positive allometry, while PCSA increased rapidly and plateaued in adulthood through senescence. Fascicle lengths remained relatively constant once maximal length was reached suggesting that changes in PCSA are driven by changes in muscle mass. Quadratic curvilinear models of each of the logged variables (total combined adductors and individual muscles) regressed against logged age were all significant. This trend was not consistently observed relative to measures of body mass likely because older individuals decline in body mass affirming the importance of the use of animal age and not size in ontogenetic research. We also used the same protocol to evaluate the ontogeny of the fiber architecture of the forearm in *M. murinus*. Through these combined studies, we can evaluate whether muscle architecture changes similarly throughout the body or whether changes in the architecture of the masticatory and forearm muscles correlate to life history stages of diet and locomotion respectively. This project was supported by the NSF (IOS-15-57125 and BCS-14-40599).

Diversity and Evolution of Trigeminal Sensory Systems in Sauropsids

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Vertebrates evolved numerous types of integumentary sensory receptors, many of which enhance facial somatosensation. Species with sensitive faces exhibit high densities of trigeminal nerve-innervated receptors at the ends of nerve branches that course through bony canals and foramina in the face and mandibles. These bony features of the trigeminal system are often used to infer facial sensation in extinct vertebrates. However, the form and function of the trigeminal system are diverse in extant reptiles, and its physiological significance and phylogenetic patterns are unclear. Extant reptiles display morphological diversity in proximal (i.e., trigeminal fossa contents and trigeminal division pathways), intermediate (i.e., inferior alveolar canal [IAC] neurovasculature and its relation to teeth and integument), and distal

structures (i.e., symphyseal neurovasculature and bill-tip-organs). These structural differences are reflected in the behavioral diversity (e.g., lingual *vs* jaw prehension in squamates, tactile-feeding in birds) across Reptilia. Using histological and CT-data, we performed morphometric analyses of the maxillomandibular foramen, IAC, and distal mandibular foramina of several extant sauropsids. Comparing IAC and associated neurovasculature cross sectional area, we find higher relative content of vascular tissue in squamate IACs in comparison to crocodylians, and accessory canals transmit mostly vascular tissue to squamate integument, suggesting reduced ability for mandibular sensation. Additionally, crocodylians distribute available neurovasculature across smaller areas of the mandible than the squamate taxa sampled, suggesting smaller receptive fields and increased sensory ability. Overall, these findings assist in reconstruction of soft tissues from osteological correlates in fossil taxa and will help uncover patterns of reptilian somatosensory ecology and evolution.

A Unique Dental Renewal Mode in the Extinct *Scheenstia* (Actinopterygii, Lepisosteiformes)

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The pattern of tooth development is genetically very stable during vertebrate evolution, while dental renewal mechanisms are much diversified. The Mesozoic fish *Scheenstia* shows a novel mode of tooth replacement not reported in any other taxon and implying a peculiar feature: the amelogenesis of replacement teeth occurs intraosseously in an upside-down position. Based on microCT-scan reconstruction, we describe the internal anatomy of a left lower jaw of *Scheenstia* sp. from the Late Jurassic of the Swiss Jura, comprising replacement teeth and their crypts, and cavities corresponding to nervous and vascular canals. We interpret this one-to-one, and likely simultaneous, renewal process as follows: amelogenesis, initiation of the 180° rotation of the enamel caps, ascension through individual replacement pores, dentinogenesis, completion of the tooth rotation and finally ankylosis to the bone through a pedicel. The reconstruction of the lower jaw also shows that it is strongly innervated, indicating a highly sensitive chin region in *Scheenstia* with the possible presence of sensitive dermal organs such as hypertrophied lips, or barbels. This replacement mode probably enhanced the protective effect of intraosseous tooth development but raises the question of its energetic cost.

Comparative Skeletal Anatomy of Neonatal Ursids and the Altricial-Precocial Spectrum of Therian Mammals

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In vertebrates, neonates exhibit a range of maturity at birth. Precocial neonates are relatively mature physically and often capable of independent function shortly after birth. In contrast, altricial newborns are born blind and helpless, requiring significant parental care. In mammals, eutherian newborns vary from highly altricial to precocial, while marsupials and monotremes are all extremely altricial at birth. Bears (family Ursidae) have among the most altricial newborns among eutherians and also one of the most extreme maternal-neonatal mass ratios in mammals. Here, we use microCT-scanning to visualize the internal anatomy of different ursid neonates and examine relative maturation levels of the skeletal system. We aim to address 1) how altricial ursid newborns are relative to other therian mammals and 2) if there is variation in relative altriciality within bears. We test three alternative hypotheses: 1) that bear neonates resemble outgroups (i.e., canids) in degrees of skeletal ossification, and only differ by the small size of newborns relative to the mother; 2) that bear neonates are more altricial than outgroups, but still conform to a eutherian pattern, or 3) that bears significantly differ from other eutherians and even exhibit marsupial-like conditions. Our survey includes neonatal skeletons of panda (*Ailuropoda melanoleuca*), sloth bears (*Melursus ursinus*), grizzly bears (*Ursus arctos*), and polar bears (*U. maritimus*) as well as the domestic dog (*Canis familiaris*), red panda (*Ailurus fulgens*) and arctic fox (*Vulpes lagopus*) as outgroup comparisons. Preliminary data suggest that most ursids do not differ significantly from canids in levels of neonatal skeletal ossification. Neonatal pandas, however, appear to have skeletal maturation levels more similar to embryonic dogs, suggesting potentially alternative skeleton developmental rates. However, no bear appears to exhibit the heterochronies seen in marsupials.

Comparative Anatomy and Finite Element Analysis of Skull of Paleognathae and Anatidae Provide Insight into the Origin of Bird Cranial Kinesis

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A fundamental dichotomy between Palaeognathae and Neognathae is recognized in almost all phylogenetic analyses of modern birds. Here, we compared the cranial anatomy of palaeognaths and neognaths, and applied Finite Element Analysis (FEA) to explore their functional features with regard to cranial kinesis. Our exemplars show that under certain force, the displacement of the upper jaw in Anatidae (goose and duck) is much larger than that of in palaeognaths (i.e., *Dromaius novaehollandiae*). A concentration of strain occurred from the nasofrontal hinge of *Dromaius* but not in Anseriformes. The thinning of nasofrontal bones and a loss of middle struct (methesmoid) innovate avian cranial kinesis. The nasofrontal hinge plays a major role in alleviating the accumulated strain that concentrates between the rostrum and the cranium, further increasing cranial kinesis in birds. The trace of this feature in Mesozoic birds further suggests that the origin of bird kinesis occurred relatively late in bird evolution.

An Upper Cretaceous (Rio Azul Formation) Elasmobranchian Fauna from Serra do Divisor, Brazilian Amazonia

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The Serra do Divisor is a chain of low hills located in the Acre state border with Peru in Western Amazonia. Unlike the remaining area of the Acre state territory, whose main geological formation is dominated by the Solimões Formation (Upper Miocene), the Serra do Divisor consists of four distinct geological units dating from the Lower Cretaceous to Paleocene: Ramon, Divisor, Rio Azul and Moa Formations. The Rio Azul Formation is constituted by fine marine clastic (gray to black shales) sediments and its position in the Upper Cretaceous is based on its overlaying the Moa Formation and correlated with other basins of Peru and Ecuador. In the last years the Rio Azul Formation sediments have yielded more than 50 elasmobranchian teeth belonging to some neoselachian coastal groups, previously unreported for this Formation and also for the Acre Basin. Oral teeth of the following orders have been identified: Rhinopristiformes (*Pristis sp.*, *Rhynchobatus sp.* [?]), Myliobatiformes (superfamilies Dasyatoidea [*Dasyatis sp.*, *Dasyatidae indet.*] and Myliobatoidea [*Rhinoptera sp.*, Myliobatidae indet.]) and Carcharhiniformes (*Galeocerdo sp.*, Carcharhiniformes indet.). The majority of the analyzed teeth is small in size (equal to or smaller than one centimeter) independent of the taxonomic group. The few elasmobranchian teeth previously described for the Serra do Divisor were correlated to the extinct Hybodontiformes and Sclerorhynchidae (Batoidea), both from the Moa Formation. Due to the reduced size of these new neoselachian teeth plus the type of sediments of the Rio Azul Formation (black shales) we infer a paleoenvironment related to coastal, or even mangrove areas. It is noteworthy that some of the taxa recovered are typical of these environments (e.g, *Pristis*, *Dasyatis*). Besides, this new elasmobranchian fauna agrees with previous reconstructions that report evidences of transgressive marine influence in the Serra do Divisor (Moa and Rio Azul Formations).

Morphology and Phylogenetic Significance of the Synarcual Cartilage in Members of Potamotrygonidae (Chondrichthyes: Myliobatiformes)

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The family Potamotrygonidae is composed of two subfamilies, five genera and 37 species. Styracuninae embraces a single genus (*Styracura*) and two species distributed in the Caribbean Sea and the Pacific coast of Central America and Colombia. Potamotrygoninae embraces the neotropical freshwater stingrays distributed throughout the main river basins of South America. The sister group relationship indicated by recent morphological and molecular hypotheses within potamotrygonins (*Paratrygon* + *Heliotrygon* and *Potamotrygon* + *Plesiotrygon*) is supported by the following morphological characters: ventral lateral line canals, skeleton, such as neurocranium, mandibular arch, scapulocoracoid and clasper, but also by the variable morphology of muscles of the mandibular arch. Some of the morphological characters that vary considerably between the two sister groups are those related to the pectoral skeleton. For instance, the pectoral skeletal elements are notoriously stouter in the clade *Paratrygon* + *Heliotrygon* but slender in the clade *Potamotrygon* + *Plesiotrygon*. This distinct morphology of the pectoral skeleton is reflected in the synarcual cartilage, an element of the axial skeleton that acts as an additional skeletal support for the pectoral girdle and fins. Accordingly, the synarcual shows modifications that are only recognizable for the clade *Paratrygon* + *Heliotrygon*, being laterally expanded, dorsoventrally flat, and associated to the scapulocoracoid by means of two condyles and one socket. On the other hand, the morphology of the synarcual in the clade *Potamotrygon* + *Plesiotrygon* is very similar with the pattern observed in *Styracura* and other Dasyatoidea: slender, cylindrical and articulated with the scapulocoracoid by means of one condyle and one socket. This remarkably distinct morphology of the synarcual and pectoral skeleton in *Paratrygon* + *Heliotrygon* may be possibly correlated to the evolution of this clade in the main channels of rivers in the north of South America.

Homology of Ethmoidal Ossifications in Neopterygians (Actinopterygii)

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Different ossifications have been identified in the ethmoidal region of teleosts: lateral ethmoids, supraethmoid, ventral ethmoid, anterior myodome bone, rostral, lateral dermethmoids and vomer. The single mesethmoid of most teleosts is a compound of two or more of these bones. Some fossil teleosts have a compound rostrodermethmoid. In holosteans, only lateral ethmoids, preethmoids, rostral and vomers have been identified. However, the homology between the nasal processes of the premaxillae of holosteans and the lateral dermethmoids of teleosts has been proposed. Although the homologies, as well as the chondral or dermal origin of these ethmoidal ossifications has been discussed by several authors, no consensus has been achieved and the teleost mesethmoid is usually treated as homologous between different lineages. After thorough survey of the literature and revision of the morphology, topological relationships and ontogeny of these ethmoidal ossifications, we evaluate hypotheses of homology and propose characters for comprehensive cladistic analyses of the Actinopterygii including also recent taxa. We accept the primary homology between nasal processes and lateral dermethmoids and between preethmoids and ventral ethmoid. The compound rostrodermethmoid includes the rostral and lateral dermethmoids, but probably also a supraethmoid. The composition of the teleost mesethmoid varies in different groups involving two or more of the following elements: supraethmoid, ventral ethmoid, rostral, and lateral dermethmoids. Therefore, independent characters are proposed for each condition. These characters are defined in a way that they should serve to test the hypotheses of primary homology and trace the evolutionary history of each of the actinopterygian ethmoidal ossifications.

Timing of Jaw Shape Remodeling during Development in Bamboo Shark and Catshark (Chondrichthyes: Galeomorphii) to Promote Species-Specific Feeding Mechanisms

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Despite elasmobranch sharks representing a rather small part of vertebrate diversity they display a wide array of life styles, reproduction, and morphological adaptations throughout their evolutionary history. The skeletal elements in the elasmobranch mandibular apparatus might appear simple at first, however they can show several modifications for specific functions. Regarding the feeding mechanisms, distinct modes are present like ram, suction, grasping, crushing and cutting, along with combinations of those actions. These mechanisms had evolved in different groups of sharks independently, like suction feeding. However the morphological changes to achieve the same feeding mechanisms do not lead to similarities in the skeletal elements. The modifications needed to achieve a functional morphology can be traced during embryonic development, and therefore allow an understanding of how this feeding behavior evolved in separated lineages. The main goal of this study is to determine the specific changes in the shape of the Meckel's cartilage occurring during the development that lead to specialized morphologies in an orectolobiform shark, *Chiloscylium punctatum* (Bamboo shark) a specialized suction feeder, and a carcharhiniform, *Scyliorhinus canicula* (Catshark) a generalist ram feeder. We also intend to understand how other elements in the craniofacial morphology are related to the changes occurring in Meckel's cartilage, like the palatoquadrate, hyomandibular arch, or the neurocranium. In this way, we will understand if these elements have become integrated as a functional unit within the jaws or if the elements function as separated modules. We employed geometric morphometric approaches to quantify the shape changes in the cartilage elements of the jaws through comparable embryonic stages to observe the patterns of divergence in their developmental trajectories that can lead to specific jaw morphologies for feeding mechanisms.

How are Anagalids Informative for the Evolution of Euarchontoglires?

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Anagalidae is a poorly studied group of Paleogene Euarchontoglires endemic to China and Mongolia. They share some dental features with both Glires and Euarchonta, being a morphological 'buffer zone' between these groups. Anagalids have tall cheek teeth (in some instances more unilaterally hypsodont than in most basal Glires) with usually heavily worn crowns. The intense wear has been suggested to be indicative of an abrasive diet. However, the earliest Glires already show a greatly reduced dental formula, whereas anagalids have a full dental set (I 3/3, C 1/1, P 4/3-4, M 3/3). Anagalids display a semi-procumbent somewhat enlarged i1, similar, to a lesser degree, to those of plesiadapiforms, instead of an enlarged deciduous i2, as is typical of Glires. They also have large, prominent canines, as is observed in plesiadapiforms, euprimates, and treeshrews. However, it is possible that the characters that link them to Euarchonta are symplesiomorphies inherited from a primitive euarchontogliran ancestor. Most mammalian phylogenies rarely include anagalids, but a few occasionally place the group relatively close to Glires. Our phylogenetic results disagree with the previous view that Anagalidae were monophyletic. Instead, anagalids are heavily paraphyletic, appearing as several offshoots at the base of Glires, which suggests that anagalids could be considered stem Glires. In terms of their ecology, anagalids peaked in diversity immediately after their appearance in the fossil record in the early Paleocene. Their diversity decreased in the middle Paleocene, and later crashed in the late Paleocene, with long gaps in the fossil record until the late Eocene. The anagalid drop in diversity appears to match with the appearance of rodents and plesiadapiforms in Asia in the late Paleocene, suggesting that anagalids might have been outcompeted by these groups. Funding sources: This research was supported by National Science Centre (Poland) grant No. 2015/18/E/NZ8/00637.

HSP90 Inhibition Causes Heterochronies in the Skull Ossification Sequences of *Pleurodeles waltl* (Urodela). Evolutionary Implications

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Heat-shock protein 90 (HSP90) is an ubiquitous chaperone in eukaryotes that facilitates folding of proteins both in normal conditions and in response to environmental stress. In addition, HSP90 is able to buffer genetic variation resulting from random mutations by regulating intracellular protein degradation mechanisms. It has been shown that experimental HSP90 inhibition produces anatomical variability during embryonic development in *Arabidopsis*, *Drosophila* and zebrafish. It is not clear whether these anatomical changes are caused by the expression of genomic cryptic mutations or by modifications of HSP90 dependent molecular pathways. However, several results suggest that HSP90 modulation is a relevant mechanism underlying the *de novo* appearance of character states. In order to test whether HSP90 is involved in the generation of apomorphic phenotypes in tetrapods, we pharmacologically inhibited HSP90 in *Pleurodeles waltl* (Urodela) embryos (n=141), by exposure to 10 μM Radicicol during the first 24 hours of development. Control specimens (n=20) received no treatment. The 54 surviving larvae were euthanized at stages 46 (n=25) and 50 (n=29), and subjected to whole-mount double staining with alcian blue and alizarin red. All the control and 7 (13%) of the treated specimens were phenotypically normal. The remaining 47 (87%) larvae showed 20 abnormal phenotypes best described as heterochronic skull ossification sequences. Interestingly, these heterochronies fit the ossification sequences described in other urodele families. We propose that modulation of HSP90 function during the embryonic development, caused naturally by environmental stress, may underlay the evolutionary modifications of skull ossification sequences in urodeles. New studies on the inheritance of the phenotypes obtained in untreated embryos from treated parents may confirm the plausibility of this hypothesis. Funding: FPU15/03209, EST17/00194 and University of Málaga.

Ventricular Myocardial Trabeculation in Chondrichthyans. Evolutionary Implications

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The formation of trabeculae (trabeculation) in vertebrates occurs during cardiac development in the three structural types of ventricular myocardium, namely, compact, spongy and mixed. The compact type is mainly composed of compacted muscular fibers and the spongy type of muscular trabeculae. The mixed type, with an inner trabecular and an outer compact layer, has been proposed as the ancestral condition in gnathostomes. In vertebrate models, trabeculation initiates following two alternative mechanisms: (1) in chicken and mouse, the endocardial cells evaginate towards the two-layered myocardium; (2) in zebrafish, cardiomyocytes from the mono-layered myocardium invaginate towards the endocardium. Trabeculation in the mixed myocardium has not been described yet. We have studied the mixed myocardium formation in the dogfish (*Scyliorhinus canicula*, Elasmobranchii) using light, scanning and transmission electron microscopy. At stage 27, the ventricle consists of a two-layered myocardium internally lined by endocardium, both separated by cardiac jelly. Trabeculation starts at stage 28, when small spaces between cardiomyocytes appear, the cardiac jelly become thinner and the endocardium focally contacts the myocardium. At stage 29, the spaces between cardiomyocytes increase in size and become lined by the endocardium, shaping the presumptive trabeculae. At later stages, the trabeculae increase in complexity and the outer cardiomyocytes proliferate and become compacted, delineating the definitive trabeculated and compact myocardia. We conclude that early trabeculation in elasmobranchs matches that described in tetrapods. Thus, the mechanism of trabeculation of the mixed ventricular myocardium has been conserved in the formation of the compact myocardium of tetrapods. Additional studies in actinopterygians with different myocardial types may uncover how trabeculation has evolved during the evolution of gnathostomes. Funding: CGL2017-85090-P, FPU15/03209, UMAJI75 and FEDER.

Bite Force Determinants in Caecilians (Gymnophiona): the Relationships between Head Shape, Jaw Muscles, and *In Vivo* Bite Force

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Caecilians are elongated limbless amphibians that are mostly fossorial. Because their head-first burrowing lifestyle puts severe constraints on maximal head diameter, the external jaw adductors are constrained in size and thus are strongly reduced compared to other amphibians. However, caecilians developed a unique jaw-closing system involving the large and well-developed *m. interhyoideus posterior* which is positioned posterior to the head instead of laterally (as is the case for the *adductor mandibulae*) and thus does not increase the head diameter. Although these additional jaw closing muscles could suggest that these animals can generate considerable bite forces, few experimental *in vivo* data have been published. In the current study we investigate the relationships between the skull and mandible shape, the architecture of the cranial muscles, and *in vivo* bite forces in seven species of caecilians. To do so we use μCT reconstructions of the skull and mandible and geometric morphometric methods to characterize shape variation. Additionally, we use PMA-stained μCT-scans and dissections to assess the morphology of the cranial muscles. As previous models have suggested that skull shape is not correlated with burrowing capacity, we expect that the mandible and skull shape will co-vary strongly with bite force. Additionally, we expect that a larger mass and physiological cross-section area of specific head muscles such as the *m. interhyoideus* will be correlated with bite force.

Not so Ridged After all: Ontogeny of Armor Biomechanics and Swimming Performance in Poachers

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Animal armor can defend against predators, serve as support and even store energy necessary for animal movement. Poachers (Agonidae) are differentiated from related sculpins and other cottoids by their heavily-ossified dermal armor. These fishes have elongate bodies entirely covered by bony plates, which vary morphologically from unadorned to intricately ornamented. We used micro-computed tomography (μCT) scanning to characterize regional variation in armor plating along the body of the northern spearnose poacher (*Agonopsis vulsa*) across its ontogeny. We also examined changes in mineral density of these bony plates, as it relates to scale morphology and ecology. *A. vulsa* cross-sections show staggered series of eight bony plates that encircle and serially-repeat along the length of the fish's body, forming eight longitudinal ridges. The arrangement and number of plates remains fixed throughout an individual's life. While the shapes of dorsal and longitudinal plates remain consistent over ontogeny, ventral plates shift from a spiked to flattened shape, as juveniles transition to adulthood. The mineral density of dorsal plates increased linearly with body size over ontogeny, as did plate volume. Since these armored plates are rigid and heavy, we also studied the effect of armor development on swimming and body mechanics in *A. vulsa* from 40mm to 162mm. Juveniles are less stiff, and therefore more flexible than adults, despite having similar numbers of armored plates. Instead, greater flexibility in juveniles stems from the lower mineral density of their armor. Since juveniles are more flexible, they have a higher tail beat frequency (12-19 Hz) and swim slower (0.4-0.6 BL/s) than adult fish (7-11 Hz, 0.6-1 BL/s). This suggests a tradeoff between flexibility and defense as fish grow.

Can Geometric Morphometric Analyses of Limb Shape Reveal Ecomorphological Patterns Across the Evolutionary History of Synapsida?

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Extant Mammalia are the only living representatives of the larger clade known as Synapsida, which has a continuous fossil record from around 320 million years ago to today. Despite the fact that much of the ecological diversity of mammals has been considered in light of limb morphology, the deep time origin of synapsid limb diversity and its influence on ecological diversity has received less attention. Here, we present shape analyses focusing on the forelimbs of the two earliest synapsid radiations ("pelycosaurs", and pre-mammaliaforme Therapsida) in comparison to a broad sample of extant Mammalia. Using an expansive geometric morphometric data set, comprised of 384 fossil specimens and 148 extant mammalian specimens, we sought evidence for ecomorphological signals that could provide insight on the ecology of the earliest synapsids. Collecting shape data of humeral and ulnar elements from an extant sample representing multiple known ecomorphologies provided the framework for a comparative exploration of extinct ecomorphologies, associated specifically with locomotion. Our results show that distal humeral shape is not informative of broad locomotor ecomorphologies in early fossil Synapsida. In contrast, proximal humeral shape shows a more complex pattern that suggests shape similarity between basal synapsids and members of extant Perissodactyla, and certain highly derived fully fossorial mammals, as just two examples. Overall, however, our findings suggest general shape analyses may have limited utility when analyzing for ecological-signal across deep time. Considering skeletal morphology in a holistic framework that considers unique combinations of shapes, as well as the use of biomechanically focused indices (such are functional proportions), may help to elucidate the more nuanced ways that locomotor ecology influenced limb shape in some of the earliest amniote radiations.

Relative Brain Volume of North American Carnivorans Does not Support the Cognitive Buffer Hypothesis

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The Cognitive Buffer Hypothesis proposes that a proportionally larger brain confers greater socioecological flexibility, allowing an organism to occupy novel or fluctuating environments. Previous research supports a relationship between environment, diet, and brain size in primates, an order occupying a wide range of habitats and with diverse ecological behaviors. Like primates, carnivorans have proportionally large brains to their body size, are successful across a wide environmental gradient, and perform a plethora of hunting behaviors. Following the Cognitive Buffer Hypothesis, we predict a positive correlation between relative brain size and variability of the environments occupied by carnivorans. We tested for a correlation between relative endocranial volume (PGLS residual from species mean body mass) and environmental variables in 31 species of North American carnivorans. Variables included annual temperature, annual precipitation, ecoregions inhabited, length of dry season, and vegetation index collected from the recorded geographic range of each species. This data was sourced from GIS maps provided by WorldClim, North American Data Atlas, and NASA/GSFC. Brain and body measurements were sourced from the literature. PGLS analysis found no significant relationship ($p<0.05$) between relative brain volume and the tested environmental variables. This indicates that while there is variation in relative brain size across Carnivora, this variation does not appear to be an adaptation to selective pressures imposed by environment. Instead, it is possible that the large brains seen in Carnivora reflect the dietary specializations of this clade. Most carnivorans are carnivorous, omnivorous, or insectivorous and, therefore, predominantly consume high quality food items. Future analyses testing for correlations between brain size and dietary niche may aid in determining the selective pressures acting on brain evolution within Carnivora.

Orbital Angle in the Australian Dingo

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Wild and domestic canids differ in relation to their field of vision. Wolves (*Canis lupus*) have narrow binocular vision that favors the detection of prey over wide distances, whereas domestic dogs (*Canis familiaris*) have a wider binocular vision as a consequence of decreased predation behavior. Correlated with binocular vision is the orbital angle, which is a morphological ratio based on width and height of specific skull landmarks on the frontal and zygomatic bones. Wolves have acute orbital angles (42° ± 5.3 SD). Little is known about the orbital angle of other wild canids, such as the Australian dingo (*Canis dingo*), that have markedly different lifestyles and prey compared to the grey wolf. This study compares the orbital angles of dingoes (n=45, sourced from South Australian Museum) and greyhounds (n=52, sourced from University of Adelaide). Skulls were photographed in the dorsoventral position from the rostral view. ImageJ software was used to calculate orbital angle measurements. Orbital angles in dingoes and the greyhound were found to be symmetrical ($p= 0.2$); thus only the right-side orbital angles were analyzed. The mean orbital angle of dingoes and greyhounds (49° and 53° respectively) were statistically different, with overlapping ranges of 46.3° - 54.6° ($t(95)=7.9$, $p<0.01$). These findings are comparable to binocular field ranges with wild canids like dingoes and the wolf having narrower binocular fields of vision (70°) than greyhounds (80°). The difference in orbital angle and binocular field is likely reflective of direct or indirect consequence of domestication and paedomorphism.

Caudal Autotomy in Mesosaurid Reptiles and its Implications for Anti-Predatory Behaviors in Early Amniotes

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Mesosaurs are a distinctive clade of early reptiles that returned to an aquatic lifestyle in the Permian period. While their status as the first reptilian group to re-invade aquatic environments makes them a particularly interesting clade, one of their most puzzling and controversial features is the potential for caudal autotomy. Several researchers have described fracture planes in mesosaur caudal vertebrae - unossified regions in the middle of caudal vertebral centra - that in extant squamates allow the tail to separate and enable escape from a predator's grasp. However, the reports of fracture planes in mesosaurs are contradictory, having never been closely investigated beyond preliminary descriptions. Here, using numerous vertebral series, computed tomography scans, and histological sections, we provide a detailed account of fracture planes in the caudal vertebrae of several mesosaur specimens, confirming earlier observations. The identification of fracture planes in mesosaurs expands the occurrence of this behavior in Palaeozoic amniotes, and also has important implications for aquatic locomotion in mesosaurs. With caudal autotomy also being present in other Palaeozoic tetrapod clades, specifically captorhinid reptiles and 'microsaurs', this trait was more prevalent among early tetrapods than previously realized, with ancestral state reconstruction indicating that it was likely a plesiomorphic characteristic of reptiles. Furthermore, despite mesosaurs apparently having the ability to autotomize their tail, it is unclear if they actually made use of this behavior, as they would have had no known predators in the inland sea in which they lived. Caudal autotomy may have been useful if they were spending time on land, as has recently been suggested. It also has implications for how mesosaurs swam; they are generally considered to be largely tail driven swimmers, the potential for autotomy suggests that the limbs would have played a larger role in locomotion.

Fetlock Morphology in Equoids (Mammalia: Perissodactyla) and its Relationship to Mass, Diet and Extrinsic Evolutionary Drivers

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The fetlock joint of equoids (Perissodactyla; Equoidea) is a highly specialized joint with multiple functions, including shock absorption, distal limb stability, and facilitating efficient elastic recoil during the swing phase of locomotion to enable sustained, rapid running. Here, we investigate how this joint has changed in shape (and potential function) from extinct tetradactyl equoids (equids + palaeotheres) to modern horses in a quantitative framework, comparing patterns of shape change with internal (mass/diet) and external (geological/climatic) ecological drivers. We used landmark based geometric morphometrics to quantify fetlock shape in Equoidea using landmarks applied to the distal metacarpal. 268 metacarpals were laser scanned and landmarked. A hypothetical ancestor was calculated from basal-most metacarpal shapes using a time-calibrated phylogeny. Divergence from the ancestral shape was calculated using ordinary sum of square distances (OSS) from geometric morphometric analysis, averaged per species (n=57). First time derivatives for body mass, hypsodonty and OSS were taken at 1 Ma intervals to study trait shifts. When examined through time, positive correlations between shape divergence and body mass/hypsodonty occurred at < 1 Ma, with negative correlations at -5 Ma. Small-bodied palaeotheres drive a divergence in fetlock shape in the late Eocene, with North American anchitheres also inducing a morphological shift away from the ancestral morphology in the late Oligocene. Increases in divergence were observed at the Grande Coupure and MMCO, with decreases at the Vallesian turnover and Quaternary Glaciation. Overall, we demonstrate that fetlock morphology in equoids is linked with fluctuations in body mass, diet regime, and with key turnover events. Localized morphological evolution also plays a key role, with morphological peaks and troughs correlating with origination and extinction of specialized endemics (e.g., *Plagiolophus*, *Nannippus*).

A New Permian-like Fauna within a Single Fossilized Stump from the Carboniferous of Nova Scotia

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Here, we report on the discovery of a fossiliferous lycopsid 'tree' stump from the Sydney Mines Formation, Upper Pennsylvanian, Cape Breton Island, that remarkably contains the remains of at least six taxa, both non-amniote and amniote, in various states of preservation and articulation. Significantly, most of the preserved taxa are otherwise only known by representation in the later, Permian ecosystems of North America. Most notable among these is a virtually complete skull of a large, pantylid recumbirostran, as well as four partial, articulated skeletons of a varanopid synapsid. As such, the new material provides new, earliest records of these taxa and reveals several evolutionary events vastly predate currently known occurrences. For example, CT-scanning of the pantylid reveals a highly specialized dental apparatus composed of opposing dental fields on the palate and coronoids. The low, conical teeth of these fields is suggestive of complex oral processing of a diet consistent with high-fiber herbivory, well advanced to that of any known tetrapod of equivalent age. Additionally, the presence of at least three partial, articulated varanopid specimens of equal, subadult size, and an associated very small fourth, alludes to the possibility of a social aggregation – a behavior otherwise known from this clade in the Late Permian. These skeletons are consistent in many regards with mycterosaurines, except for the presence of tall, blade-like neural spines, suggesting they may represent a new taxon. Together, the implications of this discovery are numerous and include revisions to the tempo of evolution of major tetrapod clades and several new additions to the Upper Carboniferous faunal record. Further detailed analyses of this material will contribute to revising our understanding of the ecosystem composition and dynamics of Upper Carboniferous tetrapod communities.

The Evolution of Body Shape, Locomotion and Ecology in Terrestrial Vertebrates

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Body shape has a fundamental impact on organismal function. Most studies on body shape in vertebrates are focused on research into squamates (mostly fossorial species) and aquatic or semi-aquatic vertebrates, but it is largely unknown (in a quantitative way) how body shape has evolved more widely in concert with changes in behavior, locomotor style and ecological niches. Here, we combine three-dimensional computer models of vertebrate skeletons with phylogenetic reconstructions to quantify the evolution of body segments and whole body shape across terrestrial vertebrates. Measures of whole body shape include a range of linear measurements, including limb bones lengths (used to calculate whole limb lengths) and gleno-acetabular distance, along with skeletal volumes (generated by automated convex hulling) for major body segments (e.g., neck, tail, thigh segments). This data is then used to generate a range of measures to describe various aspects of body shape, such as relative body length (limb length: gleno-acetabular distance), relative limb length (forelimb length: hind limb length) and proportion of total skeletal volume made up by individual body segments. We derived this data from 3D-skeletal models spanning 420 taxa across all major extinct and extant terrestrial vertebrate groups. In order to test for correlations between body shape and locomotion, behavior and ecology we assigned each taxon to a range of morpho-functional groups. To consider phylogeny in our analysis we constructed a phylogenetic tree of our sample taxa by merging the most recent consensus trees in the published literature. Statistical analysis of this data set reveals a number of strong correlations between multiple body shape metrics and both locomotor style and ecological niche. Interestingly, our analysis reveals that selectively bred animals, such as specific breeds of domestic dogs, represent statistical outliers, having body shapes that are uncharacteristic of their locomotor style and ecology, which may help explain the prevalence of musculoskeletal dysfunction in these animals. IACD are acknowledged for part-funding this research.

Ontogenetic Development of Skull Shape in *Bothrops jararaca*, with Special Emphasis on the Pit Organ and the Venom Gland

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The venomous pit viper *Bothrops jararaca* from Brazil is known to experience a dietary shift during growth, i.e., whereas juveniles initially hunt for ectothermic prey and insects, prey preference changes towards endotherms, i.e., mammals, in the adult stage. This shift is also reflected in a change in venom composition during growth. However, it remains unknown if there are also any anatomical changes resulting from this dietary change. To investigate whether this shift can be detected in the morphology of the head we generated micro-computed tomography scans of the skulls of 85 individuals of *B. jararaca* across all growth stages, and applied a geometric morphometrics approach with special focus on the imprint of the pit organ onto the maxillary bone. Also, we used Diffusible Iodine-based Contrast-Enhanced Computed Tomography Method (DiceCT) to visualize the morphology of the venom gland. Results reveal that the growth trajectory of the pit organ deviates from that of the skull, with the pit organ following a much steeper inclination and showing fast, positively allometric growth relative to the remaining skull until close to the adult stage. In addition, not only the pit organ but also the venom gland system follows its own growth trajectory. Our results suggest a relationship between ontogenetic changes in prey preference and the postnatal ontogenies of pit organ and venom delivery system in *B. jararaca.* It still remains to be tested if similar patterns are also found in other species of pit vipers without dietary shifts.

Are Rhinoceros Graviportal? Morphofunctional 3D-Analysis of Modern Rhinoceros Limb Long Bones

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Many amniote lineages display convergent evolution towards high body mass through time, which strongly impact (among others) the appendicular skeleton. Species displaying adaptations to sustain a high body mass are said to be graviportal, a term defined alternately by the relative length of limb segments, osteological features, body mass, posture or gait. Unlike elephants, rhinoceros do not fulfil all the graviportal criteria and important body mass and body size variations can be observed between the lightest rhinoceros (*Dicerorhinus sumatrensis*) and the heaviest one (*Ceratotherium simum*). Detailed study of long bone shape variation in the five living rhino species could enable to better highlight limb traits potentially linked to body mass increase in the group. Using 3D-geometric morphometrics on the six stylopod and zeugopod bones allows us to clearly discriminate the five species. The fibula displays a particularly strong intraspecific variation which questions its functional adaptive value, among other possible contributing factors. Moreover, morphological traits tend to co-vary because of common developmental origin or similar function, a tendency called integration. We completed our individual bone analysis by exploring this integrative aspect related to high body mass. While the strong differences between the lightest and the heaviest species tend to indicate an impact of body mass on the bone shape, the influence of body size, body proportions, ecology, and phylogeny are also characterized. This study allows us to propose morphofunctional interpretations of the observed shape variations between the five species and to contribute new elements to the recognition of morphological changes associated with weight bearing adaptations of the limb bones in rhinoceros.

How Informative is Joint Mobility? A 3D-Analysis of Potential *versus* Realized Joint Poses in Archosaurs

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Paleontologists have traditionally reconstructed the locomotion of dinosaurs and other extinct animals by manipulating their fossil bones and inferring the mobilities of their limb joints. But even if we could estimate the ranges of motion (ROMs) of joints perfectly, are we justified in assuming that all of an animal's potential joint poses are exploited in life, let alone in locomotion? Here, we evaluate the predictive power of joint mobility by determining what portion of a joint's full passive ROM is actually used during various behaviors. We measured the passive joint ROMs of the hip, knee, and ankle of the helmeted guineafowl (*Numida meleagris*) and the American alligator (*Alligator mississippiensis*) based on manipulations of fully intact cadavers. We then measured thousands of poses used at each of these joints during locomotor and non-locomotor behaviors using XROMM, and plotted the mobilities and poses on a common ROM map in 3D-joint pose space. We found that in all the joints studied, steady forward locomotor poses form a very small and uncentered subset of all possible joint poses. The centroid of each joint's mobility - sometimes termed the joint's "neutral pose" and thought to reflect habitual stance - has no relationship to posture or locomotion. Rather, locomotor poses, especially stance phase poses, often fall along the edges of cadaveric ROM envelopes in 3D-joint pose space. These results suggest that even well-estimated joint ROM, though critical for the elimination of impossible joint poses, is a poor predictor of the locomotor poses actually used by extinct ornithodirans such as non-avian dinosaurs and pterosaurs. Future analyses of hind limb joint surface interactions during life are necessary to further constrain paleontological reconstructions of locomotion.

A Reappraisal of the Pennsylvanian-aged Early Reptile *Cephalerpeton ventriarmatum* (Moodie, 1912) from Mazon Creek, Illinois and Linton, Ohio

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The Pennsylvanian-aged (309-307 Ma) Francis Creek Shale, 'Mazon Creek' Lagerstätte, produces some of the earliest fossils of the major tetrapod lineages. The Mazon Creek record of the early 'protorothyridid' reptile, *Cephalerpeton ventriarmatum* (YPM 796), is known from a single part concretion containing a well-preserved anterior portion of a skeleton. Aside from the reptile *Hylonomus lyelli* from the slightly older deposits of Joggins, Nova Scotia, the remains of *Cephalerpeton* are amongst the oldest known amniote fossils. *Cephalerpeton cf. C. ventriarmatum* has also been identified in the tetrapod fauna from Linton, Ohio, represented by a disarticulated cranium (CM 23055) and a single right dentary (BMNH R. 2667). Here, we re-describe the anatomy of *Cephalerpeton* from all its known fossils from Mazon Creek and the slightly younger coal deposits of Linton, Ohio, and additionally, we describe new material from the latter. Our results indicate major anatomical differences between fossils of *Cephalerpeton* from Mazon Creek and those from Linton, likely representing new taxonomic diversity. The holotype is reconfirmed as a basal eureptile sharing close postcranial skeletal similarities to other protorthyridids, such as *Anthracodromeus* and *Paleothyris*. The skull of the holotype is long and lightly built, with large orbits, and a dorsoventrally short mandible similar to most basal eureptiles. This strongly contrasts the condition seen in *Cephalerpeton cf. C. ventriarmatum* from Linton where the cranial and mandibular elements appear proportionally taller. Additionally, the anteroposteriorly narrower and dorsoventrally taller maxilla of the Linton specimen is reinterpreted as excluding the lacrimals from the nares; a similar condition is seen in 'short-faced' parareptiles such as *Colobomycter* and *Acleistorhinus*. We tentatively propose a parareptilian affinity for the reptile remains from Linton, which would represent the oldest known example of a parareptile.

Does the Muscular Anatomy of the Pelvic Fin of the Extant Coelacanth *Latimeria chalumnae* (Actinistia: Latimeriidae) Provide Information on its Mobility and Role during Locomotion?

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Coelacanths are sarcopterygian fishes that were originally known only from their fossil record and assumed extinct since the Upper Cretaceous (70My ago). The discovery of a living coelacanth, *Latimeria chalumnae*, offshore South Africa in 1938, was a surprise for the scientific community, and provides a unique opportunity to study the anatomy of this close relative to tetrapods. Its paired fins are of special interest because of their mono-basal articulation and their proximal endoskeleton, homologous to that of tetrapods. A recent study on the functional anatomy of the musculature of the pectoral fin showed that it is more complex than previously thought. Here, we focus on the pelvic fin and hypothesize that the muscles are equally complex and allow complex movements of the fins. A detailed dissection and anatomical description of the pelvic fins was undertaken on an adult specimen of *L. chalumnae* preserved in the MNHN collections, Paris. According to previous descriptions, the pelvic fin musculature presents a three-layered organization: the adductor and abductor muscles form the superficial and middle layers, whereas the pronator and supinator form the deep layer. Amongst others, our preliminary results show that the muscle bundles of the superficial and middle layers lead to adduction or abduction movements, but also to the protraction or retraction of the fin. Moreover, whereas previous studies documented about twenty muscles, we observed and described more than 70 clearly individualized muscle bundles. This complex organization of the muscle bundles

is congruent with a high mobility of the pelvic fin as quantified based on *in vivo* video recording.

Artificial Selection Reveals a Role for Ion Transport in Regulating Chondrocyte Differentiation and Bone Length Variation during Endochondral Ossification

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The developmental basis of vertebrate limb length diversity has long been a focus of study among evolutionary developmental biologists. To study the genetic basis underlying heritable limb variation within populations, we selectively bred mice for increased tibia length (Longshanks) relative to body mass. Longshanks long bone growth plates preserve the orderly transition of chondrocytes from resting to proliferative to hypertrophic states, but differ from controls in having a larger pool of proliferative chondrocytes. To investigate how changes in transcriptional regulation may lead to the observed increase in proliferative chondrocytes and bone growth rate, we analyzed gene expression in juvenile Longshanks tibial growth plates using RNA sequencing and qPCR. Surprisingly, qPCR revealed only a few differentially expressed genes in Longshanks *vs* control growth plates. The strongest and most consistent signal was downregulation of Fxyd2, a subunit of the Na+/K+ ATPase pump (NKA) which regulates efficiency of ion exchange across cell membranes. We hypothesized that this pump plays a key role in chondrocyte differentiation and, consequently, bone elongation. To test this hypothesis, we cultured whole tibiae and chondrocyte micromasses in serial dilutions of the NKA inhibitor ouabain. Histology of cultured tibiae shows that higher concentrations of ouabain inhibit tibia growth and, in particular, affects cell differentiation. Micromass qPCR shows that NKA inhibition has a dynamic effect on transcription of cartilage markers: at low concentrations, ouabain promotes an increase in Collagen2 and Sox9 expression (proliferative chondrocyte markers) whereas at higher concentrations, ouabain downregulates Collagen2, Sox9 and Collagen10 (a hypertrophic chondrocyte marker). Our data suggest that ion transport plays an important and previously unrecognized role in regulating chondrocyte differentiation and physiology during endochondral ossification.

Skull and Limb Bone Shape Variation in a Novel Chondrodysplasia Model

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Studies of skull morphology in numerous mouse models have shown how disruption of cartilage growth can produce changes in shape and covariance structure both in the affected bone and in other bones of the skull. New mutants can provide insight into ways in which altered tissue-specific processes disrupt development and morphological outcomes. The Nabo mutation affects a regulatory region important for cartilage growth, and has been previously shown to produce substantial reductions in limb length (30% in adult). Here, we used microCT and our automatic segmentation and landmarking workflow to examine covariation in the skull and limb segments across ontogeny in the Nabo mouse. Because the Nabo mutation is regulatory in nature, we predicted spatially and temporally dynamic effects on development. We find that the Nabo mutation most strongly affects the shape and size of the endochondrally ossifying cranial base early in development, but is not accompanied by substantial differences in overall skull length and shape. Over ontogeny, cranial base shape in the Nabo partially recovers, becoming more similar to stage-matched controls. In contrast, preliminary analysis indicates that stylopod and zeugopod elements maintain a strong shape difference throughout ontogeny. Shape recovery in the cranial base might reflect conserved topological and physical constraints specific in the head. The results show the importance of both intrinsic tissue-level properties as well as positional context when determining the effects of integrated developmental processes.

The Surrogate Arm: Assessing Factors Influencing Vertebral Morphology in the Avian Cervical Spine

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The avian neck allows for the head to perform environmental manipulation tasks usually accompanied by the forelimbs, which are primarily adapted for flight in birds. This additional selection pressure on the cervical system has led to a vast array of neck morphologies in modern avians, yet, no systematic study of this variation has occurred, owing to fluctuating cervical counts. Hox genes regulate axial regionalization in vertebrates and the number of cervical regions is fixed within a group of vertebrates. Thus, studying cervical regionalization overcomes problems associated with varying cervical counts. Using 3D-geometric morphometrics, Phenotypic Trajectory Analysis and multivariate statistics this study assesses how ecological and functional factors influence the morphology of these cervical regions in a diverse selection of extant birds. Across all five distinct cervical regions Phenotypic Trajectory Analysis reveals that only two ecological factors (carnivory and soaring) appear to significantly affect the morphology of the entire cervical spine. Further investigation using Procrustes distance phylogenetic GLS models reveals that many other ecological factors (both diet and locomotor mode) significantly affect vertebral morphology but only in individual regions. Functional factors have a stronger influence on vertebral morphology with body mass affecting vertebral morphology in the anterior- and posterior-most regions, and neck length in the middle three regions. Finally, we note that body mass and neck length overshadow head mass in their effect on vertebral morphology. Using regionalization as a metric, it appears

that one specific factor does not govern neck morphology in birds, and that the avian cervical column is a generalist musculoskeletal system, capable of performing a multitude of tasks on a daily basis, acting as a surrogate arm.

Comparing the Kinematics and Speed of Locomotion in the Svalbard Rock Ptarmigan under Field and Laboratory Conditions

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Traditionally, animal locomotion has been studied in animals exercising on treadmills. The uniform conditions experienced on treadmills, however, contrast with the highly variable conditions when animals move in their natural environments. Among the major differences, substrate properties may play a key role in how animals move. By using video recordings, we compared the kinematics (stride length, stride frequency, stance and swing duration, duty factor) of Svalbard Rock Ptarmigan moving in their natural environment and exercising on a treadmill. Our results suggest that kinematics for walking and aerial running speeds are similar between field and treadmill-based studies. Walking gaits were found over a mixed variety of substrates, however, aerial running is almost exclusively used when moving over hard snow. Interestingly, birds used faster and shorter steps during grounded running gaits likely as a stabilization mechanism when moving on slippery patches of snow or/and ice. Our study expands ptarmigan speed range to 2.76 ms^{-1}, however, ptarmigan preferred walking and aerial running speeds that promote energetic economy. Altogether, our study demonstrates that laboratory studies provide meaningful information for animals moving in the wild and highlight the importance of understanding how substrate could affect how animals move across in their natural environment.

An Eocene Myliobatiform (Chondrichthyes, Elasmobranchii) from Monte Bolca (Italy) Defines a New, Basal Body Plan for Pelagic Stingrays

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The end-Cretaceous niche filling scenario by benthic Mesozoic survivors resulted in a prominent increase of durophagous fish families, resulting in the appearance of the earliest representatives of several extant fish lineages, including the pelagic durophagous stingrays, a monophyletic clade of myliobatiform batoids that is characterized by derived swimming mode and feeding habits. Although the earliest members appeared in the Late Cretaceous, most of the crown genera date back to the Eocene. Among the latter, the eagle ray *Promyliobatis* Jaekel, 1894, represented by two nearly complete and articulated fossil specimens from the celebrated Bolca Konservat-Lagerstätte and dating back to about 49 million years ago, exhibits a mosaic of plesiomorphic and derived characters (e.g., tail sting displaced posteriorly on the tail, at about 50-60% of tail length; pectoral fins joining in front of the head; anterior and posterior pectoral fin margins nearly straight; compagibus laminam absent; single not fragmented mesopterygium) that clearly define a new body plan within the pelagic durophagous stingrays. The significant morphological differences between *Promyliobatis* and extant representatives of Myliobatidae, Aetobatidae, Rhinopteridae, and Mobulidae, support its placement in a separate new family. The phylogenetic placement of *Promyliobatis* within the Myliobatiformes is assessed based on skeletal and dental characters that strongly support its basal position within pelagic stingrays, although its position becomes unstable when stingray taxa known by fossil teeth only are included. Financial support to attend the conference was provided by Austrian Science Fund (FWF): M2368-B25 to GM.

Geographical Isolation Drives Developmental Modularity Shifts in the Skull of a Critically Endangered Carnivore, the Arctic Fox (*Vulpes lagopus*)

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Island populations are excellent systems to investigate the effects of genetic isolation on phenotypic variation, evolvability, and ecological adaptations. However, how genetic isolation influences intraspecific integration and modularity change are less explored. Here, we use the skull of the isolated Arctic foxes (*Vulpes lagopus*) of the Bering and Mednyi islands to explore how variation in phenotypic integration and modularity in isolated populations impact ecological adaptations to feed on specific resources. A set of three-dimensional landmarks in a wide sample of fox skulls from the mainland and from Bering and Mednyi islands were digitized. We performed a PCA to explore morphological variation of the three populations, and we analyzed morphological integration of each population at two levels: static (among adult individuals) and developmental (using fluctuating asymmetry). The results of the PCA show that the skulls of foxes from Mednyi have the shortest rostra, which increases the mechanical advantage for biting larger prey, whereas the skulls of mainland foxes have the longest rostra. In addition, the skulls of the foxes from Mednyi Island are more integrated than the ones of the mainland for both static and developmental levels. The degree of integration of the skull of the foxes from Bering Island is intermediate. Our results indicate that: (i) genetic isolation of Arctic foxes is accompanied by an increase in phenotypic integration within the skull, including the developmental level; and (ii) this stronger developmental integration has favored adaptive morphological changes for hunting larger prey in foxes from Mednyi Island. This indicates that changes in developmental integration not only can influence phenotypic macroevolution, but also microevolution.

3D-Reconstruction of the Skull of the Enigmatic Carboniferous Tetrapod *Eoherpeton watsoni* and the Evolution of the Pterygoid Flange

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The tetrapod *Eoherpeton watsoni*, from the mid-Carboniferous of Scotland, was first described over 40 years ago. While its exact phylogenetic position is unclear, most analyses place it as an embolomere/ reptiliomorph, and therefore on the lineage leading to amniotes. This makes it a key taxon for understanding changes in skull form and function during the acquisition of a fully terrestrial lifestyle. The type specimen includes a near-complete, though flattened, cranium and lower jaws. Through micro-computed tomography (μCT), the skull was digitally prepared and individual bones identified allowing for new observations of anatomy. New anatomical information includes the presence of a tooth-bearing vomer (previously unknown), an elongated parasphenoid, a pterygoid-squamosal articulation, and additional information on the shape of the basipterygoid processes and extent of the pterygoid. Of most relevance to feeding, we note the presence of a pterygoid flange, not previously described or figured. The pterygoid flange is widely considered to be characteristic of amniotes and serves as the origin of M. pterygoideus. The differentiation of the adductor muscles and appearance of M. pterygoideus are thought to have permitted a static pressure bite in amniotes. This might have resulted in higher bite forces, allowing a wider dietary scope and their diversification in terrestrial ecosystems. Incipient flanges have been found outside of Amniota, but never as stem-ward as *Eoherpeton* or in embolomeres, suggesting this feature (and associated changes in the feeding mechanism) may have evolved significantly earlier than previously thought. Additionally, data from CT-scans allowed the skull of *Eoherpeton* to be digitally reconstructed in 3D for the first time. This model will serve as the basis for future biomechanical studies to investigate how changes in skull shape impacted feeding during the evolution of early tetrapods.

Convergent Evolution of Olfactory and Thermoregulatory Capacities in Small Amphibious Mammals

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Olfaction is a key function for mammals that helps for feeding behaviors, sexual mating and predator avoidance. Despite studies related to olfaction in marine mammals, small amphibious mammals are poorly understood for that sense. We investigated olfactory capacities in amphibious mammals using a large-scale sampling representing most transition events toward amphibious lifestyle in Rodentia, Eulipotyphla, and Afrosoricida. We used a comprehensive 3D-CT-scan dataset (N=189) to infer that amphibious mammals converged towards reduced olfactory turbinal bones and might rely on poor olfactory capacities as compared to their terrestrial counterparts. Using comparative phylogenetic methods, we tested and identified a convergent loss pattern of olfactory capacities related to amphibious lifestyle. Our results are consistent with genetic and histological evidence. We further demonstrate that amphibious species convergently display large respiratory turbinal bones that reflect efficient heat conservation capacities. Indeed, mammals also use the nasal cavity as a heat-exchanger with the environment. Because body heat is lost quicker in water than in air, the nasal cavity of amphibious mammals independently evolved to limit thermal loss.

Phenotypic Variation of the Zebrafish (*Danio rerio*, Actinopterygii: Cyprinidae) Skeleton in Response to Rearing Density

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The response of individuals to novel or altered environments is defined as "phenotypic plasticity“. Plasticity is a fundamental character of the vertebrate skeleton (West-Eberhard, 2005, J. Exp. Zool. 304B: 610-618). The skeleton is active and dynamic throughout life and capable to adapt to mechanical forces and environmental changes. Here, we study how rearing density affects skeletal development in zebrafish. From 30 to 90 days post-fertilization zebrafish were reared at three different densities: high density (HD) 32 fish/L, medium density (MD) 8 fish/L and low density (LD) 2 fish/L. A connected recirculating system ensured homogenous water chemistry. At the end of the experiment, animals were whole mount stained with Alizarin red S to visualize calcified tissues. Then, the entire skeleton was analyzed for 113 malformation types (modified from Prestinicola et al., 2013, PloS One 9(5): e55736) and vertebral body malformations were subjected to histological analyses. The animals' average standard length decreased with increasing rearing density. The HD-group had the highest variety of malformations throughout the skeleton and the highest number of malformations per malformed specimen. The HD-group particularly showed malformations in the caudal region of the vertebral column, such as dislocation of neural and hemal arches, missing distal fusion of arches and malformed neural and hemal spines. Histological analyses showed a variable size of muscle segments while arches and spines align with dislocated myosepta. Vertebral centra can extend over two myosepta, the opposite of diplospondyly. Interestingly, similar malformations have been described for tbx6 mutant (fssti1) and transgenic zebrafish in which the Notch pathway was inhibited (Wopat et al., 2018, Cell Reports 22.8: 2026-2038). The mechanisms by which rearing density induces late vertebral column malformations similar to early, mutant-related, malformations remain to be elucidated.

Alternate Uses of Geometric Morphometrics in Morphology

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Geometric morphometrics (GM) encompasses a powerful suite of graphical and statistical techniques that have become an essential tool

for comparative morphology. Most conventional uses of GM include the analysis of intra- and inter-specific variation and taxonomic discrimination, but other more complex approaches, such as the assessment of evolutionary allometry, of integration and modularity, and the extent to which all the latter underlie phylogeny, also have become relatively common. However, there are many unexplored avenues of enquiry where GM can deliver its full potential and aid discovery. Importantly, these alternative approaches do not require a particular dimensional sophistication nor a deep acquaintance with complex statistics. They merely require imagining biological settings where morphology is ubiquitous and dissimilarity informative, and a thoughtful understanding of the Procrustes method (namely, what it entails to work with coordinates instead of linear distances), to ensure that the method is applicable. Of course, the scenarios that can emerge when exploiting multivariate statistics, and especially covariation methods, are almost unimaginable. I will succinctly review some published examples aimed collectively at showing diverse uses of GM other than the mainstream ones, and thereafter our preliminary results in several studies of non-avian and avian dinosaur morphology using GM unconventionally.

Feeding Behavior and Neck Mobility in the Extinct Long-Snouted Choristodera *Champsosaurus* (Reptilia: Diapsida) *vs* Crocodilia *Gavialis*

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The extinct choristoderes *Champsosaurus* and *Simoedosaurus* are characterized by large size and a long snout. Consequently, they are often described as eco-analogues of crocodiles. The wider-snouted *Simoedosaurus* has been compared with short-snouted crocodiles. By contrast, the slender-snouted *Champsosaurus* is described as “gavial-like”, implying that it fed by lateral underwater sweeps of the head and neck, as in the living *Gavialis gangeticus*. We explored the functional morphology of cervical vertebrae in *G. gangeticus* by comparison with wider-snouted crocodiles, using a combination of vertebral proportions and intervertebral joint angles. These methods were validated with μCT-scanning of fresh specimens of *G. gangeticus* and *Caiman latirostris*, in several postures. The validated methodology was then used to estimate neck mobility in choristoderes. The study revealed a unique mechanism for lateral flexion in *G. gangeticus* involving anteroposterior elongation of centra and horizontal joint articulations; lateral flexion limited to anterior cervicals; and high dorsal flexibility in the mid-posterior neck. By comparison, *Champsosaurus* and *Simoedosaurus* possess relatively short cervical vertebrae as in short-snouted crocodiles. However, whereas the cervicals of *Champsosaurus* permitted lateral flexion in the mid-posterior neck, with limited dorsal flexibility, *Simoedosaurus* had limited capacity for lateral flexion but retained dorsal flexibility. Like *Gavialis*, therefore, *Champsosaurus* may have used its slender snout to grab fish using lateral sweeps of the head and neck, but this movement occurred through the neck. Inertial feeding is unlikely, potentially explaining the role of the palatal dentition in transporting prey through the mouth. *Simoedosaurus* is less likely to have swung the neck actively during prey capture. Where these two genera co-occurred, they may have divided their niche by prey type.

Different Patterns of Developmental Truncation and the Remarkable Diversity in *Priocharax*, a Miniature Amazonian Fish Genus (Teleostei, Characiformes)

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Miniaturization, the drastic reduction of body size, is often associated with developmental truncation resulting in small organisms that may resemble early life stages of their close relatives. This is the case for many miniature fishes whose adults are smaller than 26mm standard length (SL). The Neotropical region harbors the richest freshwater ichthyofauna in the world and also houses 227 miniature fish species, more than any other system on the planet. This makes the Neotropical realm with its huge Amazonian basin a prolific source of model species to better understand developmental truncations in phylogeny. Approximately half of these species belong to the order Characiformes, comprising small tetras, crenuchids, pencilfishes and others. *Priocharax* is a genus with three of the smallest species of characiforms and is diagnosed by the retention of a larval pectoral-fin in adults, a feature known otherwise only in the miniature marine goby *Schindleria*. A detailed osteological study of *Priocharax* revealed some ontogenetic truncations in its skeleton when compared to developmental series of non-miniature characiforms, rendering *Priocharax* as the most developmentally truncated characiform known to date. Moreover, the real biological diversity in the genus is underestimated, as samples of different populations from distinct Amazonian tributaries continue to be revealed. Samples of different regions, which most probably represent distinct undescribed species, are characterized by alternative patterns of bone loss and reduction. So far, it is estimated that five species await formal description, with their main diagnostic characters being the different patterns of developmental truncation. Most ontogenetic truncations are associated with the pectoral girdle, infraorbital series and Weberian apparatus. It is obvious that biological diversification in *Priocharax* occurred through different patterns of truncation in each location, a feature that should be investigated in other miniature taxa.

Evolution of Brain Size and Morphology in Hipposideridae (Mammalia, Chiroptera), New Insights from Extinct Taxa

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Bats have some of the most spectacular morpho-anatomical modifications of mammals. They notably present modifications of their perception organs and of sensory integration in relation with the physical constraints of the aerial environment. Several studies focused on the onset of echolocation in bats and on the evolution of brain characteristics in relation to their ecology and their environment. Some chiropteran families are among the rare mammalian groups that could have experienced a brain mass reduction through time, related to flight, foraging strategies and habitat complexity. Hipposiderid bats, or Old World leaf-nosed bats, are the most diversified family of Rhinolophoidea (the sister-group of megabats in Yinpterochiroptera) and the second most diversified family of bats in the fossil record. A brain mass decrease has been proposed for Hipposideridae, but this scenario has been challenged by the inclusion of two Oligo-Miocene fossil species. Addition of extinct taxa to the picture would instead imply a relative brain-mass decrease from their common ancestor, followed by an increase until modern times. Here, we quantify and qualify the evolution of hipposiderid brain based on 3D-reconstructions of endocasts of Paleogene and Neogene taxa, including an Eocene species from the Quercy (France) deposits. Our results confirm the previous non-linear scenario of relative brain mass evolution in this chiropteran family. Moreover, we describe in detail the endocranial morphology and the pattern of basicranial foramina of paleogene hipposiderids. This allows an assessment of the evolutionary history of brain features through time in this family.

Premature Birth Impacts Feeding Performance and Airway Protection in Infant Mammals

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The coordination of swallowing and breathing are critical for mammalian survival, as the pathways for air and food cross in the pharynx. However, premature birth disrupts this coordination, which is thought to be reflected by their immature nervous system at birth. Although feeding behaviors such as sucking and swallowing, and the coordination between them improve in preterm infants, the coordination between swallowing and breathing does not improve throughout the nursing period. This discoordination could arise from a variety of factors and have multiple downstream consequences. We used high-speed video fluoroscopy to test whether discoordination between breathing and swallowing led to increased frequency of aspiration during feeding. We also tested the possibility that events occurring prior to the swallow might influence swallow safety by measuring the relationship between the shape and size of the bolus of milk being swallowed and the occurrence of aspiration. We found that preterm birth resulted in decreased mean size-standardized bolus areas and decreased milk expression from the nipple. Additionally, bolus size increased proportionally with term pigs as they grew, but preterm pigs did not increase the volume of milk swallowed as they grew and developed. Finally, we found differences in the frequency of aspiration and in the shape of the bolus between term and preterm infants throughout the nursing period. Our results show that food transport prior to a swallow plays an integral role in swallow safety and demonstrate the effects of prematurity on feeding performance and neuromotor coordination in infant mammals.

Modeling the Evolution of Vertebral Number in Snakes (Reptilia: Serpentes)

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Body elongation may be accomplished by increasing the length of vertebrae or by increasing the number of segments present. These differing approaches can have profound effects on the biology of elongate organisms, influencing flexibility and stability. Snakes have elongated via addition of many segments; however, within the clade there is a substantial range in vertebral number (from ~150 to more than 500 in the extinct *Archaeophis proavus*). Previous work has suggested a relationship between the number of segments and aspects of ecology, including habitat use and the application of constriction in prey subjugation. However, the degree to which vertebral number is under selection in snakes is unknown. Using the package SURFACE for the statistical software R, I show that an Ornstein-Uhlenbeck model with multiple optima for vertebral number is preferred to either a global optimum or Brownian motion models. The results do show extensive convergence between lineages, but there is only a weak pattern related to either habitat use or prey capture. Some aquatic and fossorial snakes appear to be under similar selective pressures for low vertebral numbers. One low vertebral number selective regime includes a mix of burrowing and aquatic snakes, as well as terrestrial crotaline species. A second includes old world typhlopids and most natricine snakes, as well as a handful of terrestrial colubrines. The highest vertebral number selective regimes include a number of constricting pythonid and colubroid species, as well as some non-constricting aquatic and arboreal species. The inclusion of species of different environments and behaviors in particular selective regimes suggests that the selective pressures snakes face are complex, and that they face conflicting constraints related to flexibility and stability. Further work is necessary to understand what factors are most important to selection on vertebral number.

The Ventricular Zone of the Lizard Brain: Cell Proliferation, Radial Glia and Evidence for Postnatal Neurogenesis

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The capacity to generate new neurons from endogenous cell populations in the postnatal brain is widely recognized as a feature common to most if not all vertebrates. In non-mammalian vertebrates, neurogenesis is associated with cell populations lining the ventricular system known as the ventricular zone. Although lizards demonstrate some of the most compelling evidence of postnatal neurogenesis, details of the ventricular zone are typically limited to areas of the cerebral cortex. Using the leopard gecko (*Eublepharis macularius*), we investigated the proliferative capacity and histology of the ventricular zone at multiple regions along the brain axis. To map cell proliferation along the ventricular zone, we used phosphorylated histone H3 and a short pulse 5-bromo-2'-deoxyuridine strategy. To identify radial glia, the neural stem cell population of the ventricular zone, we immunostained for the intermediate filaments vimentin and glial fibrillary acidic protein, along with the transcription factor SOX2. We found cells with a radial glia phenotype lining the majority of the ventricular system. Proliferative cells were most commonly observed in pseudostratified regions of the lateral ventricles, as well as the median hypothalamic eminence of the third ventricle, and the dorsal regions of the tectal ventricles. Cell proliferation was also observed within the olfactory bulbs. Taken together,

our data indicate that the capacity for neurogenesis may extend beyond the cerebral cortex. Grant sponsor: Natural Sciences and Engineering Research Council (NSERC) Discovery Grant 400358 (MKV).

The Correlation between Molar Morphometry and Familial Relatedness in Extant Eutherians

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Given an evolutionary mechanism of heritable variation over the course of many generations, we expect near relatives (e.g., human and chimpanzee) to share more of their phenotype and genotype than distant relatives (e.g., human and lungfish). This evolutionary mechanism similarly implies that, on much smaller scales, individuals from the same species resemble each other more so than individuals from different genera, or that, crucially, close familial relatives (e.g., siblings) resemble each other more so than individuals with more distant familial relationships (e.g., fourth cousins). We test this latter expectation using morphometric techniques applied to computerized tomographic data, derived from the dental hard tissues of specimens of known relatedness via Stradwin 5.4 and wxRegSurf (Turmezei et al., 2015, Eur. Radiol. 2016, 26: 2047–2054). Thus far, a highly significant correlation between first molar structural similarity and relatedness quotients has been shown to exist in several species, including *Setifer setosus* (Afrotheria), suggesting that morphometric data from teeth can accurately predict relatedness among individuals.

Effect of Implants on Mechanics of the Primate Mandible during Unilateral Chewing

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Mandible fractures caused by assault, traffic accidents, falls, congenital disorders and sporting accidents account for approximately 30-40% of craniofacial trauma. Current treatments aim to restore mandible function by immobilizing the fracture with plates and screws but are associated with post-operative complications. An important contributor to post-surgical complications may be bone strains around the fracture zone that compromise healing. Previous research has addressed the effect of plates and screws on deformation, strain and stress regimes of the lower jaw but these studies are limited by their use of non-validated finite element models (FEMs) of pig, sheep and cadaveric human mandibles and non-physiological boundary conditions. This study uses a validated subject-specific finite element model of a healthy female rhesus monkey (*Macaca mulatta*) to determine the effect of mini-plate fixation of the mandibular angle on mandible biomechanics during post-canine chewing. Preliminary results show that implants affect torsion in both mandibular corpora (chewing and non-chewing side) and increase principal strain magnitudes at the bone-implant interface by orders of magnitude. Our findings are an important first step towards the optimization of the best method of mandible fracture fixation to minimize maladaptive jaw movements and create strain environments conductive to bone healing.

The 3D-Nature of the Magpie (Aves: *Pica pica*) Functional Hind limb Anatomy Revealed

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Studies on the biomechanics of the hind limb of extant ground-dwelling birds during terrestrial locomotion exemplify how studying extant animals can shed light on the abilities and behaviors of extinct ancestors. The hind limbs are thought to be primary thrust generators for the take-off of modern birds and the well-developed hind imbs in their theropod ancestry suggests that leaping capabilities may have been key also for basal birds to take to the air. However, the 3D-biomechanics of the hind limbs are poorly understood even in modern flying birds and analyses are often limited to the sagittal plane. This study explored the capacity of the hip muscles to support the take-off jump by assessing their 3D-muscle moment arms. An ethically sourced *P. pica* cadaver was CT-scanned (450kVp/225kVp; isotropic resolution: 18.2 μm) to extract bone morphology and identify joint centers and axes. Muscles were modelled as 3D-polylines spanning origin and insertion while muscle paths were obtained by mapping digitized 2D-sketches of attachments and cross-sectional data onto the bone surfaces. 3D-muscle moment arms were assessed for 15 hip muscles across the functional joint range of motion derived from 3D-skeletal kinematics of the take-off jump obtained from literature. Robust results were found by systematically considering key sources of variation in the 3D-muscle paths through a total of 446 moment arm analyses. Attribution of muscle functions was based on peak 3D-moment arms derived from that data. 13 of 15 pelvic muscles exhibited the potential to act in multiple planes and were not restricted to the sagittal plane as previous descriptions suggest. Our findings imply that a detailed understanding of avian take-off mechanics can only be obtained if hindlimb anatomy is considered in 3D. The model developed here provides the foundations for gaining more detailed understanding of take-off mechanics and providing insight into the prerequisites needed for a successful take-off leap.

Diet and Tooth Morphology of Southeast Asian Squirrels (Callosciurinae, Sciuridae, Rodentia)

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Several authors have demonstrated a relationship between diet and dental morphology in rodents. This relationship is particularly interesting for the study of fossil material because the most abundant fossils recorded for rodents are isolated teeth. The development of dietary inference models based on these fossil remains should improve our knowledge of ecological features and evolutionary trends of extinct species. Here, we explored dental morphology through geometric morphometrics (GM) with the aim of characterizing the relationship between tooth shape and diet preferences of extant squirrels (Sciuridae, Rodentia). Squirrels have adapted to very different diets and have evolved into disparate ecomorphological types, which makes them an exceptional group for studying this relationship. We focused the study on the fourth lower premolar (p4) outline variation among 57 species of the Callosciurinae subfamily (Southeast Asian tree and striped squirrels), encompassing 5 individuals per species when available. We recorded 64 points equally spaced along each tooth outline using "StereoMorph" package in R. After the digitalization, we applied an Elliptic Fourier Analysis (EFA) to the outlines and recorded the Fourier Coefficients (FCs) of first nine harmonics (36 FC, A1–D9) using "Momocs" package in R. Shape analysis and phylogenetic comparative methods were applied to the resulting data. We were able to identify the different dietary groups (omnivores, herbivores, and faunivores) in the morphometric space described by the premolar outlines. We observed that omnivore species have more disparity than herbivore ones, and both more than faunivore species. We also observed that size had a significant impact on molar shape, where smaller p4 were rounded and large p4 were more sinuous. Finally, we conclude that changes in the p4 of squirrels may be useful for studying the evolution of shape in sciurid teeth, and these results will be essential to infer ecological preferences of extinct species.

Large Scale 3D-Geometric Morphometrics Analysis of the Ruminant Bony Labyrinth

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The inner ear is the sensory system responsible for balance and hearing. It has been shown in various placental mammals (e.g., humans, cetaceans, ruminants) that its bony capsule, the bony labyrinth, fully ossifies long before birth, at around mid-gestation. After ossification is achieved, its shape and size will not change during life in placental mammals. There is a growing consensus that bony labyrinth morphology in many taxa is largely related to phylogenetic history. Published analyses, based on 3D-geometric morphometrics, also revealed a low intraspecific variability, but a clear disparity at higher taxonomic levels. In addition, when fossils are included, evolutionary trends among lineages become obvious. Here, we present the first large scale analysis (more than 150 specimens and more than 100 species) of the ruminant bony labyrinth using 3D-geometric morphometrics. This analysis encompasses 45 million years of ruminant history, and includes all extant families and tribes as well as the extinct families. Morphological characters related to the insertion and shape of the semi-circular canals or to the overall shape of the cochlea allow a clear distinction between the different families and help understand the gradual evolution of the structure.

Phenotypic Integration in Carnivores: Covariation Patterns in Species with Hypercarnivorous *versus* Generalist Diet in Feliformia

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The whole body of an organism is a complex arrangement of anatomical structures that covary to various degrees depending on developmental, functional and phylogenetic factors. Understanding these patterns of morphological integration could shed light onto the underlying mechanisms that shape biological forms. To do so, we used the Feliformia as a model group as they display a great diversity of ecology. Numerous feliforms are recognized for their role as apex predators providing a unique opportunity to explore covariations that might be specific to a highly specialized hypercarnivorous diet. High dimensional geometric morphometric techniques were used to analyze the shape of several functionally relevant structures: the skull, mandible, humerus and femur. Covariation analyses (2B-PLS) were performed on each structure accounting for allometry and phylogeny. A covariance ratio was also calculated in order to assess the degree of morphological integration between each structure. Strong covariations are expected for highly linked functional complexes such as skull and mandible. We also predict differences in phenotypic diversity and covariation patterns depending on ecological strategies (hypercarnivorous *versus* generalist species). We also predict that hypercarnivores display lower phenotypic diversity and stronger covariation for some structures implied in hunting and food processing in comparison to more generalist species. Our results highlight different degrees of morphological integration in Feliformia depending on the functional implication of the structure, with a strong covariation between the femur and the humerus. Covariations are moderately high between the skull and the mandible as well as between the skull and the humerus. Finally, our results show that hypercarnivorous species display a stronger degree of morphological integration compared to generalist species.

Intralimb Coordination and Kinematics in Elegant Crested Tinamou *Eudromia elegans* Bipedal Locomotion

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The study of bipedal locomotion in archosaurs can provide insight into the evolution of bipedality in both the Pseudosuchia and the Ornithodira lineages, and their origin in the Triassic as well as subsequent innovations. Here, we used marker-based XROMM (biplanar high speed x-ray video recordings) to investigate the three dimensional kinematics of the pelvic limb across a range of walking and running speeds in adult *Eudromia elegans* (elegant crested tinamou). We studied these palaeognathous birds to provide complementary data to detailed published studies of guineafowl and other birds' locomotor dynamics, in order to better assess the ancestral state for hind limb motions in extant birds as well as disparity in hind limb kinematics among small, cursorial, ground-dwelling extant birds. We were also able to compare our marker-based 3D-kinematics of tinamou pelvic limbs with previous kinematic data (based on markerless quasi 3D-analysis) from the literature, allowing us to determine the influence of fine mediolateral and long-axis rotations of the limb elements as part of whole limb locomotor coordination and function. In addition to a previously reported increase in flexion/extension of the hip joint with an increase in locomotor velocity, tinamous also increased the range of femur and tibiotarsus abduction/adduction. Long-axis rotations of the femur and tibiotarsus were used to modulate the positioning of the foot to accommodate the limb coordination across different velocities, as in guineafowl and other birds. For example, the tibiotarsus rotated internally around its long axis throughout stance phase; about 20 degrees during straight level walking. We also present data for other behaviors including turning and explosive leaping. Overall our findings bolster the inference that there is a fundamental pattern of 3D-pelvic limb motion in extant cursorial birds such as Palaeognathae and Galliformes that was inherited from the ancestor of crown clade Aves.

Methods for Visualizing and Comparing Force Vectors in Two- and Three-Dimensions, with Applications for Vertebrate Feeding and Locomotion

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Because many early studies of vertebrate feeding and locomotion were focused on organisms with relatively little mediolateral motion or forces (e.g., mammals), the contributions of the third-dimension were often, justifiably, ignored. Two-dimensional allowed for ease of both calculations and visualizations of joint- and ground-reaction forces, however recent advances in 3D-imaging and accompanying computational approaches have led to an increased appreciation of the third dimension. Studies of non-mammals have emphasized the importance of considering mediolateral forces. A significant drawback has been challenges in both visualizing 3D-force vectors and in comparing across different temporal and evolutionary scales. Here, we present two approaches to visualizing and analyzing 3D-force vectors in the context of multiple scales: within an individual during a gape or step cycle, ontogenetically within a species, and across multiple individuals within or among species. First, we describe a programmatic pipeline using the Python language for marrying 3D-models with dynamically generated indicators of muscle vectors and/or joint reaction forces. These indicators can be scaled arbitrarily to show only orientation or scaled proportionately to force or load to provide a visual measure of the vector's magnitude. Second, we adapt ternary plots to show 3D-vectors in two-dimensions by decomposing a 3D-vector into its relative orthogonal magnitudes. Using this visualization, we represent ontogenetic changes in the orientation of the muscles of the feeding apparatus in the American alligator as the head flattens dorsoventrally through ontogeny. Similarly, we show how muscle force vectors change across a gape cycle and how orientations of ground reaction forces vary in both reptiles and mammals during terrestrial locomotion. In conclusion, these novel 3D-visualization techniques both allow repeatability and comparison among taxa and behaviors.

Reconstructing the Cranial Morphology of the Early Archosauromorph *Macrocnemus* using Synchrotron Microtomography and 3D-Imaging

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Macrocnemus is a genus of archosauromorph reptile from the Middle Triassic of Europe and China previously assigned to the larger clade of 'Protorosauria'. While this clade has repeatedly been found to be paraphyletic in recent analyses, *Macrocnemus* is still considered a member of the clade Tanystropheidae, closely related to the extremely long-necked *Tanystropheus*. The clade is mostly characterized by elongated cervical vertebrae. However, assessing the cranial morphology of members of this clade and *Macrocnemus* in particular has been difficult due to the nature of preservation of the specimens. Most specimens have been severely flattened in either mudstones or shales. In this study, we examine one of the specimens from the early Ladinian Besano Formation in Switzerland using synchrotron microtomography, presenting the most detailed cranial study of any tanystropheid to date. We were able to obtain a wealth of new information on the skull morphology of this taxon, particularly of the braincase elements, the palate and the atlas-axis-complex, which are usually obscured by other bones or by matrix. The braincase is unfused, and in morphology shares features of both other basal archosauromorphs such as *Prolacerta*, and the more basal diapsid *Youngina*. The palatine, vomer and pterygoid bear teeth, but on the pterygoid and palatine there is a clear distinction between the anterior and posterior teeth. The more posterior teeth are more conical and bulbous, whereas their anterior counterparts are more blade-like. Together with more detailed observations of the orbital and rostral regions as well as the mandible, which were previously hard to interpret confidently, we are able to present the first 3D-skull reconstruction of the taxon. Rendering new insight in the morphology of *Macrocnemus* aids in our understanding of Tanystropheidae, and adds to our knowledge of the evolution of basal archosauromorphs as a whole.

Phylogeny and Evolution of the Musculoskeletal System of Polynemid Fishes (Actinopterygii: Percomorphacea)

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The Polynemidae are a family of primarily marine fishes with eight genera and 42 extant species. The phylogenetic allocation of polynemids within Percomorphacea, as well as its intrafamilial relationships, are poorly understood. Polynemid morphology is also largely unknown, with little osteological and almost no myological information documented in the literature. The most remarkable feature of polynemids is their pectoral fin, divided into a dorsal lobe that retains the morphology of a typical fin, and a ventral lobe composed of elongate tactile filaments. The muscles involved in such an intricate structure are duplicated, with each single muscle serving a distinct lobe of the pectoral fin. These findings along with comparisons with outgroup taxa indicate the necessity of a novel terminology for the pectoral muscles. Even more surprising is the discovery of chemoreceptor components in the massive nerves that run along the pectoral filaments, indicating that these structures have not only tactile but also tasting functions. The *adductor mandibulae* complex of polynemids exhibits unique features among percomorphaceans, such as the *promalaris* completely lateral to all other sections of the muscle. The hypothesis of a sister-group relationship between polynemids and sciaenids is supported by myological data and several new synapomorphies derived from the muscular system are proposed for the family. A phylogenetic analysis of polynemids incorporating these myological data is currently in progress. This study was funded by the São Paulo Research Foundation (FAPESP #2017/16192-7).

Functional Morphology of Piscivorous Fishes: From Teeth to Whole Body Morphologies

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It is well known that teeth are important in capturing prey. Yet, exactly how they operate in prey capture, handling, and processing is poorly understood, especially in piscivory, one of the ecological pillars of coral reef ecosystems. In particular, it is not known how the diversity of piscivorous fish morphotypes relates to realized ecological functions. There is therefore a need to understand how piscivorous fishes perform during a predation event. We investigated the functional morphology of piscivorous fishes and conducted performance-based experiments to link morphology to behavior. We investigated morphological traits such as tooth morphotypes, gape sizes, and body and fin shapes. We quantified how teeth and gape morphology influence the feeding behavior of piscivorous fishes through performance-based feeding experiments. Body and fin shape traits were also used to identify broader ecological morphotypes. We found tooth function to be more complex than their homodont morphology would suggest. Dentition-based morphotypes also displayed differences between functional feeding traits (e.g., gapes, mouth shape, protrusion). Gape sizes were found to progressively decrease anteroposteriorly, from oral to stomach gapes. The horizontal maxillary oral gape was found to be the best predictor of maximum ingestible prey size. For body and fin shape morphology, we found three distinct ecomorphotypes: benthic, nocturnal, and pelagic piscivores. We demonstrate how basic morphologies and performance-based experiments, may open broad new avenues for elucidating the nature, and thus ecological function, of piscivory.

A New Record of Quadrate and Articular in *Discosauriscus* (Seymouriamorpha) from the Boskovice Basin (Czech Republic) Based on High-Resolution X-ray Microcomputed Tomography

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The lower Permian seymouriamorph *Discosauriscus austriacus* is known on the basis of hundreds of specimens representing mostly larval and metamorphic individuals (skull length ranges from about 15 - 45 mm). The specimens are found in the lacustrine sediments and some of them have well preserved external gills. Only six specimens are found with a skull length ranging from 46 – 52 mm. Only one specimen has a skull length of about 62 mm. In the latter specimen, the ossified quadrate and articular were identified and it was interpreted to represent a postmetamorphic, probably subadult individual. The scanning of a recently recorded specimen has a skull length of about 60 mm and also shows the presence of the quadrate and articular. We present here the 3D-visualizations of the skulls of these two rare specimens. The quadrate in the new specimen has a typically triangular shape. Its ventral, condylar portion, is well identifiable. The quadrate lamina is thin and of triangular shape. The discovery of the second specimen of *Discosauriscus* with the ossified quadrate and articular supports the correct identification of these bones in the first specimen. Further, it supports the determination of the ontogenetic condition of this size category of *Discosauriscus* specimens. The previous studies showed that in all early tetrapods the ossified bones of the jaw joint start to be identified only in the postmetamorphic ontogenetic stages. The presence of the ossified quadrate and articular in *Discosauriscus* strongly supports the interpretation that these animals are not paedomorphic, but are metamorphosed, and that they had left their water environment and lived already on land. This project was supported by the VEGA grant agency, Grant number 1/0228/19.

Going Small or Growing Apart Different: Heterogeneous Patterns of Body Size Variation and Sexual Size Dimorphism in Response to Climate Warming

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Rising temperatures and shifting rainfall patterns due to climate change have altered the ecological milieu organisms exploit for resources and reproduction. Many studies have examined distributional shifts or changes in the phenology of a species due to climate change. However, few have examined changes in phenotypic traits associated with habitat exploitation. Body size is a key phenotypic trait, because many physiological and ecological attributes scale with size. Several studies have shown a decrease in body size due to warmer climates. In this study, I examined temporal variation in mean body size of the tree lizard (*Urosaurus ornatus*) from a Sonoran desert habitat in southeastern Arizona. I measured body size of males and females at Saguaro National Park from 1985 - 2018. I supplemented these data with measurements from museum specimens between 1889 - 1980. Average mean maximum and minimum temperatures significantly increased in nearly all months of the year. In addition, precipitation patterns exhibited a shift in the amount of rain falling in winter *versus* summer. Mean body size varied from 1889 - 1980, but showed no specific trend. However, a segmented (piece-wise) regression revealed a shift in body size after 1985. The temporal pattern of body size variation differed between the sexes. Male tree lizards increased in size, whereas female lizards decreased in size. In addition, the magnitude of sexual size dimorphism also increased. Population size also declined during the 1985 - 2017 period. The changes in body size were consistent with an increase in the frequency and intensity of droughts that began after 1989. The increase in male body size may represent lower intraspecific competition resulting in higher per capita food availability. In contrast, female size may be a result of early onset of reproductive maturity and annual higher mortality. These results suggest shifts in mean body size may be more complex than described in previous analyses.

Investigating Transcription Factor Hierarchies Underlying the Formation of Hair Cells *versus* Electroreceptors in the Lateral Line System

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The mechanosensory lateral line system of fishes and aquatic-stage amphibians comprises lines of 'neuromasts' over the head and body, containing mechanosensory hair cells with a primary cilium and a characteristic stepped array of microvilli, which detect local water displacement. In all lineages except frogs and neopterygian fishes (gars, bowfin, teleosts), the lateral line system also includes ampullary organs containing electroreceptors, which detect weak, low-frequency electric fields around other animals (used primarily for hunting). Both mechanosensory and electrosensory organs, and their afferent neurons, develop from cranial lateral line placodes. The presence of two different but related sensory cell types deriving from the same lateral line placode within a single organism represents a unique opportunity for studying sensory cell type specification. We previously used differential RNA-seq to generate a lateral line organ-enriched gene-set from late-larval paddlefish (*Polyodon spathula*): *in situ* hybridization for candidate genes showed that developing electroreceptors express all the transcription factor genes known to be essential for hair cell formation, plus Neurod4, which may underlie electroreceptor specification (Modrell et al., 2017, *eLife* 6: e24197). The very short paddlefish spawning season limits functional experiments, so we are using another chondrostean, the sterlet (*Acipenser ruthenus*), to investigate the expression of all transcription factor genes from the paddlefish lateral line organ-enriched gene set, and to develop CRISPR/Cas9 to test the role of selected candidates in sensory cell specification. Preliminary CRISPR/Cas9 data suggest that Atoh1, which is essential for hair cell development, is also required for electroreceptor differentiation. We are investigating Neurod4 and other top candidates in order to identify the transcription factor hierarchies underlying the formation of hair cells *versus* electroreceptors.

A Pharyngeal Component in the Premandibular Segment of the Vertebrate Head

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The segmental formation of the pharynx represents a fundamental part of the metameric organization of the vertebrate head and face. Pharyngeal pouches maintain populations of the craniofacial mesenchyme separate, and signaling from the endodermal pouches is essential for induction and pattern of serially arranged cranial skeletal elements. Segmentation of the vertebrate head is thus orchestrated around pouching of the primitive gut cavity, of which the forward expansion is thought to be limited by the oral (stomodeal) invagination during mouth formation. Recently, we ascertained the existence of the preoral gut (POG), the rostral-most foregut pouch located dorsoanterior to the forming mouth, and thus extending to the premandibular segment. The POG represents a classical, yet forgotten textbook embryonic domain, and we argue that it presents a deep deuterostome heritage of the pan-vertebrate pharynx. The developmental and evolutionary significance of the pharyngeal pouch-like component in the rostral-most, premandibular head segment will be discussed in the context of the segmental nature of the vertebrate head.

The Lever System of the Mammalian Leg Bone to Support Its Body Mass

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Extinct animals are reconstructed based in general upon skeletal information. The reconstruction of the posture makes the basis of the study of extinct taxa. However, the relationships between skeletal information and posture in the live animal is still not revealed enough even among extant taxa. To reveal the relationship between posture of a mammal supporting its own body mass, and its skeletal geometry, this study focuses on the mammalian knee joint. Mammals extend limb joints continuously with muscles called antigravity muscles to prevent collapse due to the gravity during body support. The semimembranosus muscle, one of the antigravity muscles, runs from the ischial tuberosity to the anteroproximal end of the tibia and pulls the tibia posteriorly to extend. The muscle continues working while supporting the body mass, and thus, a mechanism is required to help the muscle work. This mechanism is a lever system. The lever system can be built as a mechanical model. The torque of the lever is maximized when the angle between the semimembranosus and the tibia is at 90°; therefore, mammals keep their tibia at that angle. To test the hypothesis, mammals kept in the zoo were videotaped and the tibia angle was measured when the hind limb was supporting the body mass. The leverage efficiency (LE), which is defined as the ratio of the value of the $\sin\theta$ when 90° is equal to 1.0, was calculated from these measurement data. This study tested 18 species in 16 genera from 14 families within five orders of extant taxa. The LE range was 0.84 to 1.0 (0.9996); the highest was the reindeer, the lowest was the maned wolf. All taxa studied except the maned wolf had a LE more than 0.9, the maned wolf having the lowest LE still of 0.84. Therefore, mammals keep their knee joint where the angle at the lever system works well. Thus, the mechanical model used in this study could be a powerful tool to reconstruct mammals, especially extinct taxa, from their skeletal geometry.

Hindlimb Posture and Muscle Actions in Stem Crocodylia

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In contrast to their living descendants, crocodylomorphs from the late Triassic are thought to have been highly terrestrial, erect, cursorial, and some have speculated that they were facultative bipedal. We used musculoskeletal modeling to characterize limb posture and muscle actions in a newly discovered, exceptionally complete early crocodylomorph ("YPM sphenosuchian") and estimate how they changed within crocodile-line archosaurs. Using CT/microCT-scans and muscle reconstructions based on extant crocodylians, muscle scars, and the literature, we compared five taxa: the "YPM sphenosuchian," another "sphenosuchian" crocodylomorph *(Terrestrisuchus gracilis)*, an early Jurassic crocodylomorph *(Protosuchus richardsoni)*, a non-crocodylomorph crocodile-line archosaur *(Poposaurus gracilis)*, and an extant crocodile *(Crocodylus johnstoni)*. Our results support a phylogenetic trend toward more sprawling posture in stem Crocodylia, with increases in width of the pelvis, range of motion in hip ad/abduction, and moment arms of hip adductor muscles. Although size-normalized moment arms were generally similar among taxa, some stood out as unusual. For example, the "YPM sphenosuchian" would have had relatively little leverage for hip adduction, which suggests that it habitually held its femur in more erect positions because femoral adductors are important for body support in more sprawling postures. *Poposaurus* had very large flexion/extension moment arms, probably reflecting some combination of erect posture, cursoriality, and large body size. More broadly, we show that substantial changes in hind limb posture and muscle actions in stem Crocodylia took place during the Triassic period. By integrating these musculoskeletal models with experimental analyses of living Crocodylia, we will be able to test how locomotor function, and perhaps even unusual gaits such as bounding and galloping, evolved along the crocodilian stem.

Geometric Morphometric Investigation of Enamel-Dentine Junction Morphology in a Global Sample of Late Holocene Human Populations

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Teeth have been studied for decades and yet continue to reveal information relevant to human evolution. Enamel-dentine junction (EDJ) morphology is highly informative because it is not subject to the same extent of wear as the outer enamel surface and thus preserves more morphology. The EDJ has been well-studied in many extinct hominid taxa but has not yet been comprehensively explored in modern humans. We used biomedical microCT-scanning to investigate dental variation in a worldwide sample (N=161) of late Holocene modern humans from archaeological populations. With this extensive 3-dimensional data set, we explored global variation in EDJ morphology, focusing exclusively on the left permanent first mandibular molar. Using geometric morphometric analyses, we find significant variation in EDJ morphology across populations when both shape and size, and only shape, are considered ($p<0.01$). We also explore the potential role of factors underlying EDJ variation such as geographic dispersal, neutral and non-neutral evolutionary processes, and body size. This study substantially increases our knowledge of modern human dental variation and contributes to our understanding of dental evolution more broadly with taxonomic implications for the primate fossil record. This work was funded by the Swiss National Science Foundation, SNF Grant #CR32I3_166053 awarded to CPEZ.

A Multiscale Approach to Explore the Postnatal Development of the Largest Subterranean Scratch-digging Mammal, *Bathyergus suillus* (Rodentia: Bathyergidae)

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Subterranean mammals show a suite of musculoskeletal adaptations that enables efficient digging activity. However, little is known about the development and adaptive processes contributing to such phenotype. We studied the postnatal development of the axial, stylopodial and zeugopodial elements of a fully subterranean scratch-digging African molerat, *Bathyergus suillus*. A multiscale approach involving morpho-functional indices, bone allometry, bone microanatomy and fusion sequences was used to assess: ontogenetic morphological change, bone growth, and endochondral and intramembranous dynamics of bone formation. A total of 184 bones (humerus, ulna, femur, tibia-fibula) from 46 individuals (juveniles, subadults and adults) of both sexes were studied. Multivariate analysis showed that juveniles differs from adults, with subadults showing an intermediate skeletal shape. Juveniles show a well-developed scratch-digging phenotype, with greater external robustness (e.g., wider epicondyles), greater humeral articular surface area for elbow stabilization, and a distal position of the deltoid crest, whereas adults develop a more robust ulna, and higher stylopodial bone compactness, which increases bone resistance during digging. Microstructural features develop synchronously with endochondral bone elongation at juvenile stages, resulting in adults having thicker cortical walls to counteract their more stylized external design. Different scaling relationships for cranial and postcranial growth relative to body size exist in *B. suillus*. In general, postcranial growth is isometric, and periosteal bone formation in limbs occurs faster as compared to endochondral formation. These results are discussed in the context of the ecology and digging behavior of this species and provide important information on aspects regulating the skeletal development of this highly specialized and largest subterranean rodent.

Ontogenetic Endochondral Fore limb Growth Patterns in African Mole-rats (Bathyergidae)

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Changes in limb proportions and allometric patterns during ontogeny are important to understand heterochrony and evolution in mammals. These changes provide evidence for relationships between ecomorphology and function, but more importantly, they provide insight into the adaptive processes modulating bone phenotype throughout the differential dynamics of bone formation (i.e., endochondral and intramembranous osteogenesis). In this study, we explore the ontogenetic patterns of bone elongation in 371 specimens of African mole-rats (AMs), involving seven species from six genera. To assess the allometric relationship (ordinary least squares regression) of body mass (BM), body length (BL) and skull length (SKL) with limb bones, we used standard linear measurements of the humerus and ulna, such as humeral and ulnar length (HL, UL), diaphyseal extension of the deltoid crest (DLH), olecranon length (OL), and functional ulnar length (FUL). In general, allometries obtained from SKL comparisons showed higher allometric coefficients (ACs) when compared to scaling relationships based on BL. This indicates that forelimb elongation occurs following a pattern similar to BL, which differs from SKL. Thus, the skulls of AMs have a different growth trend as compared to the postcranial skeleton. Features reflecting endochondral growth rates of the stylopod (HL) and zeugopod (UL) were similar among AMs. Solitary AMs showed the highest and lowest ACs for DLH, while social mole-rats showed intermediate values. Similarly, social AMs showed the highest and lowest ACs for OL, whilst *Bathyergus* has the lowest AC when the allometry is based on SKL, probably due to its scratch-digging behavior, which differs from all other AMs. The lowest FUL ACs were found in social mole-rats. The results of this study are discussed in terms of the digging mechanisms, social behavior and body size, and provide important insights to understand fundamental osteogenic limb bone patterns of subterranean mammals.

Ontogenetic Allometry of Periosteal Bone Formation in Forelimbs of African Mole-rats (Bathyergidae)

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The robust skeleton of subterranean and fossorial mammals is an adaptation to resist the increased mechanical loads imposed on their limbs during soil excavation. However, it is unknown whether this increased robusticity is the result of changes in bone elongation (limb shortening) or an effect of increased periosteal bone formation (cortical thickening). In this study, we explore the ontogenetic patterns of fore limb diaphyseal thickening in seven species of African mole-rats (AMs) (N= 371), which includes all bathyergid genera, as well as chisel-tooth diggers and scratch-diggers. To assess the allometric relationship (ordinary least squares regression) of body mass (BM), body length (BL) and skull length (SKL) with limb bone features, we used anteroposterior and mediolateral diameters of the humerus (TDH, APDH) and ulna (TDU, APDU) at mid-diaphysis. Regressions of diameter showed deviations from isometry when scaled against SKL (higher allometric coefficients (ACs) when scaling was based on BL), indicating that the skulls of AMs have a different growth trajectory as compared to periosteal bone apposition of the fore limb. The highest and lowest ACs were found in social chisel-tooth diggers (*Cryptomys hottentotus* and *Heterocephalus glaber*, respectively). This shows that *C. hottentotus* reaches cortical thickening faster than other AMs, with *H. glaber* showing a slower growth. In general, anteroposterior thickening, especially the APDU, is reached more rapidly during ontogeny as compared to mediolateral thickening. These findings suggest that zeugopodial postnatal development occurs early during ontogeny, probably to increase bone resistance to bending and torsion (even among chisel-tooth diggers). The results are discussed in the light of social behavior, digging mechanisms and body sizes of these mammals, and provide important information regarding the adaptive features of the skeleton of AMs to the subterranean niche.

Morphofunctional Diversity in Toarcian (Early Jurassic) Ichthyosaurs (Reptilia: Diapsida)

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The Early Jurassic has the highest diversity of ichthyosaur taxa in the Mesozoic, yet not the highest disparity. Two lagerstätten – the Lias Group and Posidonia Shale – have preserved abundant specimens representing this diversity, however, three-dimensional specimens are rare, and testing of ecological adaptation and niche occupation has thus far been infrequent. We use μCT-scans of two complete, 3D-ichthyosaur skulls from the Lias (Toarcian) Strawberry Bank lagerstätte of Somerset, U.K. – *Hauffiopteryx typicus* and *Stenopterygius triscissus* – to reconstruct the internal cranial hard and soft anatomy. *Hauffiopteryx typicus* possesses a narrow, elongate snout, and anteroposteriorly short postorbital region and supratemporal fenestra. The adductor cavity is large providing broad areas for muscle attachment. In *Stenopterygius triscissus* the snout is broader and more robust; the postorbital region longer and supratemporal fenestra larger than *H. typicus*. A feature of Neoichthyosauria is the posterior position of the paracoronoid process on the surangular, close to the jaw articulation. We find this – coupled with extensive muscle attachment in this region – gives a high moment action on the lower jaw, allowing the jaw to be closed rapidly even in the viscous medium of water. Morphofunctional differences in jaw action, particularly movement of the lower jaw through water, is considered important in the form of the skull. The teeth of *S. triscissus* are longer and greater in diameter than in *H. typicus*, and retained in both taxa through ontogeny. We suggest that these morphologies evidence niche partitioning between the taxa. No direct evidence of diet was found in the specimens, however, the lagerstätte preserves numerous fishes and insects and has been interpreted as a ‘nursery’ for ichthyosaurs. There is evidence for similar ecologies between *H. typicus* and the crocodyliform *Pelagosaurus typus*.

Early High Disparity and Rates in the Evolution of Ichthyosaurs (Reptilia: Diapsida)

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Ichthyosaurs were a diverse clade of Mesozoic marine tetrapods; however, the evolution of the group has been understudied. Previous work shows an evolutionary bottleneck across the Triassic–Jurassic boundary, based only on a subset of genera. Here, we present a macroevolutionary analysis of ichthyosaurs using a recently published species-level dataset. We use an established disparity work-flow to explore evolutionary rates of discrete skeletal and continuous characters related to body size. Reduction of disparity across the Triassic–Jurassic boundary is less than previously thought, followed by a long-term decrease. Post-Triassic ichthyosaurs notably occupy different morphospace compared to Triassic ichthyosaurs, supporting a substantial turnover; however, resolution and preservation is insufficient to be certain on the timing and length of this. Magnitude of early high disparity is dependent on resolution but is accompanied by high initial rates of evolution in discrete characters and in body and skull size predominantly in the Early–Middle Triassic; these trends are agnostic of the time-scaling used. Our results evidence rapid shifts in morphology associated with changes in ecology early in ichthyosaur evolution, followed by relative stasis as taxa specialize within their niches. They also build the framework for future investigations of the marine incursions of major tetrapod clades.

Vascular Patterns in the Phallus and Glans of Crocodylia

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Crocodylian phalli contain a stiff and dense collagenous shaft paired with distal glans tissues that inflate during copulation, producing a range of species-specific morphologies that may play important roles in postcopulatory sexual selection. Our previous work with American alligators (*Alligator mississippiensis*) identified vascular elements that could supply blood for glans inflation, including a pair of supracrural vascular bodies at the proximal end of the phallus which are connected to blood vessels that parallel the sulcus spermaticus and open into lateral glans sinuses. Histological examination and latex injections of the Nile crocodile (*Crocodylus niloticus*) and *Tomistoma* (*Tomistoma schlegelii*) phalli and cloacal tissues show that these species also share similar vascular morphologies. Additionally, diceCT-imaging of flaccid and artificially-inflated *Crocodylus* glans tissue confirms that sulcal blood vessels connect to a complex network of anastomosing vascular cavities inside the ridge and tip regions of the glans that expand during inflation. These results, from one representative species of each of the major crocodylian families, imply that the vascular organization of the crocodilian phallus is a basal characteristic of all modern crocodilians.

How Parodontid Fishes (Ostariophysi: Characiformes) Sing with their Ribs

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Sound communication is widespread in Teleostei. While sound production has been reported for at least 100 fish families, the mechanisms that generate sound are still poorly known for most species. For instance, there are reports of a few characiform species pertaining to five families (Anostomidae, Characidae, Curimatidae, Serrasalmidae and

Prochilodontidae) producing sound, however how it is produced is only described in detail for a handful of species. In the course of exploring the mechanisms for sound production in the families Anostomidae, Curimatidae and Prochilodontidae, we observed that the sonic apparatus is more widely distributed in those families, present in most of its genera, and also that it is present in the families Hemiodontidae and Parodontidae. In this work, we describe the morphology of the sonic apparatus for the family Parodontidae. Because Parodontidae is a small family (32 spp; 3 genera) of small fishes (maximum SL 15 cm) it was used as a model for an ongoing study of this mechanism in the Characiformes. Specimens from all three genera were radiographed, CT-scanned and/or dissected for this study. The sonic apparatus seems to be similar among all the species examined, and is present only in reproductive males. This apparatus is composed of an osteological and a muscular component. The osteological component is composed of the modification of the anterior two ribs which are thickened and expanded. These ribs are connected by sonic muscles, which also run anteriorly inserting to the anterior face of the peritoneum. While not directly observed, most likely the rhythmic contraction of the sonic muscles, cause the compression of the anterior chamber of the swimbladder, causing the gas to move to the posterior chamber producing sound. Inter- and intraspecific variation is discussed.

Convergence and Constraint in Sensory Evolution in Secondarily Aquatic Sauropsids: a Preliminary Assessment

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The invasion of marine and aquatic habitats has been a recurrent theme among sauropsid amniotes, occurring potentially dozens of times independently. Sauropterygia, Ichthyosauria, Thalattosuchia, Phytosauria, and Mosasauroidea, as well as multiple clades of turtles and birds are some of the secondarily aquatic and marine clades that diversified starting in the Mesozoic. Information on evolutionary trends in the sensory structures have been analyzed within some of these clades, but have yet to be analyzed across clades. This study seeks to decipher the role of convergence and phylogenetic constraint in the evolutionary transition of sensory structures from a terrestrial to an aquatic environment. At this early stage of the project, all major cephalic sensory systems—sight, smell, hearing, and touch—will be evaluated via segmentation of CT-scan datasets of brain endocasts and peripheral structures related to the senses (e.g., inner-ear labyrinths, orbital anatomy). Lack of soft-tissue preservation in fossils requires reference to the extant phylogenetic bracket of the extinct clades. Therefore, extant sauropsids (birds, crocodilians, lepidosaurs, turtles) are used as guides to infer soft-tissue anatomy in extinct taxa, while also making reference to mammalian examples (e.g., cetaceans). Quantitative comparison of structures within the central nervous system, such as the olfactory bulbs and optic lobes will be analyzed, as will be aspects of the semicircular canals and cochlear duct of the inner ear, the olfactory region of the nasal cavity, trigeminal ganglia, neurovasculature of the snout (premaxilla, maxilla, dentary), and middle- and external-ear structures. Sensory structures also will be compared to postcranial evidence of commitment to the aquatic environment (e.g., flippers as evidence of more pelagic lifestyles). Phylogenetic and quantitative analysis will provide in an integrated approach to unravel the sensory systems of these secondary aquatic clades.

Endocranial Anatomy and Ontogeny in Ornithischian Dinosaurs Using Computed Tomography and 3D-Visualization

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Consideration of ontogeny and developmental stages is important for accurate interpretation of the fossil record, as well as for reconstructing life histories of extinct vertebrate taxa. A rich literature on the growth stages of the iconic and relatively well-represented non-avian dinosaur genus *Triceratops* has provided an example of how ontogeny may inform functional and paleoecological questions. Yet, most of these studies focused on skeletal variation of the post-crania and external cranium. Here, we present CT-based digital models of the crania and corresponding endocasts from previously undescribed individuals, including juvenile, subadult, and adult forms of *Triceratops*. Comparisons of endocasts (and, by proxy, brains) across ontogeny show marked difference in overall size, as well as increase in relative size of the pituitary fossa, and a reduction in the cephalic and pontine flexures. Such changes represent a potential source of data for growth stage classification. Additionally, several general features—olfactory bulbs, cerebral hemispheres, cranial nerve and blood vessel canals, and the bony labyrinth of the inner ear—are observed clearly in early ontogenetic stages, indicating precociality. Interestingly, similar results have been reported previously for a handful of ornithopod dinosaurs. Congruence in ontogenetic changes in the endocranial anatomy of distantly related ornithischian dinosaurs suggests a broad distribution of a typical pattern that may form the basis for structural and functional ontogenetic hypotheses for dinosaur taxa within, and perhaps outside, Cerapoda.

Correlations between Developmental, Ecological, and Evolutionary Axes of Cranial Shape Variation in Extant Crocodylians and the Pseudosuchian Fossil Record

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Phylogenetic analyses of stem and crown crocodylians have revealed that similar skull shapes have repeatedly evolved in distantly related lineages. In living species, adult skull shape has been shown to be tightly associated with dietary specialization resulting in distinct cranial ecomorphs (blunt-, moderate-, slender-snouted forms). Recently, we demonstrated that the diversity and convergence of crocodylian skull shapes is underpinned by shifts in the timing and/or rate of ontogenetic development (i.e., heterochrony) and that ecomorph specific shapes are acquired across post-embryonic development. However, it remains unknown whether similar developmental or ecological drivers may have facilitated and/or constrained skull shape throughout evolution of the crocodylian total group (Pseudosuchia). To address this gap in current understanding, we quantified skull shape in extinct pseudosuchians and compared this to our ontogenetic data for extant crocodylians to assess skull shape variation across ontogenetic, ecological, and evolutionary axes. Among extant crocodylians, the major axis of variation among adults of different ecomorphs is highly distinct from, and nearly orthogonal to, the major axis of ontogenetic variation. The fossil record of pseudosuchians displays a complex history of skull shape evolution, and quantifying the major axes of variation at different points in the phylogeny revealed strong associations with both ontogenetic and ecological axes. Our data suggest that in certain grades (e.g., basal crocodylomorphs) skull shape diversification may be driven by similar developmental processes as in living crocodylians, while in others (e.g., basal eusuchians) similar ecological pressures appear to be more important. By integrating ontogenetic development of living species with the fossil record we are starting to understand the potential mechanisms underlying the complex evolutionary history of the crocodylian skull.

The Elongated Root of the Rodent Incisor Contributes to Strain Reduction in the Mandible during Incision

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Rodents are characterized by a pair of enlarged and continually growing upper and lower incisors (diprotodonty). Diprotodonty is present in all living and extinct rodents and has independently evolved in a phylogenetically diverse range of non-rodent mammals including the aye-aye, a primate which we have previously shown to be highly convergent in skull morphology to rodents. Previous work has also demonstrated how both mechanically important variables, such as incisor cross sectional geometry, and the extent to which the unerupted internal portion of the incisor extends into the mandible, vary among rodents. This study aims to determine whether this internal portion of the incisor contributes to reducing strain in the mandible associated with the loading encountered during incision. CTs of the cranium and mandible of a sample of four rodents and the non-rodent diprotodont aye-aye, were segmented to produce models for finite element analysis (FEA). In addition, a series of hypothetical models were produced for each species with variations in the length of the mandibular incisor and presence of the incisor crypt. The results of the FEA show that strains increase as the internal portion of the incisor is shortened. This finding indicates that the long internal portion of the incisor helps reduce bending in the mandible during incisal loading, including the repetitive loadings and high forces encountered during the iconic rodent behavior – gnawing.

A Horse of a Different Color? Tensile Strength of Bones and Tendons in Sloth Limbs

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Vertebrate limb bone is a conservative biological tissue. Fundamentally, compressive and tensile strength have been observed to be generally similar across taxa despite marked variation in limb posture and locomotor patterns. However, the material properties of limb bones from species employing suspensory habits have not been formally evaluated. Sloths are obligatory in their use of suspensory locomotion and posture, thus placing their limb bones and associated soft tissue structures under routine tensile loading. It was predicted that the long limb bones of sloths will diverge from the typical mammalian pattern and show increased resistance to tensile stress/strain at the expense of lower resistance to compressive loads to failure. This hypothesis will be tested using femora and humeri from two-toed (*Choloepus hoffmanni*) and three-toed (*Bradypus variegatus*) sloths. Limb bones were excised from specimens that were frozen immediately post-mortem and thawed prior to dissection. Bone shafts were cleared of tissue, sectioned with a wet ceramic saw blade and fine sanded with wet/dry paper to remove any imperfections prior to compressive/tensile testing using an Instron machine. In addition, the fore- and hindlimb digital flexor tendons will be loaded in tension until failure to verify a secondary hypothesis that sloths possess a suspensory apparatus with loading curves analogous to those of tendons from upright ungulates (e.g., horses), thus allowing for passive support of a large portion of their body weight while inverted to conserve energy. Evaluation of tendon loading data will also help explain our previous findings of low levels of muscle activation of the digital flexors during suspensory habits. Altogether, this study will further inform the mechanisms that permit suspensory behaviors and how bone (and tendon) properties could be modified to a greater extent than previously thought possible in relation to an extremely rare behavior in mammals.

Musculoskeletal Development of the West African Viviparous Toad *Nimbaphrynoides occidentalis* (Amphibia: Anura: Bufonidae)

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Viviparity is extremely rare in anuran amphibians. So far, only about 16 species (out of a total of over 7000) 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 onward, which necessitates a functioning musculocranial system, among other things. The extent as to which the fetal morphology differs from that of free-living aquatic tadpole larvae has been unclear though. To address this we examined and described the morphology of the chrondrocranium, branchial apparatus, and associated musculature of fetuses of *N. occidentalis* representing various developmental stages and compared these with the morphology of larval *Altiphrynoides osgoodi*, its closest relative retaining a free-living tadpole. The overall structural organization of the chondrocranium, lower jaw and branchial apparatus of *N. occidentalis* is surprisingly tadpole-like. Although some muscles are reduced or fused, the musculoskeletal system does not differ substantially from that of *A. osgoodi* and other free-swimming bufonid tadpoles. However, there are marked differences in the orientation and proportions of these structures, most prominent among them a downward flexure of the cranial base, which are seemingly related to intrauterine feeding in *N. occidentalis*.

Proboscidean Cranial Musculature and the Evolution of Jaw Mechanics and the Proboscis in Elephants

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The evolution of the elephant proboscis likely coincided with lengthening of the mandibular symphysis in early gomphothere proboscideans, with secondary symphyseal shortening resulting in a remaining long, pendulous, and dexterous proboscis. The temporalis muscle in long-jawed gomphotheres has also been qualitatively described as likely producing an orthal power stroke in feeding whereas the derived vertically-oriented temporalis in extant short-jawed elephants forms a sling permitting the masseter and pterygoid muscles to produce a proal power-stroke. Here, skulls of 18 proboscidean taxa are used to quantify angle of muscular line of action in both temporalis and masseter by connecting origin and insertion centroids for each muscle. Cranial muscle anatomy is based on dissection of an adult African elephant (*Loxodonta africana*). 2D-lever arm methods are used to quantify evolutionary transformations in these muscles, the resultant, and their mechanical advantages (MA) to interpret impact on feeding and bite force. All statistical analyses show significant results ($p < 0.05$), corroborating previous hypotheses of temporalis and masseter reorientation and its effect on jaw mechanics. A positive trend is seen from lower temporalis and masseter angles in long-jawed proboscideans to higher angles in short-jawed proboscideans. An inverse relationship is seen between increased resultant muscle vector angle and decreased relative mandibular symphysis length. Muscular MA with respect to tooth row increases with increased vector angle. Correlation between increased masseter angle and its MA is statistically stronger than that of temporalis, highlighting an increased trend toward masseter use in taxa with a vertical temporalis. Most taxa with high temporalis and masseter angles and short mandibular symphyses present with greater overall MA. These shifts in jaw mechanics help implicate evolution of feeding behavior and the importance of proboscis use in extant elephants.

Epaxial and Hypaxial Distinction from the Aspect of Neuronal Development

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Classical comparative anatomy has divided the vertebrate body into dorsal epaxial and ventral hypaxial domains. This is based on the distribution of the spinal nerve which splits into dorsal and ventral rami just after merging of dorsal (sensory) and ventral (motor) roots from the spinal cord. The epaxial and hypaxial muscles are defined as muscles innervated by dorsal and ventral rami, respectively. In fishes, these muscles are divided dorsoventrally by the horizontal myoseptum running rostrocaudally, whereas in tetrapods, the septum was lost and the boundary became obscured. In general, the epaxial muscles include intrinsic back muscles, while the hypaxial muscles contain lateral body wall and limb muscles. Spinal motor neurons (SpMNs) innervating a particular muscle group make a distinct cluster in the spinal cord and require expressions of specific transcriptional factors in their development. In some muscles, however, double innervation of dorsal and ventral rami has been reported. We investigated molecular expressions in the developing SpMNs innervating the muscles in chick. The rhomboid-levator complex and serratus muscles have been classified as forelimb hypaxial muscles, because they are mainly innervated by the brachial plexus, which arises from the ventral rami and innervates the forelimb muscles. Molecular profiles of these muscle innervations were not of a limb hypaxial pattern but of a dorsal rami pattern. The finding suggests that these muscles should not be classified as limb muscles, rather that they have a character of epaxial trunk muscles. This conclusion is consistent with the mode of muscle development. Moreover, the lateral branch of the intercostal nerve which innervates external intercostal and obliquus abdominis externus muscles also contains dorsal rami-type SpMNs. Therefore, it is plausible to assume that these muscles represent either epaxial muscles in the lateral body wall or intermediate muscles between the epaxial and hypaxial muscles.

Morphological Disparity in the Middle-Ear Ossicles of Suliforms with Implications for Behavioral Ecology (Aves: Suliformes)

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Sensory systems act as filters, transducing and modifying environmental stimuli for interpretation by the central nervous system. This mediation limits available information but functions as a barrier against damage to the system. In mammals, flexibility in the middle-ear ossicular chain is theorized to limit the intensity of stimuli reaching delicate inner-ear structures. Although the columella – the auditory ossicle in birds – is known to vary greatly in size and shape, the consequences of this diversity are underexplored. Suliforms are an ecologically-diverse clade of birds that represent a model system for evaluating the functional morphology of the sound-conduction system in birds. Cadaveric avian specimens, including species from all four major suliform clades, were μCT-scanned. Middle- and inner-ear structures were reconstructed digitally using Avizo. DiceCT-data were used to reconstruct soft tissues including musculature and neurovasculature. Specimens were also dissected and photographed to visualize additional anatomy and validate CT-based interpretations. Digitally-reconstructed columellae were qualitatively compared, and morphometric analyses were performed within a phylogenetic framework. The columellar meshes were also imported and modified in Inventor for finite element modeling. Analyses support previous claims of a phylogenetic signal in columellar morphology, but disparity is greater than previously described in Suliformes. Plunge-diving sulids exhibit a "boomerang" columellar shape that is distinct from all other sampled species. This shape may confer additional flexibility to the sound-conduction system, mitigating damage during the rapid transition from air to water during foraging. Sampling of more suliforms is necessary to account for potential allometry in the middle-ear system. Additional mechanical analyses will be used to simulate the behavior of the columella when subjected to static and dynamic loads. NSF Grant DGE-1645419 to JPN.

Differences in Post-hatching Ontogeny Shaped the Diverse Cranial Evolution of Strisoran Birds

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Evolutionary changes in development were important factors in the origin and early evolution of the avian skull, yet whether these have been also important drivers of craniofacial evolution in more recent avian radiations remains unclear. Here, we explore cranial shape variation in strisoran birds, and several outgroup lineages, at the evolutionary and ontogenetic (peri/post-hatching ontogenesis) levels using geometric morphometrics and phylogenetic comparative methods. Strisores encompasses hummingbirds, swifts, and 'caprimulgiforms', a series of nocturnal, mostly insectivorous lineages. 'Caprimulgiforms' and swifts exhibit cranial traits reminiscent of juvenile birds including large orbits, flat wide skulls, and weak ossification. Nested among this radiation are the hummingbirds, with highly divergent craniofacial morphologies. While these transitions have been generally explained as feeding adaptations, evolutionary changes in development might have been important contributors generating such diversity in cranial form within a clade. Our results suggest that a combination of ontogenetic scaling (miniaturization) and heterochronic acceleration, which are possibly linked, underlie the origin of the divergent hummingbird cranial shape from a swift-like ancestral morphology. Furthermore, we did not find any evidence of paedomorphosis in 'caprimulgiforms' and swifts. Instead, a great deal of neomorphic shape change occurs during ontogeny in all these lineages, greatly departing from the plesiomorphic ontogenetic shape change displayed by palaeognathans and galliforms. Our study reveals an unexpected disparity in craniofacial ontogenesis in birds and stresses the importance of understanding the interplay between the ontogenetic and evolutionary levels in defining the patterns of diversification in vertebrates.

Linking Virchow's Law with Williston's Law: Morphological Change in the Tetrapod Skull through Bone Losses and Fusions

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During the evolution of tetrapods the number of skull bones has diminished drastically, an evolutionary trend known as Williston's Law. Two morphogenetic mechanisms can explain such pattern: the loss of ossification centers and the fusion of ancestral bones. During craniofacial development, premature suture fusions cause skull shape changes that result in head malformations, a pathological condition known as craniosynostosis. Virchow's Law describes the skull shape dysmorphies in human craniosynostosis generated by suture fusions, offering an analogous morphological model that might be extrapolated at an evolutionary scale. The skull of vertebrates achieved a wide range of morphological diversity throughout their evolution, and the fusion of bones could have played an important role in shaping this diversity. Here, we survey the literature for known instances in which loss or fusions of bones occurred, and describe its concomitant morphological change. Finally, using Anatomical Network Analysis, we explore the possibility that shape changes in the different tetrapod lineages could be explained by the morphogenetic processes by which ossification centers are lost or fused together to form single bones during development. DRG funded by grant BFU2015-70927-R. BE-A funded by grant LCF/BQ/LI18/11630002 and MDM-2014-0370.

Toe Pad and Claw Morphological Co-variation: Investigating Evolutionary and Ecological Patterns within Geckos

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Geckos' exceptional ability to cling to and climb various vertical and inverted surfaces has principally been attributed to their unique "sticky" toes. Beyond adhesive and friction-enhancing setae found in some lizard groups, gecko toe pads comprise a hierarchical, integrated suite of structures that finely modulate setal-surface contact and enable strong, repeated attachment, particularly on smooth surfaces. Roughly two-thirds of gecko species exhibit this putative key innovation, with multiple independent origins of diverse pad forms across the phylogeny. However, many geckos also exhibit claws (the ancestral lizard condition), which penetrate or mechanically interlock with a surface and create friction. Having both structures may be optimal under different substrate conditions found in nature, such as smooth leaves and rough rock. Interestingly, some padded lineages have lost or reduced their claws; others have secondarily lost or reduced both pads and claws. However, correlative relationships between these features and the ecological factors driving their evolution have yet to be evaluated. From preserved specimens, we imaged the distal aspect of the fourth pedal digit in over 100 species and quantified pad and claw morphology, including pad micromorphology via scanning electron microscopy. We assessed co-variation among morphological variables, the extent of integration between pads and claws, and the effect of microhabitat use on these structures within a phylogenetic comparative framework. Our results show correlations between the morphologies of these attachment structures, along with a strong ecological signal. For example, claw reduction was observed in arboreal species with greater toe pad area. This study provides new insights into the morphological diversity and evolutionary trajectory of this emblematic clade, and more broadly, how complex functional systems evolve within different ecological contexts.

Macroevolutionary Transformation of the Maniraptoran Manus and Insights on the Origin of the Modern Avian Hand

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The transformation of the hand from a prensile structure to a wing component across maniraptorans (including modern birds) is a key morphological transition in tetrapod evolution. Yet, it has never been studied quantitatively at a broad macroevolutionary scale. The sustained miniaturization occurring along the lineage towards crown birds suggests that this transition could be related to allometry, but this hypothesis has not been tested either. Here, we propose a new methodological approach to study the evolutionary transformation of the hand among paravians using chord length measurements of all the hand bones of a broad sample of 174 maniraptors, including 79 fossils and 95 extant birds. Specifically, we propose the transformation of traditional lengths of the manus bones to a Cartesian coordinates system to benefit from the use of Procrustes methods. Our results show a pattern of step-wise morphological change between basal, paravian and avian derived forms, with modern birds showing a strikingly low disparity compared to stem taxa, where the morphological changes are driven by the reduction and finally loss of phalanges. Furthermore, we show that significant allometry characterizes hand shape variation in non-avian maniraptorans and basal avians, but manus size and shape are seemingly decoupled in ornithuromorphs, including the radiation of modern birds. This describes the scaling of the hand morphology along the neognathan phylogeny, which is probably anticipated in ornithuromorphan birds. These results suggest that the interplay between functional and developmental constraints shaped the macroevolution of this region of the forelimb along maniraptoran evolution.

The Osseous Labyrinth of *Cyamodus* (Sauropterygia: Placodontia) Shows Distinct Morphological Variation between Closely-Related Species

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With at least four valid species, *Cyamodus* is the most speciose genus of Placodontia, a clade of durophagous, often heavily-armoured marine reptiles known from the Middle and Late Triassic. *C. rostratus* and *C. kuhnschnyderi* both occur in the Upper Muschelkalk of the Germanic Basin and share strikingly similar cranial morphologies. However, their dentition differs somewhat, with *C. kuhnschnyderi* having relatively larger teeth and only two palatine teeth (*vs* three in *C. rostratus*). This may indicate different feeding ecologies and lifestyles in these closely-related species, resulting in differing inputs on their sensory systems. Recent work has found that sauropterygians with different modes of life exhibit disparate semicircular canal geometries in the osseous labyrinth, the bony housing of the vestibular organ which governs, among other things, the sense of balance and orientation. While observations of sauropterygian labyrinths have shown broad ecomorphological correlations (e.g., semi-aquatic *vs* pelagic taxa), it has yet to be determined whether differences can be detected at a finer phylogenetic scale. To address this, the holotype crania of *C. rostratus* and *C. kuhnschnyderi* were μCT-scanned and the osseous labyrinths were virtually reconstructed. Semicircular canal geometries are distinctly different between the two species. *C. kuhnschnyderi* follows the plesiomorphic condition seen in the placodont *Placodus* and other Triassic sauropterygians, i.e., dorsoventrally compressed and anteroposteriorly elongate vertical canals. In contrast, *C. rostratus* has an anteroposteriorly compressed labyrinth, with tall, thick vertical canals and a more rounded general appearance, a morphology reminiscent of that seen in obligate-aquatic plesiosaurs. This indicates that function appears to influence semicircular canal geometry significantly in Placodontia, even on the interspecific scale.

Quantitative Assessment of Cellular Composition of Avian Brains: Implications for Evolution of Bird Intelligence

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Using the isotropic fractionator, we determined numbers of neurons and glial cells in major brain divisions in 125 bird species representing 11 avian orders. This unique data set allowed us to establish and compare cellular scaling rules among major bird clades and between birds and mammals. Brains of birds belonging to distantly related clades differ in relative structure sizes, neuronal densities, neuronal numbers and allocation of neurons into brain compartments. While the relative proportions of major brain structures seem to reflect behavioral and perceptual specializations, neuronal scaling rules are rather conservative and strongly phylogeny-dependent. Songbirds, parrots and owls share high neuronal densities and disproportionately large numbers of neurons in the pallial telencephalon. In contrast, birds representing basal lineages, such as paleognathous and galliform birds, have lower neuronal densities, a proportionally smaller telencephalon, small telencephalic and dominant cerebellar neuronal fraction.

Brains of birds situated phylogenetically in between these two groups, such as pigeons or birds of prey, exhibit intermediate characteristics. Compared to mammals, avian brains are built in a more economical, spatially efficient way; even the lowest neuronal densities observed in brains of basal birds are equal to or higher than the highest densities found in homologous brain regions in mammalian species investigated so far. Songbirds and parrots feature extremely high neuronal densities and have a high proportion of neurons allocated in the pallial forebrain. In fact, numbers of pallial neurons in large-brained parrots and songbirds (especially corvids) equal or exceed those found in primates with much larger brains.

Dinosaurs Inherited Highly Variable and Extended Ontogenetic Pathways from their Closest Relatives and Subsequently Lost this Pattern

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Newly recovered skeletons of early dinosaurs and their closest relatives have revolutionized insights into their paleobiology, diversity, and character evolution. With a growing sample of early dinosaurs and increasing evidence that early dinosaurs and their closest relatives had complex ontogenetic patterns, we critically examined ontogenetic variation in Dinosauria and their immediate outgroups. We identified ontogenetically variable characters within the postcrania of species-level taxa of dinosaurs and their closest relatives. From these observations, we implemented a new method of examining ontogenetic pathways (using non-metric multidimensional scaling) combined with relative body size (i.e., femoral length) to estimate intra- and interspecific ontogenetic trajectories. We recovered ontogenetic pathways of these taxa, extending from smaller individuals with immature ontogenetic character states to larger individuals with more mature ontogenetic character states, although the sequence of character state transitions may be variable. Importantly, most ornithischians, tetanuran theropods, and Jurassic sauropodomorphs do not follow the common ontogenetic pathway of early dinosaurs and their close relatives. In these taxa, the character states that appear later in ontogeny in early dinosaurs are typically absent, and there are comparatively fewer changes throughout growth. These results have a number of novel paleobiological implications including: 1) ontogenetically variable characters states should not be used to differentiate early dinosaur species; 2) early dinosaurs and their close relatives had substantially different growth strategies from other reptiles and later dinosaurs; 3) these ontogenetic pathways evolved rapidly early in the Mesozoic. Careful documentation of the ontogenetic changes in early dinosaurs has led to a better understanding of character transformations and, hence, a better grasp on the relationships of early dinosaurs.

A Review of the Vocal Species of Characiformes (Teleostei: Ostariophysi)

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Sound production mechanisms have been observed in over 40 orders and 100 families of Teleostei. Among characiform fishes, such mechanisms are described for representatives of four families only: the croaking tetra (Characidae), the branquinhas (Curimatidae), the jaraquis and the curimbas (Prochilodontidae), and the piranhas (Serrasalmidae). Based on data from the literature and reports from fishermen, a prospective revisionary study based on collection specimens was carried out. Modifications comparable to those reported for the sonic apparatus of *Potamorhina*, *Semaprochilodus* or *Serrasalmus* were investigated with the aid of x-ray images or dissection of representatives of the above-mentioned families plus representatives of the other characiform families. Preliminary results indicate the presence of modifications of the *obliquus inferioris* and the anteriormost ribs homologous to the sonic apparatus of the Curimatidae and Prochilodontidae also in members of Anostomidae, Hemiodontidae and Parodontidae. Such modifications had been previously observed, but have been mistakenly interpreted by different authors as unique features for (Curimatidae+Prochilodontidae) or *Megaleporinus* (Anostomidae). So far, a sonic apparatus was not found in representatives of Chilodontidae, although members of that family present an expanded rib associated to the fifth vertebral centrum, as observed in the Curimatidae, but they seem to lack any distinctive sonic muscles. The present results also show the number of sonic species is largely underestimated within each family. Modifications were detected in at least five genera of the Anostomidae, seven of the Curimatidae, all genera of the Prochilodontidae and Parodontidae, and both species of *Anodus* (Hemiodontidae). In a phylogenetic context, our results suggest that the origin of such sonic apparatus observed in Anostomidae, Curimatidae Hemiodontidae and Prochilodontidae may be unique, secondarily reverted in the Chilodontidae, possibly associated to the distinct swimming orientation of those fishes. Additionally, the sonic ability observed in those families could also be homologous to the highly derived condition of the Serrasalmidae, and therefore a synapomorphy for a less inclusive group of the Curimatoidea, excluding the Cynodontidae.

Does Prenatal Development Support a Single Origin of Laryngeal Echolocation in Bats?

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Bats are phylogenetically divided into two major groups, Yangochiroptera and Yinpterochiroptera. Laryngeal echolocation is observed in the Rhinolophoidea clade of Yinpterochiroptera and all species of Yangochiroptera. Laryngeal echolocation is not found in Pteropodidae, a member of Yinpterochiroptera. To date, it has been highly disputed whether laryngeal echolocation was acquired by the common ancestor of all extant bats and was subsequently lost in Pteropodidae, or it evolved independently in Yangochiroptera and Rhinolophoidea. The cochlea in bats has attracted much interest, given its function and performance in receiving echolocation sounds, and the relative size of the cochlear canal in the skull at adulthood has been regarded to reflect sensitivity to high-frequency sound. Some researchers investigated the prenatal cochlear development of several species with X-ray radiograph and reported that the relative size of the fetal cochlear canal of Pteropodidae is of similar size as in Rhinolophoidea and Yangochiroptera whereas its cochlear growth rate decreases postnatally while the growth rate of the whole skull is maintained. Based on the apparent resemblance of fetal cochlear size among bats, it was proposed that the common ancestor of extant bats was possibly a sophisticated echolocator and that laryngeal echolocation emerged just once, leading to the assumption that "ontogeny recapitulates phylogeny". However, based on our extensive study of the prenatal cochlea of more than 30 bat species, this previous argumentation that the cochlear development of Pteropodidae is comparable to that of laryngeal echolocators does not hold. We demonstrate that early-stage fetuses of laryngeal echolocators were not sampled broadly enough by previous investigators and that the resulting interpretations considerably underestimate their cochlear growth. Describing various aspects of the cochlear development, we address the controversy on the origins of laryngeal echolocation.

Development and Dynamics of the Pharyngeal Dentition in Sturgeon

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Teeth represent a key evolutionary novelty of vertebrates. The dentition of the majority of extant vertebrates is present in the oral cavity associated with the jaws and palate and/or in the pharyngeal cavity associated with the last pharyngeal arch. The ancestral condition of the vertebrate dentition is, however, considered to be presence of teeth through the entire oropharyngeal cavity. Contrary to the proposed condition, the dentition of sturgeons is unique. It is significantly reduced – teeth are present only in larval stages and juvenile forms on the jaw margins, on the palate and in the anterior part of the pharyngeal cavity. Adults are completely toothless. This project aims at a developmental description of the pharyngeal dentition of sturgeon (*Acipenser ruthenus*), a detailed description of the development of individual tooth fields, experimental perturbation of addition and replacement of teeth within these tooth fields, and dynamics of tooth cycling. Although sturgeons are unique from the point of view of localization of their dentitions, their phylogenetic position as an early diverged ray-finned fish clade may account for uncovering the proposed dental characteristics of ancient vertebrates.

Development in a Domestication Framework: Morphological Change from Fowl to Chickens

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Years of research in domestication have revealed that "wild to domesticated" transition involves vast morphological variation in a short time span. For the most part, this variation has been studied from a genomic-genetic perspective, whereas a developmental or evo-devo focus on anatomical structures has been largely neglected. We examined this subject by comparing developmental series of red junglefowl (the ancestor) and four chicken breeds (white leghorn, Hubbard, shamo, and ukkokei). We focused on particular developmental "windows" and investigated changes associated with the great morphological diversity of chickens. We compared sequential morphological events, testing for convergent stages, such as the controversial "phylotypic stage" and stages where ontogenies diverge, as well as looking for variation in the timing of developmental sequences (heterochronies). By comparing embryos with a standardized method to characterize ontogenetic series (SES), we found relatively few heterochronic changes in the development of red junglefowl and chicken breeds. The changes identified, however, are related to the formation of integument, skeleton, somitogenesis, and heart. For instance, by comparing the number of somites in organogenesis, we found that white leghorn embryos develop the heart earlier than fowls and other breeds. At the phylotypic stage, we found no clear differences, except in red junglefowl embryos, where the pineal gland is present but absent in chicken breeds. In spite of much adult diversity, our analyses reveal conservation during development, and the variation found may be related with the life mode of wild *versus* domesticated forms.

A New Record of the Extinct Tusked Walrus (Carnivora: Odobenidae) from the Early Pliocene of Japan Reveals their Unknown Paleoecology

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The late Miocene and early Pliocene are important epochs for the evolution of the walruses because they shifted their feeding strategies from piscivory to durophagy during those epochs. Recently, a new fossil of a pinniped was found from the latest Miocene to early Pliocene of Japan in the Northwest Pacific. This specimen (NMNS-PV 24611) preserves almost all the skeletal bones, except for cervical vertebrae and a few others. NMNS-PV 24611 is identified as an adult male walrus in the family Odobenidae by the following features: the greater trochanter of the femur is lower than the femoral head, the lesser trochanter is not developed, the neuropore of the lumbar is large in diameter, the posterior process of the astragalus is well developed medioventrally, epiphyses of each of the bones are almost fused, and the specimen has an exceedingly long baculum. In addition, we newly discovered a tusk-like, upper canine from the same individual in this locality. The length of the tusk is 21.2 cm and the radius of arc along its posterior side is 52.4 cm, indicating that NMNS-PV 24611 belongs to the extinct walrus, *Ontocetus* sp. This taxon is well known from the Pliocene of the North Atlantic realms, but mostly known by fragmented isolated teeth and bones, which is the reason that the paleoecology of this taxon has not been clearly revealed. NMNS-PV 24611 is the only specimen consisting of almost the entire skeleton and it is therefore morphologically and ecologically informative. We compared the new fossil to the skeletons of the extant walrus (Odobenidae) and that of the Stellar sea lion (Otaridae) to reveal the paleoecology of *Ontocetus* sp. The robustness of the forelimb of *Ontocetus* sp. suggests that it was used more frequently than in the extant walrus. This indicates that *Ontocetus* sp. had a behavioral ecology more closely like that of sea lions, and accordingly suggests that there was stronger intraspecific male aggression as compared to the extant walrus.

Shape Change Throughout the Body of the Tongue during Lapping in Small Carnivorans

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In mammals that lap during drinking, the tongue transports fluid into and through the oral cavity. Like all other oral behaviors involving the tongue, lapping is performed with only a partial reliance on an external bony support system, the hyoid. Rather, the tongue is able to engage in complex movements because it functions as a muscular hydrostat. In muscular hydrostats selective contraction of intrinsic and extrinsic muscle fibers produce movements and deformations of the tongue. The objective of this study is to characterize tongue movements and deformations in three-dimensions relative to timing and phase parameters of the gape cycle during drinking in small carnivorans using marker-based XROMM (X-ray Reconstruction of Moving Morphology) with additional beads implanted in the body of the tongue. The omnivorous striped skunk (*Mephitis mephitis*, N=2) and raccoon (*Procyon lotor*, N=2) as well as the carnivorous ferret (*Mustela putorius*, N=2) were used as a model for rhythmic lapping while drinking a bariumized broth. During rhythmic drinking, the middle and posterior tongue underwent the most variation in length change in ferrets and skunks, while raccoons showed more individual variation. Maximum tongue length occurred just before maximum gape, i.e., during jaw opening, in all but one individual. In one skunk, maximum tongue length occurred just after maximum gape, i.e., during jaw closing. Minimum tongue length occurred near minimum gape in all individuals. In ferrets and raccoons, the posterior tongue underwent more variation in width than the anterior tongue, while skunks were the opposite. These results provide preliminary insight into how the tongue functions as a muscular hydrostat in order to perform complex oral behaviors. This project was supported by grants from Ohio University Student Enhancement Award and National Science Foundation (USA) grants (DBI-0922988 and IOS-1456810).

A New Paradigm for Pharyngeal Tooth Formation?

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As a corollary to the 'modified outside in' hypothesis about the evolutionary origin of vertebrate teeth (Huysseune et al., 2009, J. Anat. 214: 465-476), we previously hypothesized that the development of, allegedly endoderm-derived, pharyngeal teeth in teleost fish requires ectodermal contribution or signaling. This may have been facilitated by ectoderm invasion via the pharyngeal pouches. Here, we examine the development of pharyngeal teeth in the zebrafish (*Danio rerio*) in light of the above hypothesis, using transgenic and mutant lines, by perturbing pouch morphogenesis, and by interfering with signaling pathways. We show that (1) the epithelial component of pharyngeal teeth (the enamel organ) is derived from medial endoderm located posterior to the sixth pharyngeal pouch (P6). Still, (2) dental epithelial morphogenesis starts only after P6 endoderm has made contact with the ectoderm, and (3) invariably only after a layer of periderm-like cells have covered the odontogenic endodermal epithelium. Both, P6 contact with ectoderm, and the presence of periderm-like cells, are required, albeit not sufficient, to elicit pharyngeal tooth formation. Teeth form prior to opening of the pouches into gill slits, and late invasion of periderm through the gill slits does not contribute to formation of first-generation teeth. Signaling pathways that perturb tooth formation (Fgf and Hh signaling) do not affect P6 contact with ectoderm or spreading of periderm-like cells in the pharynx, nor does perturbation of delta/notch, ectodysplasin or Wnt signaling. Taken together, a new paradigm for pharyngeal tooth formation in zebrafish appears to emerge: three rather than two tissue layers interact to produce a tooth - a periderm-like epithelium, endodermal epithelium and (neural crest-derived) mesenchyme. Supported by Ghent University Research Fund (n° BOF24J2015001401) and by the Czech Science Foundation (17-14886S).

Acoustic Communication and Olfaction in the Pygmy Hippopotamus *Choeropsis liberiensis*

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While communication and senses are well documented issues in cetaceans, very little is known about these questions in hippopotamuses, their closest living relatives. The modern family Hippopotamidae includes only two extant species: the common hippopotamus (*Hippopotamus amphibius*) and the pygmy hippopotamus (*Choeropsis liberiensis*). Few studies document communication cues in *H. amphibius*; however, virtually nothing is known about acoustic repertoire or olfaction in *Choeropsis liberiensis*. The purpose of this ethological and morphological study is to explore olfactory and acoustic communication in Hippopotamidae. The ear region of *C. liberiensis* is here described in detailed including the auditory bulla structure, middle ear ossicles, and structures associated with the cochlear canal, innervation and irrigation of the cochlea. These detailed morphological observations are put into perspective with vocalization recordings and behavioral audiogram of captive *C. liberiensis*. The morphology of the cribriform plate of the ethmoid bone of *C. liberiensis* is also described for the first time (surface, shape, number, size and distribution of foramina) and provides a first picture of the peripheric olfactive innervation in this taxon. The impact of semi aquatic lifestyle on auditory and olfactory abilities of the pygmy hippopotamus is finally discussed.

Exploring Morphological Integration in the Pool Frog, *Pelophylax lessonae* (Amphibia: Anura), from Different Climates

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Morphological integration in the pool frogs, *Pelophylax lessonae* (Camerano, 1882), was explored from places with different climates: Latvia (n=41; annual mean temperature 5.3 °C, collection points) and Ukraine (n=138; annual mean temperature 7.4 °C). A species' distribution model (SDM, Maxent, WorldClim, Hijmans et al., 2005, Int. J. Climatol. 25: 1965–1978) was used to assess potential habitat suitability (HS). The resulting SDM shows that frogs in Latvia are subjected to less favorable (HS=0.46) environmental conditions (in bioclimatic terms) in comparison to those in Ukraine (HS=0.56). Phenotypic characteristics (relative length of the tibia (T), tarsus (Cs), and calcaneal tuber (Cin) tend to be smaller in the Northern populations (Statistica; Nekrasova et al., 2005, In: Herpetologia Petropolitana, Ananjeva N. & O.Tsinenko (eds.): 77-79). Moreover, the greatest coloration polymorphism and the largest number of anomalies were found for Ukraine. Considering the hypothesis that the evolutionary changes presumably may first affect males (Geodakjan, 1965, Probl. Inf. Trans.1: 105–113), only male specimens were included in the analysis. The overall level of inter-correlations among frog traits was measured using the variance of eigenvalues (Pavlicev et al., 2009, Evol. Biol. 36: 339-353) estimated in a principal component analysis (PCA). However, if the structure of a dataset is modular, with two or more different groups of strongly co-varying traits, then variance will be distributed more evenly across a number of principal components with low eigenvalue variance. In such a way, the eigenvalue variance provides a measure for comparison of the relative integration or modularity (Goswami & Polly, 2010, In: Quantitative Paleontology, Alroy & Hunt, eds, Paleontological Society Special Publications, pp. 213-243). The results show that for Ukrainian specimens the independent variance (77%) was totally concentrated in PC1, whereas for the Latvian specimens it was distributed between PC1 (70%) and PC2 (14%). Shifts demonstrated in phenotypic integration are related to environmental changes (Goswami et al., 2015, PNAS 112: 4891-4896). Our findings support this notion that more research is needed, particularly in terms of the amphibians' adaptation to climate change.

Morphological Peculiarities of Northern Marginal Populations of the Invasive Fish Species *Perccottus glenii* and its Registered Maximal Size in Latvia

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The invasion of the fish species, *P. glenii* Dybowski, 1877, in Latvia has been recorded since 1974. According to our observations and the results of GIS modeling (SDM, Maxent), *P. glenii* can seriously compete with both local fish (predators: perch, pike) and amphibians (*Bombina bombina*, etc.). Moreover, the SDM correlation level (r=0.64) between *P. glenii* and *B. bombina* indicates a possible expansion in similar habitats (Pupina et al., 2018, J. Env. Res. Engin. Manag. 74: 79-86). At the same time, over a period of 50 years, populations of *P. glenii* can develop specific morphological features, especially under conditions of human impact. Having analyzed 205 fish from 6 reservoirs in Latvia, we came to the conclusion that individuals with the largest body length (L) are found in urban reservoirs (pollutants may be having an effect): L=144 mm (76-308, n=21, juveniles are fewer in numbers), M (weight)=76 g (5-694), but in natural reservoirs L=111 mm (66-171, n=184), M=20 g (4-76) (no sexual dimorphism discovered, ANOVA, Statistica). Also interesting is the fact that the smallest water bodies (up to 3.4 ha) were found to have the largest fish L=142 mm (76-308), but in the largest water bodies (26 ha) there are more juvenile fish, as they provide better conditions for successful breeding. After reaching the size of 120-130 mm, there is a strong increase in body mass and it increases with growth, especially in urban areas. Females in both types of water bodies outnumber males (ratio 2:1). *P. glenii* reached its maximal registered size in marginal northern populations in Latvia in a human impacted environment: Lmax= 308 mm, Mmax=694 g (female, Trikarta lake, Daugavpils, 2015.11.05). The study was partly supported by the Latvian-Ukrainian project "The Ecological and Biological Triggers of Expansion of the Invasive Fish, Chinese Sleeper (*P. glenii*), in Eastern Europe". We thank Daugavpils University, Ministry of agriculture and Rural Service (Latvia) for cooperation.

Metabolic and Environmental Factors Shaping the Morphology of Respiratory Turbinates in Mammals and Archosaurs

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Respiratory turbinates in mammals and birds act to reduce heat and water loss via temporal counter-current exchange. This is especially important to endotherms with high ventilation rates, but would also be of adaptive value in cold and/or dry habitats, or during a global hypoxic event. Did respiratory turbinates evolve in response to elevated metabolic rates or extreme environmental pressures? Our comparative study of >150 species of mammals and birds reveals that respiratory turbinate surface area (RTSA) scales isometrically with body mass (range = 2.6 g – 2,000 kg) in both endothermic taxa, but is on average three times greater in mammals than in birds. Complexity of rostral turbinates in birds is highly variable, but experimental data from *Gallus* suggest that they do not contribute much to heat exchange. There is a strong phylogenetic signal in RTSA scaling, but no clear effect of habitat (arid/mesic, tropical/temperate). RTSA residuals correlate significantly with residuals of field metabolic rate in mammals (n=10), but not in birds (n=12). No correlation is apparent with residuals of basal metabolic rate in either birds (n=31) or mammals (n=38), or aerobic capacity in mammals (n=9). Until a larger sample size becomes available, it is impossible to conclude that metabolic signals were a selective factor behind the origin of respiratory turbinates. An alternative hypothesis argues that respiratory turbinates appeared in response to a precipitous drop in atmospheric oxygen levels across the Permo-Triassic boundary, or during the subsequent global hypoxia of the Mid-Late Triassic/Early Jurassic. Extant endotherms adapted to altitudinal hypoxia do not exhibit greater RTSA compared to their lowland relatives. Neither do extant ectothermic archosaurs raised in chronic hypoxic conditions show phenotypic plasticity in their internal nasal capsule morphology. Our data, therefore, do not support the "hypoxia hypothesis" behind the origin of respiratory turbinates.

Launch Mechanics of *Quetzalcoatlus* and Other Large Pterosaurs: A Test of Three Hypotheses

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There are three main hypotheses about how large pterodactyloids may have launched themselves from the ground: (1) a running takeoff in bipedal posture, (2) a standing takeoff in bipedal posture, and (3) a standing takeoff in quadrupedal posture, powered almost entirely by the fore limbs. Manipulation of fossils at the UT Austin Vertebrate Paleontology Laboratory enabled us to test these hypotheses. (1) Thrust from the legs during running must exceed stalling velocity, but wing stroke amplitude, which with wingbeat frequency determines the thrust of the wings, is limited by shoulder height, body size, and wing length. Because wing length is positively correlated with body size (and wingbeat frequency is negatively correlated), large pterosaurs could not have achieved a stroke reaching 40° below the horizontal (considered minimally effective for thrust) without leaping. So a simple running takeoff is unlikely. (2) The proximal hind limb segments of most large pterosaurs were nearly as long as the fore limbs, and each set of bones was three times the gleno-acetabular length. The erect parasagittal hind limbs, proportionally longer relative to body length than those of herons and egrets, needed to effect a wing-assisted jump to bring the animal to approximately three hip heights above the ground to enable a wing stroke to reach 40° below the horizontal. This appears possible, so (2) is plausible. (3) When the humerus is laterally extended, rotation effecting retraction of the forelimb is prevented by a bony stop at the deltopectoral crest. To retract the forelimb for a quadrupedal launch, it must be supinated at least 135°, and thrust must be provided by a sudden extension of the elbow and wrist joints, for which no adequate musculature is known. Hypothesis (2) appears to be the only plausible one.

What Can Wing and Girdle Shape in Birds Tell us about the Flying Ability of the Hoatzin?

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The hoatzin (*Opisthocomus hoazin*) is a strictly folivorous bird with a unique digestive physiology. Due to its foregut fermentation, the crop is hypertrophied causing modifications of the scapular girdle. It has been hypothesized that this could have functional implications by greatly reducing the sternal carina, thus reducing the insertion area for the flight muscles. However, this hypothesis remains to be tested. We quantified the morphology of bones that are functionally important during flight: the sternum, the scapular girdle, and the humerus. To do so, a 3D-surface geometric morphometric study was performed on these bones for 59 species of birds with different locomotor abilities and diet. Morphological differences in relation to diet and flying ability were explored using a principal component analysis, multivariate analysis of variance, and regressions taking into account the phylogeny. Our results show morphological differences for the bones of the scapular girdle depending on the type of flight. No relationship was found between the hoatzin metabolism and its flight type and the shape of each bone, even when body mass and phylogeny were taken into account. Considering all bird species, the shape of the scapular girdle of birds seems a very good indicator of flight adaptations, its shape distinguishing good and poor flyers. When focusing on the hoatzin, the shapes of its bones are not so different from the other birds, and resemble those of poor flyers. Bone shape of the wings and girdles can be used to infer flight type. Using these data, future analysis will be done on bone shape of extinct species closely related to the hoatzin in order to better understand the locomotor evolution of this clade.

Kinematics of Wading Birds During Terrestrial Walking *versus* Wading Illustrate a Novel Gait Transition

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When moving between terrestrial and aquatic habitats, animals must adjust their locomotion to accommodate physical changes in buoyancy, drag, and substrate characteristics. Many species will shift from walking on land to swimming when in water. However, many species do not change their locomotor mode between land and water and, instead, use walking in both environments. Species such as turtles and salamanders walk while fully submerged, showing locomotor patterns impacted by differences in buoyancy between habitats. However, a diverse range of animals engage in wading behaviors, in which their limbs move through the water, but the body is partially above the water surface. We evaluated how locomotor kinematics are impacted by changes in water depth during wading by filming the locomotion of Chilean Flamingos (*Phoenicopterus chilensis*). We predicted that locomotor kinematics would be most similar between land and deep water; however, kinematics would differ for intermediate depths in which birds would use high step heights and short stride lengths to step over the water surface and, thereby, avoid drag. Additionally, as water depth increases, we predicted that birds would decrease stride velocity, and the head and neck would move posteriorly towards the body center of mass. Our results indicate that wading birds do adjust their limb and body movements as they wade through different water depths, shifting from stepping up and over the water surface in intermediate water depths, to dragging the limbs through deeper water once stepping above the water surface becomes intractable. Our study sheds light on the potential mechanisms that long-legged animals may use to overcome the challenges of transitioning between terrestrial and aquatic habitats.

Morphological Diversification of the Skull in Marsupial Frogs (*Gastrotheca*)

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Recent broad-scale studies have investigated the morphological evolution of vertebrate skulls using high-dimensional shape data, and these undertakings have confirmed that a combination of phylogenetic history, allometric scaling, and ecological or functional parameters influence the diversification of cranium shape. These expansive studies often suffer from sparse taxonomic sampling and restricted quantification of intraspecific variation, which has limited our ability to disentangle the complex mechanisms responsible for generating the macroevolutionary patterns of shape variation. We hypothesized that by investigating the diversification of the skull in a single, diverse genus with nearly complete taxon sampling and measures of intraspecific variation, we could attain more informative estimates of the relative influence of ancestry, ontogeny, allometry, and adaptive selective pressures. To test this hypothesis, we examined skull variation within the Pouch-brooding Marsupial Frogs (*Gastrotheca*). The 70 species within this genus are distributed across diverse macrohabitats, including the Atlantic Forest of Brazil, Amazonian lowland forest, montane forest, and high-elevation Andean grasslands. Adult body size ranges from less than 30 mm to greater than 90 mm snout-vent length. Additionally, species within *Gastrotheca* have transitioned between complex and simple life cycles multiple times, rendering the group a unique system to test for the influence of life history variation on cranial anatomy. Using computed tomography and three-dimensional geometric morphometrics, we quantify skull variation across 65 species and access the potential mechanisms underlying the morphological diversification of marsupial frogs. We also conduct sensitivity analyses to test how incomplete taxon sampling in *Gastrotheca* changes the estimates of phylogenetic signal, allometry, and influence of ecology on skull shape.

Morphofunctional Background of the Bat Flight Emergence

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A key problem of evolutionary biology is the fitness of transitional forms in the process of habitat change. The emergence of the bat locomotor model is one of the most intriguing cases, especially since paleontology has not yet shown a transitional stage between a quadrupedal and flying mammal. Based on the study of the morphology of treeshrews, colugos and bats, a functionally reasonable sequence of morphological transformations that were to occur during the formation of the flapping flight was constructed and analyzed from initial preadaptations to advanced specialization. The transition of the limb action from the parasagittal plane to the frontal one is regarded as the key event. It could occur in animals combining gliding with a quadrupedal running up thick tree trunks. The formation of flying membrane and digits elongation increased fitness like in colugo. Echolocation is the second key for bat success. It was modeled based on the ecomorphological analogy with a unique arboreal blind rodent *Typhlomys*, which uses echolocation for orientation on tree branches. The resultant portrait of the ancestor of bats represents a dweller of mature forests, combining gliding from tree to tree and running up the trunks, and searching for food in the crown branches. For orientation in the dark, it uses echolocation, but (unlike *Typhlomys*) the vision is not previously suppressed. The development of the flying membrane is supplemented by the increased up and down mobility of the limbs. The scapulae can alter position from parasagittal to frontal. The clavicle is strong and firmly articulated with the sternum to support the scapula. The acetabulum loses the dorsal rim limiting the thigh elevation. The distal limb elements are elongated, but the claws remain well developed and have sharp curved tips to stick into the bark. This set of osteological features allows searching for transitional forms in the fossil record. The work was supported by the RFBR 17-04-00954-a.

Establishment of Ontogenetic Sequences for Ibero-Armorican Titanosaurs and their Implications for Phylogenetic Analysis

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Knowledge of sauropod postnatal ontogeny has greatly increased in recent years based on histological analysis. However, there is little information about how the acquisition of some morphological characteristics occurs throughout development. Understanding trends of character changes in long bones of titanosaurian sauropods during ontogeny is important for proposing more comprehensive growth models for the appendicular skeleton. The current hypothesis suggests similarities between long bones of early juveniles and adult individuals. The Campanian-Maastrichtian Konzentrat-Lagerstätte of Lo Hueco (Cuenca, Spain) has yielded a broad sample of titanosaur appendicular remains, some of them articulated with partial skeletons. Two titanosaur main morphotypes of appendicular elements have been identified in the sample, Morph I, which is related to *Lohuecotitan pandafilandi*, and Morph II that is not, for the moment, related to any other Ibero-Armorican form. The presence of juvenile specimens in the sample allows testing the acquisition of morphological features during the ontogeny of appendicular bones in two different, synchronous and sympatric titanosaurs. We use two methods based on cladistic analysis and Ontogenetic Sequence Analysis in order to describe, for the first time, morphological changes in ontogenetic sequences of Ibero-Armorican titanosaurs. These ontogenetic sequences also permit us to evaluate the impact of development in the coding of some morphological characters generally used in sauropod phylogenetic analyses.

A Niche Partitioning Scenario for the Titanosaurs of Lo Hueco (Upper Cretaceous, Spain)

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Previous analyses performed on cranial material found in the associated remains of the titanosaurian sauropods of the Campanian-Maastrichtian fossil site of Lo Hueco (Cuenca, Central Spain) indicate the co-existence of, at least, two types of titanosaurs (Morphotype I, which includes *Lohuecotitan pandafilandi*, and Morphotype II) that may have exploited different ecological niches. Sauropod niche partitioning has been interpreted in some Upper Jurassic-Lower Cretaceous fauna, e.g., the sauropod communities of the Tendaguru (Tanzania) and Morrison (USA) Formations. This partitioning includes differentiation between high browsing and low browsing feeders. High feeder sauropods are generally interpreted as gracile taxa or taxa with some specialization in the proximal appendicular skeleton (e.g., *Giraffititan*). On the other hand, low feeder sauropods are represented by a complex array of more robust taxa. A similar distribution in gracile and robust forms has been identified in the Lo Hueco sauropod association. The previous hypothesis about niche partitioning for the titanosaurs of Lo Hueco based on cranial material is tested for the appendicular skeleton based on the recognition of the morphofunctional appendicular specializations, which are correlated with different feeding capabilities. We used the geometric morphometrics tool kit and a measurement data matrix including sauropod taxa from the Tendaguru and Morrison Formation, as well as several high and low browser feeder titanosaurs. Our analyses show significant differences in the length and robustness of the forelimb and distal hindlimb between high browsing and low browsing feeders. The more robust Morphotype I of Lo Hueco is congruent with a low feeder titanosaur, while the Morphotype II corresponds to a high feeder titanosaur.

Comparative Myology of the Hindlimb of the Thick-tailed Opossum *Lutreolina crassicaudata* Desmarest, 1804 (Marsupialia: Didelphimorphia)

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Traditionally, the Virginia opossum *Didelphis virginiana* (Kerr, 1792) is used as a model for myology studies in marsupials, with most New World marsupials lacking a detailed descriptive analysis. The thick-tailed opossum *Lutreolina crassicaudata* is a Neotropical species with anecdotal evidence compared to placental carnivores, but few studies assessed its morphology and adaptations. The aim of this work is to describe the fore limb myology of *Lutreolina* in order to comprehend its functional implications. Using standard dissection techniques, equipment and nomenclature, we compared the fore limb myology of *Lutreolina* with that of *Dasyurus geoffroii* Gould, 1841, a carnivorous marsupial from Australia, and *Didelphis albiventris* Lund, 1840, the white-eared opossum. Our results showed that *Lutreolina* has similar muscle attachments as in *Dasyurus*, such as origin, insertion and the division in three of the *m. deltoideus*, in *d. acromialis*, *clavicularis* and *scapularis*. Their origins lie closer to each other, and all the insertions culminate in the deltoid ridge of the humerus. The main differences were in the attachments of the pectoralis muscle group. The *m. pectoralis major* origin in *Lutreolina* does not comprise the clavicle, and we did not identify the *m. pectoralis abdominis* either in *Lutreolina* or *D. albiventris*, the only feature considered derived in *Dasyurus*. The fusion of the *m. pectoralis abdominis* with the *m. pectoralis minor*, or its absence, was already considered variable in *D. virginiana*. We conclude that the fore limb myology of *Lutreolina* is broadly similar to that in *Dasyurus* and *D. albiventris*, particularly in traits considered plesiomorphic. Despite the similarity in general body shape, we could consider that *Lutreolina* and *Dasyurus* forelimb myology do not show obvious features adapted to carnivorous habits, being more associated to the generalist opossum *Didelphis*.

Phylogenetic Disparity of Radical Skull Shape in Early Tetrapods

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The traditional model of early tetrapod evolution posits an initial period of low morphological diversity during which the tetrapod body plan adapted to life on land and a later period of rapid morphological diversification in which tetrapods filled diverse terrestrial and semiaquatic niches, forming a classic adaptive radiation. Many of the taxa implicated in this late adaptive radiation have been historically assigned to the 'Lepospondyli,' a morphologically diverse group of small-bodied animals with a wide range of specialized skull morphologies. Recent work has suggested that one 'lepospondyl' lineage, the limbless Aïstopoda, may have originated separately from the remainder of the group within a predominantly Devonian diversification, whereas a second, the Recumbirostra, may represent a specialized lineage of early reptiles. However, the phylogenetic relationships of other 'lepospondyls' remain uncertain. We here use microCT to amend this by describing the cranial and endocranial anatomy of a number of 'nectrideans,' the group of 'lepospondyls' with the most divergent skull shapes. We find that the highly divergent external morphology of nectrideans corresponds with major differences in endocranial organization, including substantial differences in organization of the hypophyseal region, basicranial articulations, cranial nerve organization, and occipital arch. These differences in major endocranial organization correspond to phylogenetic variation across early tetrapods, suggesting that 'Nectridea', like 'Lepospondyli', may be an artificial grouping of phylogenetically and morphologically disparate early tetrapods. The potential position of some disparate 'nectrideans' deep within the tetrapod stem group demonstrates the capacity for extreme morphological diversification of the tetrapod skull well before the completion of the fin-to-limb transition. We suggest that terrestrialization was the consequence of, rather than cause of, adaptive radiation in early tetrapods.

Amphibian Metamorphosis: A Delayed Embryonic Differentiation Program?

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Metamorphosis in amphibians is a rapid period of postnatal development that typically involves a transition from an aquatic larval stage to a terrestrial or semiaquatic adult, permitting ecological partitioning between larva and adult. Metamorphosis is common in modern salamanders and ubiquitous among modern anurans, but the origins of this process remain uncertain. Metamorphosis has traditionally been thought of as a condensation of a conserved postnatal ontogenetic trajectory inherited from a nonmetamorphic ancestor but attempts to identify such a postnatal ontogenetic trajectory in fossil ancestors of modern amphibians have been unsuccessful. We here review the timing and cellular dynamics of metamorphosis in two model amphibians: the axolotl salamander (*Ambystoma mexicanum*) and the African clawed frog (*Xenopus laevis*), to review these hypotheses. We are able to identify a number of conserved features of amphibian metamorphosis as well as a range of unique events associated with metamorphosis in salamanders and frogs. Rather than a condensed ontogeny, these events appear to represent a single cohesive shift in homeostasis of tissue-level processes. Comparison with caecilians and with fossil relatives of modern amphibians shows that developmental events associated with post-embryonic metamorphosis are instead part of late embryogenesis in caecilians, amniotes, Palaeozoic total-group amphibians, and tetrapod outgroups. We propose a new model for the origin of amphibian metamorphosis where embryonic differentiation processes, ubiquitous in early total-group amphibians, are delayed in metamorphic amphibian lineages.

Cenozoic Reptile Body Size Increase Coordinated with Mammal Size Increase and Climatic Cooling

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Body size is a fundamental character of species; it is correlated to many life history traits and can help to reconstruct extinct animals' ecologies. Body size trends have previously been studied in fossil mammals, which increased in size dramatically following the extinction of the dinosaurs, but how the body size of reptiles, one of the most diverse vertebrate groups today, has changed throughout the Cenozoic has not previously been analyzed at a broad scale. Metabolic theory predicts reptile body size increase in warmer climates; as poikilotherms, non-avian reptiles' body size is important for thermoregulation. Here, we examine the histories of body size change in reptiles during the Cenozoic in order to assess the relative influences of climatic variables and ecological interactions with mammals on the maximum body size of different clades. We compiled the maximum body size of Cenozoic reptile clades at sub-epoch temporal resolution, based on specimen examination and literature. Our analyses reveal that reptile body size peaked concordantly with mammal size in the Late Miocene and that size is correlated in the two clades over time. Results also show that maximum body size is inversely correlated to global temperature (from benthic Foraminifera $\delta^{18}O$ records). These results suggest common factors govern size change across terrestrial vertebrates over long time scales. Evolution to large body sizes is linked to climatic cooling, even in extant reptile clades within which large size is concentrated in the tropics. Cooling may facilitate body size increase because sea level change with glaciation leads to increased continental land area over which vertebrate species can range. This cross-clade comparison of body size trends enables us to identify climatic and ecological constraints on size changes that are shared across vertebrate groups, improving our understanding of how terrestrial vertebrate communities have evolved.

Evolution of the Sound Producing Apparatus in the Monophyletic Serrasalmid Fishes

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Within piranhas, sound production is known in carnivorous species whereas herbivorous species were thought to be mute. As these carnivorous sonic species have a complex sonic apparatus, we hypothesize that transitional forms could be found in some serrasalmid species. We investigate sound production in different species covering the entire Serrasalmidae phylogenetic tree to understand the evolution of the sonic mechanism in this family. The results highlight the evolutionary transition from a simple sound-producing mechanism without specialized sonic structures in the herbivorous species (*Piaractus* and *Myloplus*) to a sonic mechanism involving large, fast-contracting sonic muscles allowing vibration of the swimbladder in the genera *Pygocentrus* and *Serrasalmus*. Hypaxial muscles in herbivores primarily serve locomotion, but some bundles cause sound production during swimming accelerations, meaning these muscles have gained a dual function. Sound production therefore seems to have been acquired through an exaptation event, i.e., the development of a new function (sound production) in existing structures initially shaped for a different purpose (locomotion). In further evolutionary stages (*Catoprion* and *Pygopristis*), some bundles are distinguishable from other hypaxial muscles and insert directly on the swimbladder. At this stage, the primary function (locomotion) is lost in favor of the secondary function (sound production). In the last stage (*Pygocentrus* and *Serrasalmus*), the muscles and insertion sites are larger and the innervation involves more spinal nerves, improving calling abilities. The comparison of sounds and sonic mechanisms shows the evolution of acoustic communication corresponds to a trajectory where the initial exaptation event is then subject to adaptations. TEM observations of the different muscles support clearly our evolutionary hypothesis.

Sprouty 2 in the Early Development with Focus on the Jaws and Limbs

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Sprouty proteins are known as negative regulators of the pathways downstream of receptor tyrosine kinases (RTKs), including fibroblast growth factor (FGF) pathways. FGFs are involved in osteoblast proliferation, differentiation and bone formation. Especially FGFR3 affects chondrocytes in the growth plate; gain-of-function of FGFR3 is responsible for chondrodysplasia syndromes. Sprouty2 plays an important role in embryonic development, such as development of limb, kidneys, pulmonary branching and morphogenesis of teeth. Sprouty2 knock-out results in supernumerary tooth formation in the diastema of the mandible, abnormalities of skull shape or cleft palate. In the frame of this project, we aimed to determine associations between Spry2 and sonic hedgehog (Shh) genes in the craniofacial area and in the limb buds. *In situ* hybridization, immunohistochemistry were used to show expression patterns of Spry2 and Shh genes and proteins. Cre-loxP technology has been used to trace the fate of Shh expressing cell population in the jaws and limbs of Spry2 knock-out mice. Financial support: GAČR 18-04859S.

The Enigmatic Electric Knifefish *Tembeassu marauna* Triques, 1998 (Gymnotiformes: Apteronotidae): Osteological Description Using Microcomputed Tomography and Phylogenetic Inference

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The monotypic electric knifefish *Tembeassu* was described based on three specimens collected at Ilha Solteira, in the Rio Paraná basin (Mato Grosso do Sul, Brazil). The genus was originally diagnosed solely by the presence of an enlarged fleshy lateral lobe on the chin. A subsequent study using radiographs indicated the presence of a rostral patch of extra teeth on the upper lip, a unique condition across the Neotropical electric knifefishes of the order Gymnotiformes. Since its description, no additional specimens of *T. marauna* were captured. As a consequence, information of its anatomy is restricted to the external morphology and few osteological characters observed in the radiographs. We reanalyzed the external morphology and performed microcomputed tomography in the types of *T. marauna* in order to provide a robust diagnosis to the species and infer its phylogenetic position. Our results corroborate previous studies, and indicate that *Tembeassu* is further diagnosed from all other members of the order by the presence of a prominent extension of the lower lip. Conversely, the presence of a lobe on the chin was proven to be a homoplastic character, evolving more than once independently within Apteronotidae. However, only *Tembeassu* has an oval-shaped hypertrophied lobe. Likewise, results from microcomputed tomography allowed the investigation of a number of morphological characters. For instance, the dorsal portion of the rib of the fifth vertebra of *Tembeassu* is extremely modified, with a pitted posteriorly directed wing-shaped expansion, which apparently contributes to the Weberian apparatus structure. This condition is also found in a few other apteronotid species, and additional comparative studies could clarify its homology and function. Preliminarily phylogenetic analyses assign *Tembeassu* either as the sister-group of Apteronotini or into a large polytomy at the base of Apteronotidae.

Myological Characters in Phylogenies: Dorsolateral Head Muscles in Gymnotiformes (Teleostei: Ostariophysi) and an Application of Bremer Partitioned Support

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Anatomical studies in Gymnotiformes have followed the usual trend in Teleostei, with an inordinate emphasis on osteology. Other relevant anatomical systems, such as myology, remain mostly unexplored. The present study attempts to fill this gap by focusing on the head musculature of Gymnotiformes within a phylogenetic scenario. Detailed comparative study comprising the entire order identified 56 myological characters which were concatenated with a larger phenotypic matrix including characters from several different sources. After analysis, about 20 new myological synapomorphies were recovered for all major lineages in the Gymnotiformes. Gymnotidae is proposed as sister group to Sternopygoidei, the latter composed of monophyletic Rhamphichthyoidea and Sternopygoidea. We applied Partitioned Bremer Support (pbs) to investigate the influence of myological characters in the phylogeny. All families and superfamilies received positive values from the general and myology partitions; and less inclusive groups (e.g., Apteronotinae, *Steatogenys* + *Hypopygus*, and *Platyurosternarchus* + *Sternarchorhynchus*) received neutral or negative pbs values from myology. Our results indicate that the set of myological characters provides neutral or contrary evidence (i.e, pbs ≤ 0) for more than half of the subclades below family-level, but positive values (i.e., pbs > 0) for family or superfamily relationships. Thus, there is clear tendency for facial musculature characters to be informative about deeper regions of the phylogeny of gymnotiforms. Results indicate that characters from myology can significantly improve both support and resolution of important components of phylogenetic hypotheses.

Evolution of Locomotor Abilities in Frogs: Evidence from the Mesozoic-Paleogene Fossil Record

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Limbs appear to have played a key role in the adaptive radiation of anurans (frogs), showing morphologies associated with diverse locomotor abilities. Particularly, it has been shown that these abilities correlate with variations in limb proportions, which evolved convergently across the anuran tree. It has been proposed that early salientians (stem-group anurans) were good jumpers and that the origin of the bizarre anuran Bauplan might have been related to jumping adaptations. However, it has recently been shown that distinct postcranial morphologies shared by earliest salientians and frogs would not have originally been linked to a saltatory locomotion. Herein, we explore the evolution of limb proportions and locomotor abilities in Salientia over most of their history. Based on length measurements of the limb bones in more than 300 extant and 40 extinct species encompassing the Mesozoic and the Paleogene we: 1) performed a PCA to investigate the occupation of the limb morphospace over geological time; and 2) inferred locomotor behaviors (i.e., jumping, swimming, hopping, walking, burrowing) in extinct species by LDA and FDA. In the reduced morphospace PC1-PC2, extant 'archaeobatrachians' and neobatrachians overlap, with the latter more widespread in all directions, and group according to locomotor behavior. Jurassic, Cretaceous, and Paleogene species also overlap between them and with extant taxa. Based on the classification of extinct taxa, the earliest inferred long-distance jumpers are from the Early Cretaceous, whereas Jurassic taxa, including *Prosalirus*, are recovered as hopper/walkers or swimmers. In conclusion, a limited range of limb proportions has been convergently explored since the Jurassic, with new morphologies mostly evolving after the neobatrachian radiation. Interestingly, our results agree with recent work based on different lines of evidence and data suggesting that saltatory locomotion might have not evolved early among salientians.

Three Dimensional Computer Simulations in the Cave Bear Skull Reveals a Trade-off between Adaptation to Glacial Climate and Dietary Niche Versatility

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The abundant fossil remains of the cave bear (*Ursus spelaeus*) found in different places across Europe makes it one of the most well-known Pleistocene species. However, although disentangling the cave bear diet could give essential clues to further understanding potential extinction causes, its feeding preferences are still controversial in the literature. Here, we perform a biomechanical analysis of different biting scenarios of the skull of the cave bear (*Ursus spelaeus*) to investigate the biomechanics of its feeding behavior. We perform a Finite Element Analysis from CT-scans of the skull of all living bear species and all species/subspecies described for the cave bear complex (*Ursus spelaeus* sensu lato): *Ursus ingressus* and *Ursus spelaeus* (*U. sp. spelaeus. U. sp. ladinicus. U. sp. eremus*). Our results indicate that the species/subspecies of cave bears adapted to high-alpine habitats were less able to withstand large stresses when simulating different biting scenarios than those that inhabited low altitudes. The large sinuses present in high-alpine cave bears explain their low ability to resist stresses during feeding behavior. In contrast, having large sinuses may help high-alpine cave bears to increase their efficiency of thermoregulation during hibernation. In the light of this new evidence, the potential causes of the cave bear extinction is discussed.

Oriented Clonal Cell Dynamics Enables Accurate Growth and Shaping of Mammalian Facial Cartilage

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Control of shape and size during growth of the mammalian face is highly enigmatic. Complexly shaped cartilage structures in developing face provide a great model system to tackle this question. We investigated major principles of facial cartilage induction and scaling up. We found that basic 3D-blueprint of facial cartilages is induced as early mesenchymal condensations by combinatorial signals derived from epithelia and nervous system. We also revealed that the final shape and size of every solid cartilage structure in the embryonic head are achieved through two processes going in parallel: incremental addition of adjacently-induced chondrogenic condensations combined with scaling up of the pre-laid cartilage. The scaling is accomplished through a previously unknown mechanism of growth based on introducing oriented clonal units into existing cartilage from the perichondral cell layer. We took advantage of various molecular tools to demonstrate how specific clonal dynamics in cartilage enables uncoupling lateral expansion from thickness control as well as geometrical fine-tuning.

Hunting in the Deep: The Musculotendinous System of Mesopelagic Fishes (Teleostei: Stomiiformes)

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Every night the greatest migration on Earth starts in the deep-pelagic, where organisms move up to the meso- and epipelagic to find food then return during the day. The most dominant fish taxa undertaking vertical migrations are the lanternfishes and blackchins (Myctophiformes) and the dragonfishes (Stomiiformes). However, the functional aspects of locomotion and the architecture of the musculotendinous system in these fishes have never been examined. Usually, the musculature is organized in segmented blocks of specific three-dimensional 'W-shaped' foldings (myomeres) separated by thin sheets of connective tissue (myosepta) that can be additionally characterized by ossified/mineralized tendons (fishbones). Together with the fins, these structures form the functional unit of locomotion in fishes. For this study microdissections of cleared and double stained specimens of six stomiiform genera (*Polymetme*, *Gonostoma*, *Astronesthes*, *Chauliodus*, *Malacosteus*, and *Eustomias*) have been conducted in order to investigate their musculotendinous system. Additionally, soft tissue has been investigated non-invasively by using microCT-scans stained with iodine. In the investigated stomiiforms, the typical 'W-shape' of a myoseptum cannot be seen in the anteriormost myosepta as the anterior cones are missing. These cones appear and elongate gradually with the presence of the dorsal and anal fins. The amount of connective tissue in the myosepta is very low anteriorly, but increases gradually with body length. Red musculature lies laterally on the body in separate cones. The myoseptal tendons of the posterior body segments attach in a highly complex interwoven pattern on the caudal fin. The combination of these characters indicates that the posteriormost myosepta are equipped for a multisegmental force transmission towards the caudal fin. This unique anatomy might be essential for fast starts during hunting behavior, when prey is rarely available.

Scaling of Passive and Active Visco-elastic Mechanical Properties in the Bluegill Sunfish, *Lepomis macrochirus*

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The bodies of fishes are composed of flexible materials that interact mechanically with the fluid around the fish. While the behavior and mechanics of fish swimming have been studied for decades, few studies have investigated the role of internal body mechanics in swimming performance. Fish generate propulsive forces by activating muscles that bend their bodies from side to side. Their muscles, however, can also change the effective mechanical properties of their bodies. In this study, we measured the viscoelastic mechanical properties, both passive and when the muscles were active, of the bodies of bluegill sunfish over a range of sizes (100 to 170 mm SL). We used an oscillatory bending apparatus in which fish were connected to a servomotor, while the other end of the fish was attached to a six-axis force transducer. The bodies were then bent back and forth at different frequencies (1 – 7 Hz) and amplitudes (2.5, 5, 7.5, 10, 12.5, and 15 degrees) while body torques were measured with the force transducer. For active measurements, muscles were stimulated at different phases during the bending cycle. We made these measurements at two body regions: between the 1st and 3rd dorsal fin ray and between the 1st and 3rd anal fin ray. We aim to answer several questions, including (1) how does muscle activity change the effective mechanical properties? (2) do the body regions differ mechanically?, and (3) how do these properties change across ontogeny? We found that body torques increased with increasing amplitude, but remained unchanged across frequencies, indicating that the body does not have a resonant frequency in the range of normal swimming frequencies, and that the damping decreases as frequency increases. Local flexural stiffness increased with frequency, but remained unchanged with increasing amplitudes. Both body torques and local flexural stiffness increased with increasing body size.

Repeated Development of Distal Hind Limbs in the Evolution of Snakes

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Reduction and loss of external hindlimbs, combined with body elongation, are key adaptations in the evolution of snakes. Hind limb elements are only present in basal divisions among extant snakes, where they are highly reduced and function for communication, but controversial hypotheses for the evolutionary interrelationships of fossil snakes with well-developed hind limbs require either multiple episodes of loss or 're-evolution' to explain the presence of limbs within Serpentes. Developmental studies demonstrate retention of limb-patterning mechanisms during *Python* embryogenesis, suggesting a potential mechanism for evolutionary reacquisition of hind limbs; however, the extreme reduction of limb elements in extant taxa has not previously provided support for the evolutionary polarity of hindlimbs in fossils nor the role of developmental modification in potentially re-establishing limbs. Here, we combined high-resolution microCT comparative anatomy of the pelvic region in extant snakes with Ancestral State Reconstruction (ASR) methods to model the evolution of distal limb elements in the evolution of snakes. We discover the first unambiguous evidence for zeugopodial ossifications, homologized with the tibia, in extant taxa and map their distributions across competing phylogenetic hypotheses for Serpentes. ASR analyses reveals multiple histories of redevelopment of an ossified zeugopod for all topologies, regardless of the interrelationships of limbed fossil taxa, and demonstrate the persistence of late-stage limb patterning throughout snake phylogeny. These results support concepts of complex anatomical system reacquisition through deep time and are permissive of hypotheses of derived interrelationships of limbed fossil snakes.

Species Differentiation among Sixteen Animal Species Using the Elemental Profile of Carpus and Tarsus Bones

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The bones collected from different animal species contain a different elemental composition due to genetic background, food and habitat. In this study, we used the elemental profile of bones for species differentiation. The carpus and tarsus of 16 animal species including human, dog, cat, pig, deer, goat, sheep, cow, horse, tapir, hyena, tiger, elephant, monkey, dolphin and ostrich were used. The elemental profile of each bone was analyzed by X-ray fluorescence (XRF) at 15 kV and 50 kV and then discriminant analysis was performed to distinguish those species. Our results showed that Rh was detected only in dog's carpus at 15 kV whereas at 50 kV, Rh was higher in tapir. Moreover, specific elements were found only in tarsus bone: at 15 kV, Ti and Tl were present in goat and Zr was observed in sheep. Ti was present in goat at 50 kV. Furthermore, Si and S showed the highest amount in pig, at both voltages. The results suggest that elemental profiles can be used for discriminating these species: the highest accuracy rate for species classification is observed at 15 kV (79.2% and 78.4% based on carpus and tarsus, respectively). The highest accuracy rate increased at 50 kV (86.6% and 93.2% for carpus and tarsus, respectively). In conclusion, the elemental profile by XRF can be used to distinguish human from non-human bones and serve as an efficient tool for species classification.

Extracting the Lifestyle from Bone Trabecular Architecture: The Study of Humeral Metaphyses of Extant Reptiles

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Lifestyles of extinct tetrapods are often difficult to reconstruct in the absence of clear morphological adaptations such as swimming paddles. According to our assumptions on bone functional adaptation (commonly referred to as Wolff's law), the architecture of trabecular bone follows the principal stress trajectories associated to loading. Previous studies have shown a clear relation between trabecular architecture and locomotor behavior, mainly in mammals and birds. However, a link between trabecular architecture and lifestyle has rarely been examined. Here, we analyzed trabecular architecture of different clades of reptiles characterized by a wide range of lifestyles (aquatic, amphibious, generalist terrestrial, fossorial and climbing). Humeri of squamates, turtles and crocodylians have been scanned with microCT. We selected spherical volumes of interest centered in the proximal metaphyses and measured trabecular spacing (Tb.Sp), thickness (Tb.Th) and number (Tb.N), degree of anisotropy (DA), bone volume density (BV/TV) and connectivity density (Conn.D). Only BV/TV showed a significant phylogenetic signal and its significant difference between squamates and other reptiles could be linked to their physiologies. We found negative allometric relationships for Tb.Th and Tb.Sp, positive allometries for Conn.D and Tb.N, no dependence with size for DA and BV/TV. The different ecologies were well separated in the morphological space using linear discriminant analyses but a cross-validation procedure indicated a limited predictive ability of the model. In turtles and squamates, the anisotropy showed higher values in amphibious taxa than in terrestrial ones. The allometric scalings, previously emphasized in mammals and birds, seem to be valid for all amniotes. Discriminant analyses gave a good distinction of lifestyles, which however remain difficult to discriminate accurately. Trabecular architecture analysis seems to be a promising tool to infer lifestyle of extinct tetrapods.

Skin Morphology in Context of Thermoregulation and Heat Dissipation in the Social African Mole-rat *Fukomys mechowii*

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Avoiding overheating is a major challenge for mammals that spend their whole life in relatively warm and very humid subterranean burrows. This is especially pronounced during and after digging of new burrows, which leads to production of large amount of metabolic heat. In addition, strictly subterranean mammals, such as African mole-rats (Bathyergidae, Rodentia) lack body appendages such as tails and auricles that are used in many mammalian species to dissipate surplus metabolic heat. Thus, conduction via less haired body parts, so called thermal windows, seems to be the only relevant way of cooling. Previous studies performed using IR-thermography determined these thermal windows mainly on ventral side of the body, which is in agreement with a lower insulative volume of fur (shorter and less dense) in the same area. We examined the skin morphology with an emphasis on characteristic adipose tissue in the giant mole-rat *Fukomys mechowii.* Thickness of the dermis, epidermis and fat layer was measured and the connectivity of fat tissue was evaluated in the anterior, central and posterior part of the trunk on the dorsal and ventral side. Thickness of the dermis does not differ between the dorsal (0.79 ± 0.25 mm) and ventral (0.82 ± 0.28 mm) body side, but was

significantly different between anterior, central and posterior part ($p<0.0001$), and is the thinnest in the central part of the ventral side. Thickness of the fat layer was not different between dorsal (0.17 ± 0.09 mm) and ventral (0.16 ± 0.07 mm) body part, and the difference between anterior, central and posterior part was significant only on the dorsal side ($p=0.0172$). The fat tissue connectivity seems to be lower on the ventral side, but the difference was not significant. Due to the absence of remarkable differences in skin or fat between dorsal and ventral side of the body, we assume that the heat dissipation could be influenced by differences in fur quality or vascularization. This research was supported by Czech Science Foundation, 31-17-19896S.

Microstructural Analysis of Zubron (*Bison bonasus* hybrid) Tongue in Relation to its Parental Species European Bison (*Bison bonasus*) and Cattle (*Bos taurus*)

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Crossing domesticated animals with wild species in ruminant breeding is a phenomenon often applied to implement wild features to increase the productivity of domesticated animals. Well known crossbreeds with signs of improved morphological and physiological features are known as beefalo, dzo or yakalo. There is little research that describes the anatomical and histological features of the hybrids in relation to parental species. The *Bison bonasus* hybrid, called zubron, is an interspecific species between cow and the bull of the European bison. The aim of the LM and SEM studies is to describe structural features of the zubron tongue in relation to the parental species in order to indicate species-specific features in the examined breed. The outline of the tongue is similar to that in the parental species, but the length of the zubron tongue is similar to values obtained for cow. Among investigated species only in zubron do we observe a median sulcus on the apex and body of the tongue. On the surface of the tongues studied, filiform, conical, fungiform and vallate papillae are observed. Arrangement of fungiform papillae on the body and on the ventral surface of the hybrid tongue are species-specific traits. The number of vallate papillae in zubron is similar to that in European bison; its arrangement resembles that in the cow. The microstructure of these papillae is characteristic only for the crossbreeds examined. Morphometry reveals the similarity of the size of fungiform papillae on the apex of the hybrid tongue to the situation in cow, whereas the size of the fungiform papillae on the torus is close to that in the European bison. Noteworthy to mention is that the thickness of the mucosal epithelia on the papillae in the hybrid are the lowest in the species studied, but the stratum corneum is 9% higher than in parental species. In conclusion, zubron as an interspecific species has an outline and distribution of lingual papillae similar to the parental species and other ruminants, but also has some species-specific traits.

How Head-Shape of Crocodile and Ribbed Newts (Salamandridae) and their Extinct Relatives Correlate with Ecology and Life History

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The cranium is composed of various individual, articulated bones, while most other bony body parts of the postcranial vertebrate skeleton comprise only a single bone element. This is especially true for tetrapods. The cranium also houses most of the sensory organs and is responsible for various tasks such as feeding and the perception of the environment. These many tasks and the structural design forced and allowed vertebrates to evolve very distinct head morphologies. Nevertheless, among phylogenetically non-related taxa similar shapes of head morphologies evolved, particularly when different species occupied similar niches and requirements of sensory organs and structural design were analogous. Despite an enormous morphological variation in the cranial skeleton, still conclusions on a species´ ecology can be drawn. Via two-dimensional geometric morphometrics and micro-computer tomography-scans, we investigated how external and osteological cranial morphology of ribbed and knobby newts (genera *Echinotriton*, *Pleurodeles* and *Tylototriton*) differed among species inhabiting variable habitats and how it relates to ecological and life history traits. Our analysis also included the fossil record of closely related extinct *Chelotriton* in order to obtain a better estimate of the evolution of head shape in salamanders.

The Killer's Toolkit: Quantifying Canine Tooth Shape in Mammalian Carnivores

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Canine teeth are the daggers of the animal world. They are the main tool used by mammalian carnivores to catch, kill, and consume their prey. Like a human tool, the shape of a tooth determines how effectively it performs. So, how do these killing tools vary in mammalian carnivores? In this project we used novel measures of sharpness as well as 3D-geometric morphometrics to examine the variation in canine tooth morphology. We sampled a wide range of mammalian carnivores including teeth from all Carnivora families as well as the marsupials Dasyuridae, Thylacinidae, and Didelphidae. We created 3D-digital models of unworn upper and lower canines from surface scans of museum specimens. These were measured and analyzed in order to, first, map the variation present across mammalian carnivores and, second, investigate the relationship between canine morphology, phylogeny, diet, hunting technique, and tooth position. Sharpness data were collected for six functional regions of the tooth (anterior, posterior, labial, and lingual edges, and tip in sagittal and lateral orientations) and principal component analysis was undertaken in order to create a morphospace mapping the shape variation. We found that both tip and edge sharpness varies significantly between canine teeth and that the sharpest teeth belong to the Felidae and the bluntest to the Mustelidae. 3D-geometric morphometric analysis of canine morphology shows two major axes of variation: curvature and taper. Interestingly, there was no clear correlation between canine morphology and phylogeny, diet, or hunting technique. However, most striking was the difference between upper and lower canines. For a majority of the families upper and lower canine morphology differs within the same individual, with the uppers being thinner and straighter than their lower counterparts. This study demonstrates for the first time the variation in 3D-morphology of canine tooth forms, shedding light on their hidden complexity.

Revisiting the Cranial Anatomy of *Lycosuchus vanderrieti* (Therapsida: Therocephalia) from the Middle Permian of South Africa, Based on CT-Reconstruction

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Therocephalia is one of the major therapsid clades and ranges from the middle Permian to Middle Triassic. The earliest therocephalians were large-bodied predators whose fossils are common in middle Permian rocks of South Africa, but have received little study. One such middle Permian therocephalian, *Lycosuchus vanderrieti*, was initially very briefly described based on a complete cranium and mandible. Since that description, *Lycosuchus* has received some additional anatomical attention, but numerous aspects of its cranial and particularly endocranial anatomy remain obscure. Here, we present a redescription of the skull of *Lycosuchus* based on a specimen in the Museum für Naturkunde Berlin (MB.R.995) from the Tapinocephalus Assemblage Zone near Beaufort West, South Africa, which consists of a partial snout, braincase and left mandible. Using a micro-computed tomographic reconstruction of this specimen, we describe for the first time several endocranial features of *Lycosuchus*. Our results provide new insights into the internal skull anatomy and nervous system of *Lycosuchus*, including the highly ramified maxillary canal and the bony labyrinth. The labyrinth exhibits a cochlear recess, a feature previously only known within Therocephalia from the highly specialized Triassic taxon *Microgomphodon*. MB.R.995 preserves one of the few complete mandibles known from *Lycosuchus*. Examining the medial surface of the mandible revealed an unfused prearticular and one small coronoid, both of which are obscured in the holotype. Moreover, the jaw articulation of MB.R.995 is exceptionally well preserved and clearly shows that the glenoid fossa is composed of both the articular and the surangular – unlike other early therocephalians, where it is composed solely of the articular. In general, our CT-reconstruction of *Lycosuchus* reveals a mosaic of features indicating a complex history of character acquisition and loss in Therocephalia.

Cranial Skeletogenesis in Non-Teleost Fishes: Towards the Understanding of Developmental Strategies of Fish Craniofacial Diversity

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Skeletal tissues are generally considered key novelties of vertebrates. The ray-finned fishes represent the most numerous and successful recent vertebrates, and they consequently exhibit endless varieties of skeletal architectures. In order to depict fundamental principles of fish cranial skeletogenesis, the developmental formation of skeletal architectures was described, compared, and analyzed using members of early branching fish lineages, that exemplify very different strategies of skeletogenesis. While African bichirs and Tropical gars are heavily armored forms with massive exoskeleton and hyperossified dental structures, European sturgeons, on the contrary, possess a mostly cartilaginous skeleton and reduce their dental structures during early development. We have applied (i) morphometric approaches that allowed quantitative investigations of mineral tissue development, (ii) determined disproportions in patterns of temporal and topographical organization of cartilaginous and bony condensations, and (iii) demonstrated that early shifts in the relative timing of gene expressions have a significant impact on patterns of fish craniofacial architectures. Our comparative data thus revealed several crucial factors responsible for disparate cranial morphotypes, which might further allow to define the developmental strategies of craniofacial mesenchyme to generate fish craniofacial diversity.

The Tongue Morphology in the Rodents of the Families Anomaluridae and Pedetidae (Mammalia, Rodentia)

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The tongue morphology was studied in all extant genera (except *Zenkerella*) of the families Anomaluridae and Pedetidae using modern microscopy. Both families belong to one of the branches of the rodent basal radiation (Anomalurimorpha) and are characterized by a distinct morphological specificity. Significant intergeneric differences in the tongue structure between *Anomalurus* and *Idiurus* have been identified. These differences affect even such taxonomically important features as the number of circumvallate papillae (three in *Anomalurus*, two in *Idiurus*), and the distribution pattern of fungiform papillae. A parallel interspecific variability has been observed within the genera. It manifests itself in a decrease of the fungiform papillae number. The tongue structure in *Anomalurus* corresponds to the generalized version, basal for the order, whereas in *Idiurus*, it has clear signs of morpho-functional specializations. The high specificity of the tongue structure in *Pedetes* is shown which is manifested in its proportions in the distribution of different types of papillae on its dorsum. The fixed part of the tongue is long, whereas its root part is greatly shortened. The lateral organ is substantially enlarged. The circumvallate papillae are absent. The complete reduction of these papillae is a unique feature of the springhare. The fungiform papillae are concentrated in two zones: on the tip of the tongue and on a low eminence at its base. The tongue of *Pedetes* is generally more similar to the tongue of *Anomalurus* than that of *Idiurus*. The similarity in the tongue morphology in Pedetidae and Anomaluridae concerns the traits specific not only for these families but occurring also in other rodent taxa. Despite the extreme specificity of the tongue in *Pedetes*, the data obtained do not contradict the hypothesis of a sister relationship of the above families, though not definitely confirm it.

Sensory-Skeletal Integration and the Development of Cranial Asymmetry in Blind Cave-Dwelling Fish

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Deviations from symmetry are common among cave-dwelling organisms. Laterality in the cranium was among the first characterized aberrations discovered in Mexican cavefish following their discovery in 1936. Early researchers were unclear of the origin of these asymmetries, suggesting they may have arisen from a wound inflicted in life, or during post mortem handling. Several populations (and decades) later, it became clear that certain asymmetries – those associated with bone fragmentation – were a normative component of the cranial skeleton in cavefish. Interestingly, these aberrations are never observed in surface-dwelling fish, enabling comparative analyses in the two morphotypes. Certain components of the cranial skeleton are controlled by asymmetric genetic loci, i.e., QTL detected when analyzing one side of the head. Here, we describe the presence of three subtypes of cranial asymmetry. The first component is a cranial “bend” that appears late in the cavefish life history, nearly always associated with the left side. A second component is facial bone fragmentation, which is mediated by two unusual ossification processes. The first process involves ectopic centers that largely coalesce back into the developing dermal bone. The second process, which is more common, involves the spontaneous dissolution of a bony channel through mature bone. The third component of asymmetry involves the dermal bone positioning of the suborbital series. We demonstrate that primary ossification centers are associated with the positions of early canal neuromasts. The presence/absence of certain neuromasts is associated with presence/absence of associated bones. Moreover, shorter distances between embryonic canal neuromasts appear to predict fusion of neighboring suborbital bones. In conclusion, cranial asymmetry is a complex phenotype in cavefish, which is underpinned by distinct developmental aberrations. Current studies are devoted towards understanding how sensory-skeletal integration may underlie adaptation to the extreme environment of the cave.

Osteohistology of Disparate Limb Development in Ducks

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Birds exhibit diverse ontogenetic strategies referred to as the avian precocial–altricial developmental spectrum which also defines characteristic locomotor skills through ontogeny. Functional performance of legs and wings ranges from the most precocial galliforms that can run and fly soon after hatching to the most altricial passeriforms that perform proper bipedal and aerial locomotion only at or close to adult size. Transitional strategies show different functional maturation not only between hatchlings of various species, but also among different anatomical units within the hatchling’s body. For instance, anseriforms are characterized by functional modularity in limb development with their legs following precocial, whereas their wings altricial development. We studied how this developmental disparity is reflected in the diaphyseal limb bone tissue in an ontogenetic series of ducks (4, 8, 30, 50 days posthatching [dph]). Wing and leg bones were prepared as petrographic (~80 μm thick) and paraffin embedded, stained (5 μm thick) histological sections. We found disparity between fore- and hind limb osteohistology in both pre- and posthatching cortex. Precocial leg bones show more developed osteons, higher vascular density and a large amount of woven bone in the prehatching cortex, and an indistinct or invisible hatching line, contrasting altricial wing bones. An unusual posthatching cortical tissue, likely indicating very high growth rates but still to be characterized, was also identified in hind limbs but not or rarely in wing bones at 4 and 8 dph. This and the higher porosity in the outer fourth of the cortex in wing bones at 30 and 50 dph are in line with the delayed growth burst of the altricial wing. Secondary remodeling is prevalent in leg bones but largely absent in wing bones at 30 and 50 dph. These results also provide the first comparative osteohistological data to explore the evolution of ontogenetic locomotor skills in the lineage of paravian dinosaurs.

Angioarchitecture of Uterine Tubes and Uterine Horns in Domestic Cat (*Felis silvestris catus*) during Prenatal Development

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Uterine tubes (oviducts) and uterine horns in domestic cat develop at different rate. The differentiation of mucosa and muscularis in uterine horns occurs between the 44th and 46th day p.c. (post conceptionem) while in uterine tubes between the 53rd and 55th day p.c. An important issue during development of genital system is formation of an intramural vascular system. The aim of the study was to compare the angioarchitecture of the uterine tubes and uterine horns in domestic cat during prenatal development. The study was carried out on female fetuses of the domestic cat, aged from 36 to 63 days p.c., obtained from veterinary clinics. The observations were made using LM and SEM of vascular microcorrosion casts. The results revealed that the vascular system of tubal segments of paramesonephric ducts between the 36th – 40th day p.c. is simple and consists only of capillaries arranged in loose connective tissue. After the 40th day p.c. the main blood vessels in the uterine tubes differentiate into arterioles and venules. At the 55th day p.c. the intramural vascular system in the uterine tubes is complex and consists of a subserosal and mucosal vascular networks. The uterine segments of paramesonephric ducts between the 36th – 40th day p.c. supply an arteriole, which divides into capillaries. Between the 44th and 46th day p.c. two main vascular networks are established in the wall of the uterine horns, i.e., a subserosal and a mucosal network with subepithelial capillaries. During development of the vascular system, sprouting and intussusceptive angiogenesis occurs. The main process responsible for the formation of the subserosal and mucosal vascular networks in both studied organs is predominantly intussusceptive angiogenesis. In conclusion, the vascular system of the uterine horns starts to develop earlier than in the uterine tubes. The rate of development of subserosal and mucosal vascular networks in the genital system correlates with the time of differentiation of the tunica mucosa and tunica muscularis.

Unique Ectoderm-Endoderm Interactions during Mouth Formation in Basal Actinopterygian Fishes

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In most vertebrates, early development of the oral region is generally considered rather uniform and well understood. It comprises early formation of the mouth by means of ectodermal stomodeal invagination, and later its opening by means of rupture of the ecto-endodermal oral membrane. Here, we analyze development of the oral region in embryos of basal actinopterygian fishes (African bichirs, European sturgeons, and Tropical gars), where the mouth formation is influenced by development of the endodermal pre-oral gut. Early evagination of this endodermal domain affects the nascent mouth, resulting in the presence of the foregut-derived endodermal cells in front of the mouth opening and, eventually, on the external surface of the head. Our analyses further describe this unique situation and ectoderm-endoderm interactions during development of the oral region in basal actinopterygian fishes, demonstrating underestimated diversity of vertebrate craniofacial development.

Can we Determine the Role of Trophic Ecology as a Driver of Deep Time Macroevolutionary Patterns? Texture Analysis of Tooth Microwear and Niche Partitioning in Sympatric Species

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The fossil record should provide crucial evidence to test and constrain models linking trophic ecology and macroevolution through deep time, but this potential is generally unrealized. In large part this is because of the difficulty, for fossil taxa, of obtaining evidence of diet, resource use and partitioning that is independent of the morphological data from which macroevolutionary patterns are themselves derived. Non-morphological proxies for diet, including microwear texture analysis, can break this circle, and quantitative approaches to analysis based on parameterization of surface texture are increasing the robustness and repeatability of this widely used technique. Discriminating between taxa *within* dietary guilds has the potential to significantly increase our ability to determine resource use and partitioning in fossil vertebrates, but how sensitive is microwear texture analysis? Can it detect differences between sympatric species exhibiting niche partitioning with significant dietary overlap? To address these questions, we combined detailed dietary data with tooth microwear texture analysis of sympatric populations of shrew species (*Neomys fodiens*, *Neomys anomalus*, *Sorex araneus*, *Sorex minutus*) from Bialowieza Forest, Poland. Dietary analysis reveals that these populations exhibit varying degrees of niche partitioning with greatest overlap between the *Neomys* species. *Sorex araneus* also exhibits some niche overlap with *N. anomalus*, while *S. minutus* is the most specialized. Multivariate analysis based only on tooth microwear textures recovers the same pattern of niche partitioning, demonstrating that validated microwear texture analysis can provide very subtle dietary discrimination in fossil insectivores. Application of these results to a combined dataset of extinct and extant taxa has some surprising implications.

Cranial Anatomy of the Early Cynodont *Galesaurus planiceps* and the Origin of Mammalian Endocranial Characters

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The cranial anatomy of the early non-mammalian cynodont *Galesaurus planiceps* from the South African Karoo Basin is revised on the basis of a computed tomographic reconstruction of the skull. Previously, little was known about internal skull morphology and the nervous and sensory system of this taxon. The endocranial anatomy of various cynodonts has been intensively studied in recent years to understand the origin of mammalian characters in the nasal capsule, brain, and ear. The earliest cynodont taxon those studies have focused on is the Early Triassic *Thrinaxodon liorhinus*, which is phylogenetically crownward of *Galesaurus*. Accordingly, *Galesaurus* provides a useful test of whether the morphologies observed in *Thrinaxodon* were present even more basally in cynodont evolution. Our results indicate mosaic evolution of these features, with *Galesaurus* exhibiting some characters more primitive than those to *Thrinaxodon* and others shared with probainognathians (the cynodont subclade that includes mammals) to the exclusion of *Thrinaxodon*. The morphology of the maxillary canal differs markedly between these taxa. In *Galesaurus* it has relatively few ramifications, more similar to those of probainognathians, and its caudal section is very short, a primitive feature shared with gorgonopsians and therocephalians. The otic labyrinth of *Galesaurus* is generally similar to that of *Thrinaxodon*, but differs in some notable features (e.g., proportional size of the anterior semicircular canal).

Additionally, the use of computed tomography allowed us to recognize unusual, possibly autapomorphic features of the braincase of *Galesaurus* (unusually large paraflocculi of the brain and a distinct medioventrally-located notch on the anterior surface of the tabular, which forms the dorsal border of the large parafloccular lobe), which are unique to *Galesaurus* among therapsids with reconstructed endocasts. However, additional sampling is needed at the base of Cynodontia to test this.

Phylogenetic Affinities of the Fossil Elapids *Naja romani* and *Naja antiqua* (Serpentes: Elapidae)

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The genus *Naja* Laurenti, 1768 comprises 32 extant species of venomous snakes, commonly known as "cobras", allocated in four distinct lineages (Wüster et al., 2007, Mol. Phyl. Evol. 45:437–453): the Asian spitting-cobras (11 species, subgenus *Naja*), the African spitting-cobras (seven species, subgenus *Afronaja*), the African non-spitting open area clade (six species, subgenus *Uraeus*) and the African non-spitting forest clade (seven species, subgenus *Boulengerina*). In recent years, the diversity of the genus has grown considerably, mainly given to taxonomic revisions based on new molecular analyses and new discoveries in the field. Furthermore, while the taxonomy of the genus is now considered stable, its evolutionary history remains poorly understood, especially within the known lineages. Apart from the extant species, the genus *Naja* also presents a rich fossil record that spans from the Early/Middle Miocene to the Late Pliocene in Africa and Europe. This fossil record has been studied in the past, with important remarks on their distribution throughout the European continent (Bachmayer, F. & Szyndlar, Z., 1985, Ann. Naturhist. Mus. Wien, 87:79–100; Szyndlar, Z. & Rage, J. C., 1990, Amphibia-Reptilia 11:385–400; Szyndlar, Z. & Zerova, G. A., 1990, Ann. Naturhist. Mus. Wien 91A:53–61). Szyndlar & Rage (1990) provided an osteological description of the genus based on both extant and extinct species, in an important contribution showing their geographic distribution. However, no attempts have been made to conduct a broader phylogenetic analysis until then. Here, we present the first attempt to elucidate the phylogenetic history of the genus, with a morphological analysis that includes 26 of the 32 extant species along with key-fossil taxa from the Miocene *Naja antiqua* and *Naja romani*) and the Pliocene (*Naja depereti*).

Softshell Turtles as a Model for Testing the Framework of Dollo's Law

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Softshell turtles (Pan-Trionychidae) are a highly specialized extant group of strictly aquatic taxa with a long evolutionary history dating back to the Early Cretaceous. Their most peculiar character is a heavily reduced shell with the complete loss of the peripheral bony ring of the carapace. The only species with a partial peripheral ring are the Indian flapshell turtles (*Lissemys* spp.). Structural and developmental homology of this partial peripheral ring with the peripheral bones of other turtles has been previously demonstrated based on histology and ontogeny, but whether they represent primarily ancestral or secondarily reversed states remained unclear because of the basal position of *Lissemys* and the phylogenetic uncertainty around the extinct stem lineage of softshell turtles. We comprehensively revised previous morphological datasets of living and extinct pan-trionychids through the help of first-hand observations of key Mesozoic taxa. Parsimony analysis of the dataset employing a molecular scaffold and equal character weighting resulted in a topology that is in a fundamental conflict inconsistent with molecular divergence date estimates of deeply nested extant species. In contrast, implied weighting retrieved Lower Cretaceous fossil taxa as stem-trionychids, which is fully consistent with their stratigraphic occurrence and an Aptian-Santonian molecular age estimate for crown-trionychids. These results indicate that the lack of peripheral elements (i.e., the condition in crown-trionychines) is primitive for softshell turtles and that these elements were subsequently reacquired in *Lissemys*. The Indian flapshell turtle therefore demonstrates a homologous partial reversal of dermal bone loss and provides a model for testing Dollo's law of character loss-irreversibility in deep time. The reacquired peripherals may therefore be adaptive, urging the modern revision of the previous preliminary functional interpretation as insertions for neck retraction muscles.

Evolution of Sciuromorphy in a Supposed "Protrogomorphous" Rodent

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For 20 million years, a grade of rodents known as "protrogomorphs" dominated Northern America and Eurasia, from the late Paleocene to Oligocene. Today, there are few 'protrogomorph' species, such as the mountain beaver *Aplodontia rufa* and some bathyergids. Unlike other living rodents, but similar to other mammals, the origin of the masseter muscle in protrogomorphs is restricted to the zygomatic arch. Other extant rodents have an extended masseter, whereby it attaches onto the rostrum and in some cases, invades an enlarged infraorbital foramen. Here, we consider the cranioskeletal anatomy of fossil 'protrogomorphous' rodents using 3D-reconstructions produced from microCT-scans, traditional methods of observation and geometric morphometric methods. Particular attention is paid to an articulated skeleton of a new species of *Ischyromys* from the late Eocene of West Canyon Creek, Wyoming. We find that the rostral anatomy of supposed 'protrogomorphs' is variable and that the new species of *Ischyromys* exhibits myological similarities to those of 'sciuromorphous' species, such as squirrels and gophers. It has a large surface area on the rostrum (zygomatic plate) to accommodate the attachment of the lateral masseter onto the rostrum. It also has a large infraorbital foramen, smaller than that seen in 'hystricomorphous' rodents, but larger than in sciurids or *A. rufa*. Although geometric morphometric analyses place the specimen within a cluster of crown rodents, it possesses cranial and postrcranial characters that are absent or rarely seen in Rodentia, such as a robust fibula and masseteric fossa posterior to m2. *Ischyromys* and other fossil 'protrogomorphs' are therefore useful in informing our understanding of mosaic evolution in rodents and highlight the need to consistently distinguish between anatomical and cladistic terms.

Validating an Echidna (Mammalia: Monotremata) Musculoskeletal Model to Inform Mammalian Forelimb Evolution

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The ecomorphological success of therian mammals has been linked to their unique and highly versatile forelimb morphology: fully mobile scapula, ventrally oriented ball-and-socket shoulder joint, and 'parasagittal' limb posture and movement. In contrast, the earliest synapsids ("pelycosaurs") had bulky and constrained 'sprawling' forelimbs and limited ecological scope. Although the morphological transformation of the forelimb is striking, the functional consequences of this profound reorganization is not well characterized. Here, we explore the ramifications of forelimb morphology on function by modeling the musculoskeletal anatomy of the monotreme echidna. Monotremes are sister to therians, but possess anatomical features reminiscent of earlier forms (e.g., numerous large interlocking pectoral bones anchoring the forelimb to the body, a saddle-shaped glenoid, and a sprawling gait dictated by apparently constrained forelimb mobility). As such, monotremes can be particularly useful in guiding and validating functional reconstructions of extinct taxa. Previously, we have estimated range of motion and muscle moment arms in a published model of an echidna forelimb. For refinement and validation, we have now added to this minimalist model: more accurate 3D-muscle paths using iodine-enhanced contrast staining, muscle architecture, and experimentally-obtained passive limb kinematics using XROMM. Overall, we found some types of mobility limited by the skeletal morphology of the forelimb, as well as by the soft tissues. Important aspects of the echidna's posture and gait (e.g., internal humeral rotation) were reflected in model estimates of moment arms and torques. Several muscles have different functional roles compared to therians, concomitant with their differing size and positions. Our model not only allows correlation of musculoskeletal anatomy and function in this unique animal, but also offers guidance in building and interpreting models of fossil taxa spanning mammalian evolution.

Stabilizing Occlusion of Tooth-like Elements in a Jawless Mouth: Bilateral Asymmetry and Allometry as Alternate Solutions in Late Devonian Conodonts

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Conodonts are an extinct group of jawless vertebrates, which were equipped with a complex feeding apparatus composed of several tooth-like elements. Contrary to most vertebrates in which occlusion associates upper and lower teeth, in conodonts occlusion occurred between right and left elements. The evolution of morphological differences between occluding structures had thus to evolve as bilateral asymmetry. Within the apparatus, platform elements were composed of a free blade which contributed to align the occlusion of platforms involved in the comminution of food particles. The shape of such elements was described by a geometric morphometric approach in a Late Devonian set of samples of the genus *Polygnathus*. The main axis of variance corresponded to an asymmetry of the platform, differently expressed in right and left elements. This bilateral asymmetry may have been of functional relevance because morphological features such as lateral processes opposed to grooves on the opposite platform have been shown to increase the precision and stability of the occlusion. In other *Polygnathus* species, bilateral asymmetry was absent but a pronounced allometry existed from small heart-shaped to large lanceolate elements. Laterally expanded platforms of heart-shaped elements might have been an alternate way to ensure the stability during occlusion, by allowing a better anchorage in the soft tissues. Platform asymmetry and heart-shape may thus constitute two solutions to a same functional problem of ensuring precise occlusion in a jawless system. The diversity of solutions to this problem in the different contemporary *Polygnathus* groups shows the evolvability of their tooth-like elements. Possibly, the constraints exerted on developing teeth by the surrounding jaw bone did not exist in jawless animals such as conodonts, and this may have contributed to the lability of the covariation patterns between elements of the occlusal system.

How is a Dental Change Accommodated by the Jaw System: the Case of Orkney Mice

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House mice were introduced on Orkney following Viking invasion. They diversified locally, displaying an important diversity in tooth shape. On some islands, molar teeth display additional cusplets and unusual phenotypes that may constitute case studies for evaluating the potential functional relevance of dental changes. Two extreme dental morphologies were selected in wild-derived lab strains. 2D- and 3D-geometric morphometrics, dental topography, dental wear, biomechanics, estimation of masticatory muscle force, and *in vivo* bite force were quantified on a set of specimens from these two strains. The geometry of the upper and lower molar rows strongly differed between the two strains, despite the fact that additional cusplets only occur on upper molars. In agreement, dental topography differed for the upper row only. Surprisingly, the most unusual molar morphology appeared as the least complex because tooth simplification overwhelmed the signal related to the occurrence of additional cusplets. The two strains displayed similar bite force and muscle forces, showing that the difference in dental morphology was accommodated without major change in the rest of the masticatory apparatus. No functional counter-selection impeded this morphological evolution, since the unusual phenotypes did not disrupt occlusion and mastication.

Morphological Changes in the Skull of *Astyanax mexicanus* (Teleostei: Characidae) Associated with Eye Loss

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The concept of form agglutinates information about size, shape, orientation, and functional integration of parts within systems. The degree to which the form of living things is determined by genetic or non-genetic factors (such as physical or mechanical constraints) is still a subject of great debate. To study the origin of morphological diversity at a micro-evolutinary scale can help us understand more about morphological evolution in biological systems. The Mexican tetra, *Astyanax mexicanus*, consists of an eyed surface-dwelling form and several cave populations with different degrees of eye degeneration. Although spatially isolated and locally adapted, the two morphs remain interfertile, providing a valuable system for experimental evolutionary biology. Besides the dramatic reduction in eyes, a reduction in brain size and alterations in cranial morphology have also been documented for the cavefish. To investigate how morphological differences in the skull might result from alterations in soft tissues, 2D- and 3D-morphometric analyses were conducted on the cranial and axial skeleton of both morphs. These revealed a ~20% reduction in the braincase volume of the cavefish. Contrast-enhanced CT-scans of both morphs show differences between the cave and surface fish in the size, shape, and orientation of cranial muscles in contact with the eyes and mainly associated with the operculum and palate. These changes correlate with the results of shape analyses that have found previously unreported differences in individual cranial bones related to the orobranchial system. Since the concept of functional matrices argues that evolutionary modifications in the head may be driven by changes in soft tissues, which will then bring about appropriate changes in functionally related portions of the skeleton, *Astyanax mexicanus* offers an outstanding opportunity to study morphological evolution not just through genetic crossings but also tissue manipulation experiments.

Functional Implications of Extraordinary Fore Limb Shape and Low Elbow Mobility in the Weird Extinct Marsupial Megafauna Palorchestidae (Diprotodontia: Vombatomorphia)

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Reconstructing the paleoecology of extinct taxa is challenging, particularly when they have no living representatives and their anatomy differs greatly from other animals alive today. The Palorchestidae were an especially bizarre group of Australian megafauna known from the Oligocene through to their disappearance in the late Pleistocene. Distantly related to the modern wombat, they are best known for their 'tapir-like' crania and supposed flexible proboscis. In addition to this unusual skull, their skeleton also differed markedly from that of related marsupials. Their robust, oddly-proportioned forelimbs had near-flat humeroulnar articulations, which, along with their huge narrow claws, raise significant questions about how palorchestids used these limbs during life. Here, we present the first analysis of palorchestid postcrania to investigate how they may have used their forelimbs in locomotion and feeding. We used 3D-geometric morphometric and virtual range-of-motion analyses to determine how palorchestid forelimb shape and mobility differ from other marsupials, and whether other clawed mammals may be better functional analogues. Using a broad comparative sample, we found that palorchestid humeri more closely resembled wombats and some ground sloths in shape than their closest relatives, suggesting potential functional similarities. However, when examining the elbow joint, we saw that the largest species *Palorchestes azael* had the lowest range of motion of any mammal measured, making the adaptive purpose of this morphology unclear. Our results show the palorchestid lineage underwent changes in humeral shape and reduction in humeroulnar mobility with body size increase, indicating very different functional capabilities than their kin. We propose that the uniquely fixed elbow in *P. azael* was an allometric adaptation for stability in response to mass increase in a lineage already committed to specialist forelimb use in food acquisition.

The Lateral Line System of *Polypterus*, *Lepisosteus*, and *Amia* (Osteichthyes: Actinopterygii)

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We describe and compare the lateral line system of the non-teleost actinopterygian genera *Polypterus* (Cladistii: Polypteriformes), *Lepisosteus* (Holostei: Lepisosteiformes) and *Amia* (Holostei: Amiiformes). We combine the analysis of ethanol-preserved specimens, stained and cleared-and-stained specimens, and 3D-models generated by CT-scanning, and incorporate data of ontogeny and innervation. We redescribe and compare the number and distribution of canal neuromasts and lines of superficial neuromasts, their innervation, the course of lateral line canals in the head, and their association to skull bones. We also propose a unifying terminology for canals and lines of superficial neuromasts that highlights phylogenetically relevant characters. The lateral line system of these groups is representative of the plesiomorphic condition for Actinopterygii, and can be used as a reference for comparison with members of the hyperdiverse clade Teleostei, in which the lateral line system is highly diversified. This study is funded by São Paulo Research Foundation (FAPESP).

New Insights into the Cranial Circulation and Innervation of Baenid Turtles

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Variation to the internal carotid and cranial innervation system has played an important role in the systematics of fossil and living turtles.

Baenidae, for instance, a clade of freshwater turtles that persisted from the Early Cretaceous to the Eocene, is diagnosed as a member of Paracryptodira, one of the primary clades of crown turtles, by the location of the foramen posterius canalis carotici interni halfway along the suture between the pterygoid and basisphenoid. Numerous foramina are highlighted in descriptions of baenid skulls, but the exact path of the canals they highlight is typically obscured within the skull making it difficult to assess their true homology. CT-scanning and 3D-modeling of the internal carotid, lateral head vein, and facial nerve (VII) of a well preserved skull of *Eubaena cephalica* from the Hell Creek Formation of North Dakota revealed that the second bifurcation along the path of the internal carotid canal corresponds to the split with the vidian nerve (VII) and not the palatine branch of the carotid artery. This contradicts previous ideas about the circulation system of baenid turtles, as the palatine branch of the carotid artery was persistently discussed as being present in paracryptodires. As the absence of the palatal branch questions the monophyly of paracryptodires and may have significance to the systematics of turtles, future work will need to clarify the distribution of this pattern across turtles.

Strength Indicators, Shape Variation and Modularity of Palearctic Mustelids (Carnivora: Mustelidae) Mandible

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The mandibles of 14 extant species of Palearctic Mustelidae from the genera *Enhydra*, *Gulo*, *Meles*, *Lutra*, *Martes* and *Mustela* were analyzed through traditional and two-dimensional geometric morphometrics. A set of 16 landmarks was digitized on the mandibles of 290 specimens and used in geometric morphometrics to investigate shape variation, morphological integration and modularity in mustelid mandible. The analyses were conducted for the original data, size-corrected data and phylogenetic independent contrasts. The two-module hypothesis (subdivision of mandible into the alveolar region and the ascending ramus) with the masseteric fossa included in the corpus was supported for all sets of data, though a clear modularity in the mustelid mandible is seen at the interspecific level. The allometry correction reduces covariation, and correction for phylogeny increases integration of the mustelid mandibles. Principal component analysis and canonical variates analysis were performed on Procrustes coordinates to explore the relationship between mandibular shape and diet in mustelids. Two variants of mandibular ramus shape are observed in mustelids. Height of the mandibular corpus under the canines and molar complex, length of the carnassial, slicing and crushing area of the molar complex and premolar row length are related with certain food objects. The differences in mandibular traits of the species studied are partly determined both by their evolutionary history and ecological preferences. Calculated strength indicators for the mandibular corpus and teeth (lower and upper canines and carnassials) display the different loads on the jaw structures due to different trophic specialization.

Periderm Invasion Contributes to the Epithelial Lining of the Teleost Pharynx

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The gnathostome pharyngeal cavity functions in food transport and respiration. In amniotes the mouth and nares are the only channels allowing direct contact between internal and external epithelia. In teleost fish, gill slits arise through opening of endodermal pouches and connect the pharynx to the exterior. Using zebrafish (*Danio rerio*) as a model, we investigated the nature of the pharynx epithelium, in particular whether external epithelia migrate into the pharynx via the pharyngeal pouches (presumptive gill slits) early in development. Surprisingly, we find that the pharyngeal endoderm becomes overlain, not by ectoderm, but by cells with a peridermal phenotype. In a wave starting from pouch 2, peridermal cells from the outer skin layer invade the successive pouches until halfway their depth. Here, the peridermal cells connect to cells inside the pharyngeal cavity that express periderm markers. The latter population expands along the midline from anterior to posterior until the esophagus-gut boundary. The result is a bilayered pharyngeal epithelium composed of endoderm overlain by periderm-like cells. This finding of a mixed composition of the pharyngeal epithelium is relevant in view of (1) the contribution of the epithelium to various pharynx-derived organs, (2) the importance of signaling between pharyngeal epithelium and underlying neural crest derived mesenchyme for the development of pharyngeal derivatives (including the visceral skeleton), and (3) the mechanism of lumen formation in the pharynx. Supported by Ghent University Research Fund (n° BOF24J2015001401).

Visualizing the Cellular Pathways for Transforming Amphibian Larval Cartilages into Adult Shapes

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Unlike most vertebrates, salamanders and frogs have two periods of development (embryogenesis and metamorphosis), which produce great ontogenetic variation in skeletal morphology within each group, but relatively little phylogenetic variation compared with other major vertebrate clades. This discrepancy between ontogenetic and phylogenetic variation is most evident in the pharyngeal arch (PA) skeleton, which supports very different feeding and breathing behaviors in larval and postmetamorphic stages, and persists largely as cartilage throughout larval growth and metamorphosis. I have proposed that this unusual retention of cartilage derives from tissue properties that distinguish cartilage from bone and enabled the evolution of dramatic shape changes in lower jaw, ceratohyal and branchial arch cartilages. Whereas bone grows by depositing matrix on external surfaces, cartilage grows by cell division, cell death, matrix secretion and changes in cell size and shape in its interior. Investigations of the cell behaviors involved in the remodeling of PA cartilages in salamanders and frogs suggest three distinct cellular pathways are involved: 1) *de novo* condensation and differentiation of cells adjacent to a larval cartilage to add new parts, 2) spatially integrated cell behaviors within a larval cartilage that reshape it without disrupting its structural or functional integrity, and 3) spatially segregated cell behaviors that drive the morphogenesis of a new adult cartilage within a largely resorbing larval cartilage. This talk provides evidence for pathways 2 and 3 occurring in frog lower jaw and hyoid cartilages respectively, and for pathway 1 in salamander hyoid and first ceratobranchial cartilages. It also addresses how choice of pathway relates to the amount of shape change required to transition from larval to adult function, the cellular ontogeny adopted by the larval cartilage, and the necessity to remain load bearing throughout metamorphosis.

Climate Change and Its Effects on Lizard Body Shape: Is This Affecting *Tropidurus catalanensis* (Squamata:Tropiduridae)?

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As global warming continues, it is important to highlight that environmental changes can influence animal physiology, morphology and behavior, especially in small ectotherms like lizards. Among phenotypic traits, morphology relates to animal performance, thus influencing an individuals' survival and reproduction. In Brazil, the genus *Tropidurus* (Squamata:Tropiduridae) has undergone high ecological and morphological diversification and wide distribution over different biomes, making it a great biological model for studies focused on understanding the influence of environmental parameters on morphological changes. In this context, we aimed to investigate associations between body shape and temperature and precipitation rates in *Tropidurus catalanensis*. We measured 22 morphological traits related to limbs, head, tail and snout-vent length, totaling 237 specimens (males and females) from herpetological collections. We then performed Principal Component Analysis (PCA) on all morphological traits, and investigated correlations between morphology and climatic parameters (accessed from inmet.gov.br database). We accessed temperature and precipitation data based on the year and locality that each individual was collected in the field, in order to access mean values of climatic parameters experienced by an individual during its lifetime. Our results show significant correlations between female body shape and temperature regimes, while in males this relationship was less clear. Precipitation regimes were also associated with body shape, although there was no single pattern defining such relationship: males and females only from specific localities presented a correlation between these parameters. From these preliminary results we conclude that males and females respond differently to temperature and precipitation regimes during their lifetime, with the associations between temperature and female body shape the most significant.

Killing them Softly: Ontogeny of Jaw Mechanics and Stiffness in Mollusk-Feeding Freshwater Stingrays

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Durophagous predators consume hard-shelled prey such as bivalves, gastropods, and large crustaceans, typically by crushing the mineralized exoskeleton. This is energetically costly from the point of view of the bite forces involved, handling times, and the stresses inflicted on the predator's skeleton. As such, it is not uncommon for durophagous taxa to display an ontogenetic shift from softer to harder prey items, implying that it is relatively difficult for smaller animals to consume shelled prey. Batoid fishes (rays, skates, sawfishes, and guitarfishes) have independently evolved durophagy multiple times, despite the challenges associated with crushing prey harder than their own cartilaginous skeleton. *Potamotrygon leopoldi* is a durophagous freshwater ray endemic to the Xingu River in Brazil, with a jaw morphology superficially similar to its distant durophagous marine relatives, eagle rays (e.g., *Aetomylaeus*, *Aetobatus*). We examined the arrangement of the jaw materials of *P. leopoldi* to resist bending (2nd moment of area) and jaw mineralization over ontogeny using computed tomography (CT) scanning. We found that the jaws of *P. leopoldi* do not resist bending nearly as well as other durophagous elasmobranchs and possess a skeleton that is stiffest nearest the jaw joints rather than beneath the dentition. While jaw stiffness has similar material distribution over ontogeny, mineralization of the jaws under the teeth increases. Neonate rays have very low jaw stiffness and poor mineralization, suggesting that *P. leopoldi* may not feed on hard-shelled prey early in life. These differences in the shape, stiffness and mineralization of the jaws of *P. leopoldi* compared to its durophagous relatives show there are several solutions to the problem of crushing shelled prey with a compliant skeleton.

Unveiling the Invisible: a New Approach for the Selective Contrast Enhancement of Integumentary Structures in X-ray Tomography

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The development of micro-computed tomography (μCT) conveniently allows to display and analyze morphology in 3D. However, in spite of the routine application of μCT in various biological disciplines, several problems with simultaneously capturing fine details of the surface and the internal anatomy with sufficient contrast still persist. This is mainly due to the low X-ray absorbance of many delicate integumentary structures. We developed a new approach that relies on readily-available, conventional sputter coaters to overcome this shortcoming: covering samples with a thin layer of gold prior to μCT-scanning selectively enhances the contrast of the integumentary surface. We applied this new method to a wide array of taxa and achieved an average gain of surface contrast of 1008% if compared to untreated samples. Contrast was not only enhanced, but even previously invisible (i.e., X-ray transparent) structures such as the barbules of avian feathers now become distinguishable from background noise. Furthermore, the increased contrast of surface structures relative to internal tissues allows the automatic, threshold-based mesh extraction of the sample's surface (e.g., epidermis), which, without coating, frequently has similar gray values in μCT-scans as internal anatomical structures. We expect that this methodological advancement consequently will be instrumental for a number of biological disciplines that depend on accurate morphological data of internal as well as external structures.

Seismic Signaling: Morphological Adaptations to the Hind Limb in Three Species of African Mole-rats (Bathyergidae)

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Seismic signaling using hind foot drumming plays a crucial role during communication in several species of African mole-rats (Bathyergidae). These signals are produced by striking the ground repeatedly at rapid speeds with alternating hind limbs using flexion and extension of the hip and knee. This study aimed to determine if the hind limb osteology and musculature differed between drumming and non-drumming species of Bathyergidae. Both left and right formalin fixed hind limbs N=48 (n=16 of each species) of two drumming species, *Georychus capensis* and *Bathyergus suillus* and one non-drumming species, *Cryptomys hottentotus natalensis* were dissected to determine the origin and insertion of muscles. After dissection, all soft tissue was removed by maceration. The bones of the hind limb and pelvis were photographed and exact origins and insertions were mapped onto the images. The ilial shaft, distal femoral shaft and the tibia were more robust in the drumming species (*G.capensis* and *B. suillius*) compared to *C. h. natalensis.* The origins and insertions of all three species were similar except for the *m. gracilis*. In both drumming species the *m. gracilis* was a large single muscle; in contrast in *C. h. natalensis* an additional caudal part of the *m. gracilis* was observed. In all three species, the *m. tensor fasciae latae* was absent. It is unlikely that the *m. gracilis* plays a role in hind foot drumming as the singularity or doubling of this muscle has been reported in numerous non-drumming rodents. The ilium, femoral shaft and tibia are the main origin and insertion sites respectively of several muscles that act during flexion and extension of the hip and knee. Therefore, the more robust nature of these bones in the drumming species could be caused by the additional muscular force exerted during rapid flexion and extension of the hip and knee during drumming.

Cranial Diversity and Evolution in Shieldtail Snakes (Serpentes: Uropeltidae)

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As with other aspects of the biology of fossorial taxa, the diversity and diversification of cranial morphology of head-first burrowing vertebrates is relatively understudied. Shieldtails (Serpentes: Uropeltidae) are a family of small fossorial snakes, endemic to Sri Lanka and peninsular India. There are eight genera and 55 species currently recognized. This is a poorly understood group, partly due to their secretive habits and confusing taxonomic history. Although uropeltids seem to exhibit high levels of morphological diversity and have some highly distinct phenotypic features, their morphology has not been studied using a quantitative approach. Combining 3D-geometric morphometrics (from microCT-data) with a new, dated multigene phylogeny, we determined phylomorphospace occupation of skull shape, and investigated patterns of morphological diversification across time and space. We assessed the degree to which skull shape is influenced by variables such as body size, geography and phylogeny, and tested hypotheses including i) that rates of lineage diversification are correlated with morphological diversification, and ii) that patterns of diversification are similar in mainland and island lineages. Uropeltid crania vary in features including snout shape and elongation of the occipital region, which might be indicative of differing burrowing styles. Analysis of phylomophospace reveals convergence of head shape between some Indian *Uropeltis* and Sri Lankan *Rhinophis*, so that head shape variation is not only partitioned phylogenetically, but that behavioral and/or ecological factors likely also influence morphology in the group.

Think Big, Evolutionary Allometry as a Major Factor in Rates, Trajectories and Scaling of Morphological Evolution of the Primate Brain Shape

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Primates constitute one of the most successful and diverse mammalian clades. One key factor in their diversification is the evolution of their peculiar brain morphology. However, the evolutionary and developmental processes determining the relevant shape changes in the primate brain remain largely unknown. In this study, we used 3D-geometric morphometrics, phylogenetic comparative methods and Bookstein's novel concept of scaling in shape variation to understand the factors influencing rates, trajectories and scaling of brain shape in a sample of 146 species including members from each major primate clade (excluding *Homo*). We found that only Hominoidea and Cercopithecinae showed a significant evolutionary allometry after controlling for phylogeny, whereas Strepsirrhini, Colobinae and Platyrrhini did not. However, Hominoidea and Cercopithecinae both showed markedly high rates of morphological evolution, whereas Strepsirrhini and Platyrrhini display a significant slowdown. As a consequence, Hominoidea and Cercopithecinae have different trajectories and magnitudes of shape changes when compared to the remaining clades. Apes, lesser apes and cercopiths tend to have an overall globular brain shape with more developed frontal lobes. Furthermore, there is a large-scale effect (global pattern of variation) of size on brain

shape in Hominoidea and Cercopithecinae, whereas size better describes smaller scales of variation (local pattern) in the slowly evolving clades. In conclusion, our results suggest that the evolution of allometry may have favored shape changes at larger scales and promoted the rapid evolution exhibited by Hominoidea and Cercopithecinae. On the other hand, the smaller scale effect of size on brain shape of Strepsirrhini and Platyrrhini might have had a key role in their reduced evolutionary rates.

Three-Dimensional Deformation of Tendon-Bone Insertions under Load

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The insertion of the Achilles tendon into the calcaneus transmits forces between soft and hard tissue. From an adaptionist perspective, the insertional tissues are expected to distribute stress homogeneously, in spite of the abrupt change in tissue elastic behavior. But it remains yet unclear, whether and how they achieve those properties. Based on the curved course of the tendon fibers within the entheseal fibrocartilage, we developed a simplistic mechanical model to predict deformation. These predictions are compared to three-dimensional images of relaxed and loaded Achilles tendon insertions of mice [*Mus musculus*, strain C57BL/6J, n = 3], acquired using synchrotron radiation-based micro-computed tomography with propagation-based phase-contrast. According to the model, higher stress is expected to occur in the deep fibers, than in the superficial fibers of the fibrocartilage. Several factors that could mitigate an inhomogeneous distribution of stress were identified: (1) Compliance of the fibrocartilage could be low. (2) Layers of collagen fibers could exhibit length reserves adapted to the taut arrangement or (3) an adaptive tensile behavior. The tomographic images are the first to render the three-dimensional deformation of intact tendon insertions. The compression of the fibrocartilage is substantial under the permanent load of the experiment. Fibers in the deep tendon have a wavy course in the relaxed and a straight course in the loaded state. Hence, length reserves in the deep tendon could contribute to a more homogeneous stress distribution at higher loads. The fibrocartilage does not contribute to a homogenization of the expected kind of stresses in a static load case. But it still is a candidate factor under more dynamic physiological loads.

Anatomical Specialization in the Largest of Caimans: the Girdles of *Purussaurus mirandai* (Alligatoridae) from the Miocene of Venezuela

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Crown-group Crocodylia are amphibious, carnivorous large reptiles found in various aquatic environments in the Tropics and Subtropics. With a low flattened body profile and long powerful tails, they are well suited for swimming, but all also venture on land for frequent basking and for nesting and oviposition, while employing various types of locomotor patterns on land, including bounding and galloping gaits in some taxa. Independent of size, taxonomy, and locomotory capabilities, however, the precaudal vertebral count in all crown-group crocodylians is remarkably conservative, consisting of 9 cervicals, 15 dorsals and 2 sacrals. It is only in non-crocodylian crocodylomorphs that deviation from this pattern is evident. Here, we report on the first member of crown-Crocodylia, the late Miocene giant caimanine *Purussaurus mirandai* (which reaches body lengths exceeding 10 m), that has three sacrals, two true or primordial sacral vertebrae and one dorsosacral, which articulate with the ilium. Following recent discussions in the literature of hox gene expression in relation to axial compartmentalization, we propose that an earlier timing of gene expression of *Hox11* and partial suppression of *Hox10* could be coupled with the formation of an additional dorsosacral in *P. mirandai*. The deviant vertebral count in this extinct species is also supported by the ilium morphology, which shows three distinct attachment areas for sacral ribs in several specimens, thus ruling out a pathological condition of a single individual. In the pectoral region, *P. mirandai* has narrow scapular blades oriented dorsally and posteriorly, ventromedially and slightly posteriorly oriented coracoids, as well as a narrow scapulocoracoid contact (lacking an anterior expansion) between both girdle elements; a condition that again differs strongly from extant crocodylians. We speculate that the peculiar girdle morphology is related to the giant animals' size and body mass.

Comparative Waterfall-climbing Kinematics and Performance of Juvenile Gobiid Fishes: How Conservative are Novel Functional Behaviors?

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Functional innovations can contribute substantially to the diversification of lineages. Older functional innovations might show greater variation than more recent innovations, due to the accrual of evolutionary changes through time. However, functional complexity and many-to-one mapping of structure to function might complicate such expectations.

To test the robustness of these expectations, we compared kinematics and performance by juveniles from multiple species of gobiid fishes for two novel waterfall-climbing behaviors: the ancestral style of "powerburst" climbing, and more recently evolved "inching", which is restricted to species of a single genus nested within the clade of powerburst climbers. Kinematic analyses suggest tight adherence to the respective powerburst or inching climbing style within the respective climbing behavior. Similar net climbing speeds across inching species seem, at first, to indicate that the more recent innovation exhibits less functional diversity. However, these similar net speeds arise through different pathways: *Sicyopterus stimpsoni* from Hawai'i move more slowly than *S. lagocephalus* from Reunion, but spend more time moving. Thus, interpretations of relative functional diversity might be masked by many-to-one mapping of structure to function. Moreover, similarity in net performance between these two climbing styles indicates that selection on climbing performance was likely not a major factor promoting the evolution of inching as a novel behavior, implicating processes such as exaptation in the origin of this functional novelty.

Application of Kinematic Analysis in Toxicology: Using Predator Avoidance Performance to Predict Population Decline as a Result of Pollutant Exposure

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Kinematic analysis of vertebrate behaviors has been integral to our understanding of phenotypic selection for well over a century. Many studies have focused on natural selection based on food availability, predator density, and habitat variability. The substantial body of knowledge gathered through these investigations and the resultant robust experimental designs may also inform the consequences of anthropogenic environmental alterations to population sustainability. In the current study, we connect predator avoidance performance with predation trials and population modeling to assess the adverse effects of fish exposure to the common environmental contaminant 17*b*-estradiol (E2) at environmentally relevant concentrations. Response latencies were approximately 40% greater in E2 exposed larval fathead minnows (*Pimephales promelas*) which also exhibited a nearly 20% decline in escape velocities in a standardized behavioral assay. Predation trials determined that these larvae were approximately 20% more likely to be captured and consumed by their native bluegill sunfish predator *Lepomis macrochirus* than unexposed larvae. Incorporating these data into a stage-structured population model demonstrated that enhanced predation mortality as a result of E2 exposure can result in a reduction of adult fathead minnow abundance by almost 60% relative to pristine conditions. These results indicate that subtle shifts in the behavior of individuals due to anthropogenic environmental change can affect species interactions causing substantial population-level consequences. This study also highlights the potential of vertebrate functional morphology to inform decision-making processes in applied sciences such as toxicology.

Armored with Skin and Bone: The Integumentary Morphology of the Antsingy Leaf Chameleon *Brookesia perarmata* (Iguania: Chamaeleonidae)

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Madagascar's ground-dwelling leaf chameleons (Brookesiinae, including the genera *Brookesia* and *Palleon*) form the sister taxon to all other chameleons (which are included in the Chamaeleoninae) and can readily be recognized by a number of unusual features. These Malagasy endemics possess a limited ability of color change, a rather dull coloration, and a non-prehensile tail that assists locomotion in the leaf litter on the forest floor. Morphologically, most species of the genus *Brookesia* stand out due to the presence of a peculiar "*Rückensäge*", a spiky row of dorsolateral projections of the vertebral column and an aberrant vertebral structure that has been subject to several osteological studies. In addition to the pronounced *Rückensäge*, the Antsingy leaf chameleon *B. perarmata* exhibits conspicuous, acuminate tubercle scales on the lateral flanks and extremities, potentially indicative of some form of integumentary armor. Such structures are not known for any other chamaeleonid and despite an appreciable interest in chameleon integumentary research in general, so far it was completely unknown what these tubercles truly are. μCT-imaging and various histological approaches revealed that the tubercle scales consist of osseous, multi-cusped cores embedded within the dermis, and that they consequently can be interpreted as osteoderms. To the best of our knowledge, this is the first record of osteoderms in the Chamaeleonidae. In some aspects of their tissue composition and location within the dermis, the osteoderms of *B. perarmata* differ from those known for lepidosaurians so far, but rather are somewhat reminiscent of crocodilian osteoderms. Therefore, our histological data also contribute to the knowledge on the structural diversity of lepidosaurian dermal armor in general.

Mammaliaform (?Haramiyida) Petrosals from the Berezovsk Coal Mine (Itat Fm., Bathonian), Siberia, Russia

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Three partially preserved mammaliaform petrosals from the Middle Jurassic Berezovsk coal mine (Krasnoyarsk Krai, Western Siberia, Russia) are tentatively assigned to Haramiyida. The vertebrate fossils of this locality are found in fluvio-lacustrine claystones and fine grained sandstones overlaying a coal layer of 50 m thickness. MicroCT-scanning and virtual 3D-reconstruction revealed a unique autapomorphic perforated

bony bar on the medial side of the cochlear nerve foramen inside the internal acoustic meatus in all three specimens. The short and protruding bony bar is fully preserved in two of the specimens, but broken in the third. Such a structure is not present in morganucodontans, docodontans (also known from the Berezovsk coal mine) or paulchoffatiid multituberculates. This thin perforated bar differs from the sieve-like cribriform plate of monotremes but resembles the primary bony lamina inside the cochlear canal of modern mammals. The bone of each petrosal is strongly vascularized and shows two main venous passage-ways crossing the cochlear canal, embracing the cochlear nerve entrance anteriorly and posteriorly. The petrosals are similar to those of other mammaliaforms such as *Morganucodon*, *Sinoconodon*, *Haldanodon*, and *Borealestes* by their inflated promontorium and short, curved, and apically inflated cochlear canal. These two derived characters exclude a tritylodontid (also abundant at Berezovsk) origin for the petrosals. The coiling of the bony cochlear canal of about 180° and the presence of an apical inflation (associated with a lagena) as well as a perilymphatic foramen clearly distinguish the Siberian petrosals from those of dryolestoids and more derived mammals. A prominent ridge on the ventral side of the promontorium (derived character) arranged perpendicularly to the crista interfenestralis is very similar to that seen in the Jurassic haramiyidan *Arboroharamiyia* and supports closer affinities to that taxon. After docodontans, haramiyidans are the second abundant mammaliaforms in the Berezovsk locality.

Jaw Kinematics, Tooth Wear and Digestive Physiology in Equids

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Despite copious documentation of wear patterns in numerous vertebrates, the etiology of dental wear is not completely understood. Central questions are whether wear features can be attributed to forage properties and/or chewing movements, and how wear, chewing efficiency and digestibility are interrelated. In an 18-month feeding study with six Shetland ponies (*Equus ferus caballus*), we explored the impact of alfalfa chaff and grass hay on the geometry of the postcanine wear surface and mandible movements. We applied dental treatments combined with mesowear analysis to periodically quantify macroscopic wear and quantified the chewing movements using marker-based 3D-high-frequency cinematography. Moreover, we measured the fecal particle size (FPS) as an indicator of chewing efficiency and the crude fiber and lignin contents as indicators of fiber digestibility. We found a diet-specific tooth wear pattern; when feeding on alfalfa chaff, the occlusal surfaces renewed after 2-3 weeks, while this was the case for grass hay after 4-7 weeks. There is a higher chewing frequency for alfalfa chaff compared to grass hay, with smaller rotational anterio–posterior but similar medio-lateral jaw movements. The degree of particle comminution was correlated with fiber digestibility, and FPSs were larger on alfalfa chaff as compared to the grass hay. Our data suggest that a decreased fiber digestibility is tolerated within physiological limits and that fiber digestibility improves with increasing chewing efficiency. Tooth wear is clearly the result of variations in forage physical property, and modulating chewing frequency is a way to adjust to these variations. This research was supported by the Max-Planck-Society.

Does Inner and Middle Ear Morphology Link to an Aquatic Adaptation in Crocodylomorphs (Crocodylomorpha: Thalattosuchia)?

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Bony labyrinth morphology and tympanic air spaces provide powerful proxies for ecological adaptations in vertebrates. The labyrinth is responsible for the sense of hearing, and balance and equilibrium. Semicircular canal morphology is influenced by locomotion and behavior, the cochlear duct however, by hearing sensitivity. Here, we investigate ancient crocodylomorphs that underwent a major evolutionary transition from semi-aquatic to marine environments. Thalattosuchia thrived from the Early Jurassic to the Early Cretaceous. They originated in shallow marine environments, but one subclade, Metriorhynchidae, evolved a streamlined body plan with paddle shaped limbs and a vertically orientated tail fluke. Besides obvious osteological changes, understanding shifts in cephalic sensory organs will be key to understanding how these ancient animals adapted to a radically new ecosystem. Using μCT-scanning we digitally segmented the bony labyrinths of various extinct and extant crocodylomorphs. This allows us an insight into how their morphology changed and adapted during the land-water transition. In protosuchians and extant crocodylians, the middle ears are acoustically coupled by two sinus pathways, dorsal and ventral to the brain endocast. Thalattosuchians, however, lack the dorsal pathway. The ventral pathway in basal thalattosuchians is formed by either: the basioccipital diverticulum (BaD) and median pharyngeal sinus (MPs), or by the recessus epitubaricum and the MPs (or both in some taxa). In Metriorhynchidae the BaD is lost, indicating lower sensitivity to low-frequency sounds. Within Metriorhynchidae the anterior and posterior semicircular canals are dorsoventrally shortened. Similar adaptations occur in other marine reptiles. Furthermore, the cochlear duct shortens in metriorhynchids, possibly related to a reduction in hearing sensitivity. Our results indicate that metriorhynchid ear morphology can be correlated with an adaptation to marine ecosystems.

Functional Morphology of the Chewing Mechanism in a Neotenic Sirenid Salamander

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Food processing describes any kind of mechanical reduction or preparation of food items prior to deglutition. The most commonly used processing mechanism in gnathostomes is ‘chewing’. Chewing is defined as any form of intraoral processing by rhythmic jaw movements and represents the most common processing mechanism in tetrapods. Non-mammalian tetrapods typically have a hinge-like jaw joint that only permits simple arcuate (open/close) movements of the mandible during chewing. By contrast, the specialized jaw systems in most mammals permit complex 3D-movements of the mandible involving propalineal (longitudinal) as well as transverse (lateral) movements. However, only limited information is available on intraoral processing mechanisms in reptiles and lissamphibians. In fact, it was generally accepted that many reptiles and most lissamphibians do not process food intraorally but rather swallow it whole and unreduced. Here, we use biplane high-speed fluoroscopy and 3D-kinematics analyses to show that the neotenic salamander *Siren intermedia* not only uses intraoral food processing but also relies on a mandibular motion pattern involving propalineal (11.72 ± 3.49 % of cranial length) as well as transverse (4.95 ± 2.05 ° angular displacement at the mandibular symphysis) movements. The mandibular motion pattern seen in *Siren* involves a complexity not previously documented for non-mammal tetrapods. Our data on intraoral food processing in lissamphibians also challenge the commonly held view that complex chewing movements are restricted to mammals.

Functional Classification of Dynamic Hand Shape in Primates

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Manipulation ability provides many animals with adaptive advantages in activities such as food acquisition and locomotion. Among primates, since they lack claws, this manipulation is primarily achieved by friction between the skin surfaces of the digits and palm of the hand and the object. The morphology of the bones in the hand has been extensively studied but there is little information on the dynamic shape the hand adopts during different grasping tasks, which limits the functional interpretation of hand morphology. This lack is primarily due to the difficulty in obtaining kinematic data from living primates whilst performing grasping tasks. Here, we demonstrate a novel technique based on markerless motion capture using video photogrammetry that allows us to capture three-dimensional finger kinematics during hand use. We then define and measure a mid-task pose for a specific action and use Procrustes superimposition to compare the fingertip and finger joint locations both between taxa and between tasks in a standardized fashion. We have measured the hand shape during foraging tasks for three primate species: *Macaca fuscata*, *Ateles beelzebub*, *Cebus apella*. Each monkey performed three different reach and gather actions with food items of different sizes. We also compared foraging poses with the grasp patterns associated with locomotor tasks (horizontal pole walking and vertical pole climbing). We demonstrate that there are task specific poses that are chosen across multiple taxa and we suggest that these reflect optimal hand use strategies for these tasks. We also use this information to develop task specific multibody dynamic computer simulations to provide a direct link between morphology and function, with the ultimate goal of establishing a better theoretical framework for primate manipulation and predicting the hand use capabilities of fossil primates. We thank Norihiko Maeda and the Kyoto University Primate Research Institute for their help and support.

Morphofunctional Transformations of Wings in Early Birds and the Evolution of Flapping Flight

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Flight origin in the transition between non-avian paravians to avians is a classic issue deeply explored. However, how the first steps of flight evolved among early Mesozoic birds has remained far less explored. In this study, we examine the potential flight strategies of a large number of stem avian lineages spread throughout a new comprehensive cladogram. We thus identified ancestral strategies and their related morphological variations, tracing the evolutionary pathway in the earliest stages of birds' flight. Our results illustrate a transition from a limited-term flapping flight capacity of *Archaeopteryx* and confuciusornithids to a flap-assisted gliding flight of *Jeholornis* and other stem pygostylians. This was mainly correlated to the elongation of their wings relative to the body mass that entailed efficient gliding phases, which allowed flap-gliding pre-ornithothoracines to perform prolonged flights. A subsequent transition from flap-assisted gliding to a sustained flapping capacity took place crownwards, among Ornithothoraces. This transition required an increase of flapping efficiency, which correlated to mass and wing length reduction—and the associated reduction of aerodynamic drag—, as well as to the enlargement of the olecranon, which improved the lever arm of the triceps for flapping. Such a flapping improvement shown by our results is consistent with other features that appeared in Ornithothoraces (e.g., supracoracoideus pulley in the shoulder, new arrangement of the trailing edge in flight feathers). Thus, several strategies that birds use today were already used by their Mesozoic counterparts. This highlights mechanical constraints acting on the long evolution of birds and limiting the basic modes of flight to just a few.

Forever Young: Linking Genome Size to Regeneration in Salamanders

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Salamanders are unexcelled among vertebrates in their ability to regenerate body parts throughout life. Salamanders also stand out in the accumulation of massive amounts of non-coding genomic DNA, mostly transposable elements, that has occurred repeatedly and independently in nearly every salamander lineage, with extensive variation in genome size between species. The selective advantage of regeneration is obvious, but that of large and variable genomes is not. In fact, large genomes can impose significant morphogenetic constraints in the form of cell size relative to body size, rates and patterns of reproduction and somatic development, and even life history traits, some of which appear to be maladaptive. Here, we explore the idea that both the ability to regenerate and genome expansion reflect a key developmental trait that evolved in the common ancestor of all living salamanders: systemic developmental retardation (SDR), such that salamander tissues are populated throughout life with weakly differentiated cells. This idea is supported by experimental evidence indicating that adult salamander tissues are populated with cells that can easily convert to stem cells capable of re-activating developmental programs necessary for regeneration. Thus salamander tissues are "histologically paedomorphic". We hypothesize that SDR has been achieved by allowing introns to grow through the accumulation of transposable elements and other kinds of selfish DNA leading to a global slowdown of gene expression across the genome ("intron delay"). This suggests a novel function for introns as non-coding regulators of gene expression, not just by their location, but also by their physical size (length). This also presents a novel view of genome expansion and its phenotypic consequences in salamanders as unavoidable trade-offs for the prodigious ability of salamanders to regenerate lost body parts.

Adaptive Radiation and Developmental Homeostasis of the Lake Tana Large African Barbs g. *Labeobarbus* (Cyprinidae; Teleostei)

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Fishes display multiple examples of adaptive radiation (AR). In many cases, AR proceeds in an explosive manner and is accompanied by genetic, ontogenetic and morphological perturbations. One of the questions is whether such perturbations are stressful for diverging forms and decrease their developmental homeostasis. To clarify this issue, we studied the sympatric forms of the African barbs g. *Labeobarbus* (Cyprinidae; Teleostei). These fish are members of the young species flock inhabiting the Lake Tana (Ethiopia). Their rapid AR is accompanied by the divergence of ontogenetic trajectories due to heterochronies leading to the formation of form-specific morphological traits. Despite the absence of robust isolation mechanisms impeding the gene flow, the ontogenetic differences between forms have a genetic background. To evaluate the influences of genetic and ontogenetic perturbations on developmental homeostasis, we analyzed the developmental instability in the ancestral and several morphologically distinct sympatric forms. Developmental instability is a characteristic of developmental homeostasis, depending on the genotype-environment interactions, and measured by the level of fluctuating asymmetry. A comparison of fluctuating asymmetry of the meristic and morphometric traits of barb skull bones in nature and under experimental conditions, during which all fish developed under standard conditions, did not reveal significant differences. Thus, genetic and ontogenetic changes accompanying AR do not disturb the developmental homeostasis of the diverging forms. Our finding allows hypothesizing that at early stages of AR morpho-functional adaptations may not arise *de novo* but "reflect patterns of ancestral developmental plasticity" as was proposed by M.J. West-Eberhard (2003, Developmental Plasticity and Evolution; Oxford University Press, New York). This hypothesis is supported by the experimentally detected ability of an ancestral form to follow the various ontogenetic trajectories in response to the alterations of hormonal status.

Community Limb Morphology of Artiodactyla as an Environmental Predictor

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Ecometric analyses quantify assemblage-level functional trait responses to environmental change and can be used to estimate paleoclimates from fossils preserved in a community or assemblage from a past location and time. We provide an ecometric model of Artiodactyla using gear ratios of postcranial bones that can be used to improve our understanding of the relationship between morphology and environment. The gear ratio is a measurement of the overall length of the element divided by the length of the in-lever. A low gear ratio indicates a long in-lever and a more plantigrade stance whereas a high gear ratio indicates a short in-lever and a more unguligrade stance. Previous research has established a relationship between the calcaneal gear ratio of carnivorans and ecoregion province, vegetation cover, and mean annual temperature. This work has not yet been expanded to artiodactyls, who have a nearly global distribution and frequently overlap geographically to create a myriad of unique communities. Here, we present ecometrics developed from gear ratios calculated using linear measurements of calcanea and radioulnae. Using community lists at 50km equidistant points, communities were sampled for mean and standard deviation of gear ratio as well as each of the environmental variables. A maximum likelihood approach was used to discern relationships between morphology and environmental variables, including temperature, precipitation, and vegetation cover. Anomalies were calculated between the actual values and the estimated values. For precipitation, anomalies produced by the calcaneum ranged between -6.30 and 2.60 (mean = -0.26) whereas anomalies produced by the radioulna ranged between -6.77 and 3.24 (mean = -0.14). An understanding of community morphology and environmental characteristics will enable better predictions of responses to expected future changes and, with this ecometric framework, fossils of artiodactyl postcrania can be used to interpret paleoenvironment.

Variation in the Bony Labyrinth (inner ear) of Anurans

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The inner ear provides sensory information of position and acceleration of the head during movement. It is thought that spatially specific behaviors influence the shape of the inner ear, as morphology will change to maximize sensitivity to these behaviors. In birds and mammals with agile and spatially complex movements, differences in canal shape, more specifically canal radius of curvature, are thought to enhance sensitivity to these behaviors. Documentation of inner ear variation in caecilians and fossorial snakes indicates that both groups may have adopted novel morphological traits thought to enhance sensitivity to movement below ground. However, it is not well understood if these relationships extend across vertebrates. By surveying the morphological variation within the inner ears of anurans, we can compare the morphological diversity against ecological niches to better understand how form relates to the life history of these animals. We present a survey of the morphological diversity of the bony labyrinth of anurans across 52 of the 55 extant families. Inner ear endocasts were generated from high-resolution micro-computed tomography (μCT) data, and we document significant variation in the size and shape of the inner ears across species. We investigate the influence of allometry, ecology, and phylogeny on inner ear morphology using 3D-geometric morphometrics and phylogenetic comparative methods. Implications regarding behavior and life history are also discussed. This project is made possible through the oVert (openVertebrate) NSF funded initiative.

Tips and Fits: Tricks to 3D-Puzzle Making

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Engaging the public and successfully articulating complex ideas about our scientific research are essential for promoting public awareness and support of science. The growing popularity of 3D-printers and CT-scanning have opened new avenues for engaging the public with biodiversity research. Large-scale digitization efforts of museum specimens such as oVert are making 3D-models of real specimens widely available via online platforms such as MorphoSource. These models, especially those of skeletons, easily lend themselves to creative outreach opportunities, such as puzzle making. Puzzles are easy to approach, provide hands-on experience, and can demonstrate complex problems in an engaging way. Here, we present our process for developing 3D-skeletal puzzles from the specimens available at the Florida Museum of Natural History. We explore a selection of specimens, reconstruction practices using VG Studio Max 3.2, printer types, plastic types, coloring, and attachment mechanisms. These newly created puzzles were created for the purpose of presenting easily identifiable homologous structures to the public in hands-on learning activities. Puzzles can be made more complex or simple depending on the learning objectives and the audience. Educators, students, and the general public can freely download these 3D-files for printing at home or in the classroom.

Mandibular Morphology Reveals the Ecological Dynamics of the Archosauromorph Diversification through the Early Mesozoic

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The radiation of the Archosauromorpha in the Triassic helped re-establish stable ecological dynamics following the end-Permian extinction, and established archosauromorph-dominated faunas that later fostered the rise of dinosaurs. However, most quantitative studies of the radiation neglect the basal archosauromorphs and Archosauriformes, and instead focus on dinosaur and pseudosuchian (crocodile-line) archosaur evolution in the later Triassic. Here, we provide an extensive, eco-morphological study of archosauromorph macroevolution through the early Mesozoic to develop a holistic understanding of their diversification. We use geometric and functional morphometrics alongside multivariate phylogenetic methods to infer patterns of trophic ecology and evolution from the mandibular morphology of 163 archosauromorph genera. We find that mandibular disparity, morphospace, and rates of evolution through time allow us to characterize the initial archosauromorph diversification in the Early Triassic as an adaptive radiation. Our results suggest that opportunism following extinction events was key to dinosaur success, providing the impetus for their diversification at the beginning of the Late Triassic and again in the Jurassic. Our study reveals a complex picture of archosauromorph trophic evolution involving both biotic and environmental factors. Our results support an extrinsic driver for the rise of the dinosaurs, but suggest there were some intrinsic pressures on trophic evolution in Late Triassic, which indicates that intrinsic factors may have played a greater role in driving archosauromorph macroevolution than previously thought.

Ossification Sequences in *Acrocephalus scirpaceus* (Aves: Passeriformes) and *Chroicocephalus ridibundus* (Aves: Laridae), with the Emphasis on Evolution of Avian Sternum and Wrist

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Our knowledge of the ossification sequences in extant birds is based primarily on the embryonic period. However, while some bones are known to ossify or fuse to other bones only after hatching, studies of the skeletal development in the posthatch period are rare and usually concerned with precocial species such as galliforms. We therefore compared the posthatch ossification sequences in two phylogenetically distant birds – an altricial passerine, *Acrocephalus scirpaceus*, and a semiprecocial gull, *Chroicocephalus ridibundus*. The order of ossification is very similar in these two species. At hatching, the skeleton of *A. scirpaceus* is relatively well-developed for an altricial bird despite a rapid posthatch growth in this species. However, the skull and leg bones are further developed in *C. ridibundus*. The order of ossification of the wrist bones closely follows the sequence observed in the fossil record, with the semilunate carpal and major metacarpal fusing first, followed by the alular metacarpal fusing with the major metacarpal, and then the major and minor metacarpal fusing proximally. The development of the sternum shows pronounced differences. In *C. ridibundus* it starts with a single, median ossification center which is then followed by two small mediolateral centers and several lateral centers (two large and two-three very small centers, located next to the sternal ribs). In contrast, in *A. scirpaceus* two lateral ossifications appear first, and the median center appears afterwards. This suggests a developmental retardation of the median center

(or, possibly, an acceleration of the lateral centers) in the passerines, although more species must be studied in order to define the entire clade that was affected by this event.

The Ortho- and Parakeratinized Epithelium of the Tongue in Birds – New Insight to Keratinization Processes

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Generally, it is defined that lingual mucosa in birds is covered with stratified keratinized epithelium, but the latest micro- and ultrastructural investigations revealed the presence of two different types of keratinized epithelium i.e., ortho- and parakeratinized epithelium. The aim of the present work is to order the nomenclature of birds' lingual epithelia by noting the structural differences between epithelia and determining the occurrence of those epithelia in functionally different areas of the bird's tongue. The studies were conducted on the tongue of adult birds characterized by different diets and feeding mechanisms (pecking, grazing, filter-feeding) and was performed by LM, SEM, TEM, IHC and Raman spectroscopy analysis. Both ortho- and parakeratinized epithelium are composed of three layers: basal, intermediate and cornified layer. The main structural differences in the parakeratinized epithelium are the presence of flattened cell nuclei in the cornified layer and an arrangement of keratin fibers in the cell cytoplasm of the cornified layer. The molecular analysis reveals that ortho- and parakeratinized epithelium accumulate alpha-keratin mostly in the lower epithelial layers and corneous beta proteins in the cornified layer. The percentage amount of corneous beta proteins in the cornified layer is higher in orthokeratinized epithelium. The morphometric analysis indicates differences in the thickness of the epithelium and the cornified layer in both types of epithelia. In conclusion, the orthokeratinized epithelium is generally located in places involved in food intake like lingual nail and mechanical papillae, whereas the parakeratinized epithelium is present in areas of food transport. The epithelia are characterized by different ways of performing their protective function, either through a thick cornified layer with higher amount of the corneous beta protein (orthokeratinized epithelium) or by a higher epithelium (parakeratinized epithelium).

Microstructure of the Lingual Mucosa in Anseriformes in View of Diverse Mechanisms of Food Intake

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Anseriformes are characterized by complex mechanisms of food intake i.e., pecking, grazing and filter-feeding. Until now, the morphology of the areas of the avian tongue involved in each mechanism was not established. The aim of the present study is to provide a detailed description of mucosal microstructures in view of the diverse diet and mechanisms of food intake in Anseriformes. The study was conducted on tongues of adult domestic duck (Anatidae) and domestic goose (Anserinae) observed in LM and SEM. The structure involved in pecking both in Anatidae and Anserinae is named lingual nail. This cornified plate of lingual epithelium is located on the ventral surface of the apex, projects from the front of the tongue and acts as a spoon. The small and large conical papillae of the body are engaged in grazing. In Anserinae, both types of conical papillae of the body are directed caudally, fit to lamellae of the beak and participate in grass cutting. In Anatidae only large conical papillae are directed caudally and are engaged in grazing. The conical papillae consist of distinct connective tissue cores covered with well cornified epithelium. Filtering food from water is possible due to the filter-feeding apparatus, which is composed of small and large conical papillae and filiform papillae. The filiform papillae as cornified processes of the epithelium are arranged among conical papillae in Anserinae. In Anatidae filiform papillae form dense and long bristles covering small conical papillae. The comparison of cornified microstructures of the lingual mucosa indicates that Anatidae are well adapted to life in the aquatic environment and to collecting food mainly by filter-feeding and pecking. Anserinae as terrestrial birds collect food predominantly by grazing and pecking. It is worth mentioning that Anserinae are less adapted to filter-feeding and Anatidae are suited to perform grazing.

Testing the Ancestral Embryonic Origin of the Gnathostome Gill arch and Paired Fin Skeleton

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Paired appendages are one of the most iconic examples of anatomical innovation in the evolutionary history of vertebrates, yet remarkably little is known about how they arose. The 19th century comparative anatomist Carl Gegenbaur proposed that gill arches and paired fins were built on a common plan, and that paired fins evolved as gill arch serial homologues. There are, however, no fossils documenting the transformation of a gill arch into a fin along the gnathostome stem and Gegenbaur's gill arch hypothesis is widely discounted owing to the presumed distinct embryonic origins of gill arches and paired fins, the former deriving from neural crest, and the latter from lateral plate mesoderm. Here, we use gene expression and histological analyses to characterize the development of the neural crest and lateral plate mesoderm in a cartilaginous fish, the little skate (*Leucoraja erinacea*), and cell lineage tracing to experimentally test the contribution of these tissues to the gill arch and paired fin skeletons. While we find that the skate gill arch skeleton derives predominantly from cranial neural crest, and that the pectoral girdle and fin skeleton derives exclusively from lateral plate mesoderm, we note that the transition from neural crest to mesoderm-derived skeletogenic mesenchyme is likely to reflect a continuum rather than a sharp boundary. For example, we find evidence of lateral plate mesodermal contribution to the posterior pharyngeal arch derivatives, including minor contributions to the posterior gill arch skeleton. Together with chimera-based and genetic lineage tracing data from chick and mouse, a scenario is emerging where the posterior gill arch skeleton of gnathostomes may have ancestrally received contributions from both neural crest and lateral plate mesoderm, implying Gegenbaur's serial homology hypothesis need not necessarily be rejected on the grounds of embryonic origin.

Some Details of the Green Frog's Skull Anatomy of the Genus *Pelophylax* (Anura, Ranidae)

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Despite the fact that frogs of the genus *Pelophylax* Fitzinger, 1843 are important for research on comparative anatomy of vertebrates, some details of skull anatomy of green frogs not previously described were found. At the base of the lateral branches of the nasal bones (nasale) we found sharp protrusions that are not described in the literature. They were called "spike-like" protrusions and could arise from retardation of ossification of the nasale. We showed that the maxillary bone (maxillare) in the upper jaw overlaps with the square-zygomatic bone (quadratojugale) for about 3mm. The quadratojugale is developed by ossification of the connective tissue ligament between the maxillare and the ossified lateral part of the square cartilage (pars quadrata palatoquadrati) or part of the square bone (quadratum). The quadratojugale is fused with part of the quadratum. We found that in green frogs a smaller part of the ligament that forms the quadratojugale is retained and connects the oral end of the quadratojugale to the medial side of the maxillare. Therefore, we can consider this ligament in green frogs to be homologous to the ligament between maxillare and quadratum in the upper jaw of Urodela, allowing to suggest a similar evolution of batrachian skulls. In the caudal part of the quadratojugale of green frogs, a flat process was found, that not described in other representatives of Anura and that we called "scaly". It has been found that in the lower jaw of green frogs the reduced dental bones (dentale) overlap by their rostral ends with the mento-mandibular bones (mento-mandibulare) and are fused with them. The details of the frog's skull anatomy of the genus *Pelophylax*, described here, may arise due to loss of bone, retardation to ossify, and fusion of the bone primordia. These details reflect simplification of structure as general evolutionary trajectory of batrachian skulls.

Functional Morphology of Trabecular Bone in the Lumbar Spine of Shrews (Mammalia: Soricidae)

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The nature of the form-function relationship varies across organisms, scales, and structures, and is especially difficult to understand for extreme or unique morphologies. Extra bony reinforcements have evolved in the lumbar spine of the shrew genus *Scutisorex*, but it is unclear what purpose these reinforcements serve. The extreme and unusual shape of *Scutisorex* lumbar vertebrae makes them difficult to compare with other shrews using conventional homology-based morphological analyses. To circumvent this problem, we used X-ray micro computed tomography (μCT) to analyze the internal structure of the vertebrae in a phylogenetically and ecologically broad sample of shrews (family Soricidae), including both currently known species of *Scutisorex*, which have different degrees of external vertebral modification. Internal trabecular bone architecture (TBA) correlates to *in vivo* bone loading, and is therefore informative about an animal's behavior, locomotion, and ecology. We used phylogenetic comparative methods and a variety of measurements collected on soricid TBA, including trabecular orientation and degree of anisotropy; bone volume fraction; and trabecular number, spacing, thickness, and connectivity; to test the following hypotheses: i) vertebral loading schemes vary across Soricidae according to locomotor type rather than size or phylogeny; and ii) a greater degree of external modification (within *Scutisorex*) corresponds to a vertebral column that is superior in bearing high *in vivo* loads. Because our sample includes one of the smallest known terrestrial mammals (*Suncus madagascariensis*), we also discuss the limitations of using TBA to investigate bone function in animals with extremely small vertebrae (maximum dimensions in the order of a few millimeters).

Exploring the Evolution of the Amniote Forelimb Musculature by Studying its Embryology

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In amniotes, cells from the dorsal portion of the somite, the dermomyotome, delaminate and migrate to invade the limb bud, in contrast to non-tetrapods in which at least some somitic extension takes place. Reaching the limb bud, these cells aggregate into a dorsal and ventral mass of pre-muscular cells. These two masses subdivide, forming smaller divisions that will eventually split into individualized recognizable muscles of the adult. The pattern of cleavage of the shoulder and arm muscles has been described only in a handful of species, representing urodeles, lizards, turtles, marsupials and birds. Since the time of these seminal investigations, the embryonic pattern of muscle development has been used sometimes as a tool for understanding homologies across amniotes, but we remain limited to the information provided by the few species investigated and the constraints of the available technologies at the times of these studies. Half a century later, we have a clearer picture of the phylogenetic relationships among clades and new tools for studying and visualizing developing anatomy. We studied the development of closely spaced embryonic series of different species of mammals, archosaurs, lizards and turtles, comprising most major groups of amniotes alive, and studied the embryology of forelimb muscles, along with the developing nerves and skeleton, by using fluorescent immunostaining and confocal microscopy. Our data reveals a sequence of early events and muscle division much more conserved across amniotes than previously described, also placing these early divisions in the context of the rest of the developing anatomy of the arm. We also tracked and followed the embryonic origin of each adult muscle, comparing it with their supposed homologues across different clades. Based on our results, we propose a reconsideration of some assumed homologies and provide new important information regarding the development and evolution of the amniote forelimb musculature.

Effects of Artificial Selection for Increased Voluntary Wheel Running on Hindlimb Skeletal Shape in Mice

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The combination of genetic programming and phenotypic plasticity in response to mechanical loads determines an individual's skeletal morphology. To explore how locomotor systems change under the influence of ontogeny and evolution, we used a mouse model to examine the effects of selective breeding for increased locomotor activity on hind limb skeletal shape and exercise response. A founding population of Hsd:ICR outbred mice was divided into closed "high runner" (HR) and control (C) lines. HR-mice were bred for increased voluntary wheel-running distance for 82 generations, while C animals were randomly bred. Young male HR (lab-designated Line 8) and C (Line 2) mice were randomly assigned to be permitted or denied wheel access, creating 4 groups: C wheel, C no wheel, HR wheel, and HR no wheel. After 4 weeks, mice were euthanized and right hindlimbs were microCT-scanned. Shapes of the os coxa, femur, and tibia were defined by digitizing three-dimensional landmarks on each specimen. Individual bones were scaled to the geometric mean of all possible linear distances among landmarks. Between-group differences were analyzed using canonical variates analysis and localized using the Euclidean distance matrix analysis (EDMA) Form procedure. EDMA Growth procedure was used to compare the trajectories of exercise-induced skeletal plasticity between HR and C animals. Shape analyses revealed HR- and C-mice differed in the mean shape and the plastic exercise response of the os coxa and proximal femur. Additionally, throughout the hindlimb, the non-exercised morphology of HR-mice did not resemble the exercise response of C-mice, indicating the wildtype plastic response was not genetically assimilated into HR-morphology. Our results suggest localized sensitivity to plastic and evolved morphological change in the hindlimb skeleton, provide further evidence of genetic regulation of the exercise response in bone, and inform our understanding of the evolutionary lability of the skeleton.

Braincase Pneumaticity in the Rhynchosaur *Mesosuchus browni* (Reptilia: Archosauromorpha) and its Implications for the Development of Pneumatic Sinuses in Archosaurs

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Pneumatic sinuses are invasions of air-filled chambers into surrounding bones. Their connection to the originating chamber leaves a foramen in the bone, through which they can be recognized when soft tissue is not present, such as in fossils. Pneumatic sinuses are present in living birds and crocodilians. They have been considered to be related to weight reduction and flying in the former, and to directional hearing and detection of low-frequency sounds in the latter. The fossil record shows that pneumatic sinuses were more widespread, being found in a number of extinct groups like sauropodomorphs or pterosaurs. However, they seemed to be absent in basal taxa of both clades and in stem-groups. Here, we report for the first time the presence of a pneumatic sinus in the braincase of a stem-archosaur. The braincase of the rhynchosaur *Mesosuchus browni* was CT-scanned and an open space in the basal tubera could be safely identified as a pneumatic sinus, occupying most of the basal tubera. However, its precise extent could not be assessed. The sinus opens externally through a pair of foramina into the suture between basioccipital and basisphenoid. Comparing the sinus in *Mesosuchus* with the ones of theropods and crocodylians, we conclude it is more similar to the latter and thus likely derived from the pharyngotympanic system, making the foramina homologous to the openings for the true Eustachian tubes. Braincase pneumatic sinuses may be more widespread in stem-groups than previously acknowledged as indications exist for the presence in rhynchosaurs like *Howesia* and *Hyperodapedon*, and in other archosauriforms like *Erythrosuchus*. Its function is still unclear, but the presence of a pneumatic sinus in *Mesosuchus*, and possibly in other stem-archosaurs, may indicate similar patterns of development and selective pressures were taking place outside the crown.

Redescription and Novel Information on the Cranium of the Triassic Archosauromorph *Euparkeria capensis*

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Archosauria (birds, crocodiles, and their extinct relatives) form a major part of terrestrial ecosystems today, and came to dominate the land during most of the Mesozoic after radiating following the Permian-Triassic extinction event. The archosauriform *Euparkeria capensis* from the Middle Triassic (Anisian) of South Africa has been of great scientific interest since its original description in 1913, because its anatomy suggested a close approximation to the common ancestor of crown clade Archosauria. As a result, *Euparkeria* has been widely used as an outgroup in phylogenetic analyses and when investigating patterns of trait evolution among archosaurs. Although described monographically in 1965, subsequent years have seen great advances in scientific understanding of early archosaurs and imaging techniques. We redescribe the cranium, excluding the braincase, of *Euparkeria* using all available fossil material and micro-computed tomographic data. Anatomical details that were previously unclear are fully described, including vomerine dentition, the epiptergoid, the number of premaxillary teeth, and the anterior palatal arrangement. The ectopterygoid is shown to be two-headed as in pseudosuchians, and the previous observations regarding of a number of other features used as phylogenetic characters are corrected. A new cranial reconstruction has been made, with cranial proportions and shape differing from previous estimates. *Euparkeria* can be placed within wider tetrapod evolutionary tendencies, including reduction in cranial element number, reduction of the vomeronasal organ, increase in brain and eye size, and increased focus on the marginal rather than palatal dentition. However, *Euparkeria* shows

a mosaic of features including a unique pattern of palatal dentition. The skull of *Euparkeria* continues to be very similar to that expected for the archosaur common ancestor, and the taxon remains a close outgroup to Archosauria.

Coronary Artery High Take-off in Rodents and the Possible Involvement of Smad2

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The coronary arteries (CAs) supply the mammalian heart with oxygenated blood. They arise from the right and left aortic valve sinuses at the aortic root. In humans, the occurrence of a CA arising ectopically from the tubular aorta, a condition called high take-off (HTO), is rare (<0.4%) and predisposes to sudden cardiac death. We have shown that HTO is relatively frequent in some laboratory mouse strains, and preliminary studies suggests that the Smad2rs29725537:C>A (Smad2C>A) allele is associated with HTO in this species. In order to test whether HTO occurs in association with Smad2C>A in rodents, we examined the anatomical origin of the CAs, by means of stereomicroscopy and a corrosion cast technique, in 3,388 specimens belonging to 17 rodent species. In addition, Smad2 DNA sequence from *M. musculus* was compared by Blastn analyses with that from six of the species examined in which this sequence is known (*Mus spretus*, *Rattus norvegicus*, *Apodemus sylvaticus*, *Myodes glareolus*, *Mesocricetus auratus*, *Microtus agrestis*). HTO occurred in nine out of 17 species studied. The incidence of HTO ranged from 0.4% to 6.5% (low) in three species and from 15.9% to 25% (high) in six species. The Smad2 sequence showed similarities higher than 75% for the whole gene, and higher than 71% for the intron sequence that includes the rs29725537:C>A Single Nucleotide Polymorphism. The Smad2C>A allele was identified only in *M. spretus* and *A. sylvaticus*, with high incidences of HTO, whereas the other four species showed low or null incidences. We conclude that HTO is a common trait in rodents, which does not lead to cardiac pathology probably due to the intramyocardial condition of their CAs, as opposed to the human subepicardial CAs. The Smad2C>A allele may be involved in the development of HTO and probably other phenotypes in different rodent species. Funding: CGL2017-85090-P, FPU15/03209, UMAJI75 and FEDER.

Looking for the Perfect Source of Taxonomic Characters: Bony Labyrinth Morphology of Suids (Mammalia: Suidae) Displays a Low Intra-specific Variability

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Paleobiological analyses crucially rely on correct specific identifications of fossil specimens. This identification is frequently hindered by difficulties in disentangling inter- and intra-specific variabilities. Craniomandibular, dental, and postcranial remains usually display a strong intra-specific variability that results from sexual dimorphism as well as ontogenetic, geographic, and idiosyncratic variations. For example, suid third molars are widely used in taxonomic studies but are also extremely variable within a species, both in terms of size and number of cusp(id)s. Ideal taxonomic characters used to define morphospecies should be much less variable within a species than between species. Here, we quantify intra-specific variation of the bony labyrinth (bony capsule of the inner ear) within large CT-scanned samples of two suid species: *Sus scrofa*, extant wild boar from France (n = 21) and '*Kolpochoerus*' *phacochoeroides*, a Plio-Pleistocene suid from Ahl al Oughlam, Morocco (n = 14). We quantified bony labyrinth shape and size using 3D-landmark-based geometric morphometrics. Shape variation along the first axis of the Principal Component Analysis shows a clear distinction between both species. The bony labyrinth shape is significantly different between the two species (Canonical Variate Analysis, p-value < 0.0001). Combining all PC-dimensions into a hierarchical analysis (that can be assimilated to a phenetic tree), we conclude that both species display an intra-specific variability that is much lower than the inter-specific variability. In addition, we could not detect any significant effect of neither sex nor age on the inner ear morphology within the sample of extant wild boars. Overall those results suggest a strong potential of inner ear morphology as a source of taxonomic characters that will form the basis for subsequent paleobiological analyses (e.g., phylogeny).

Physiological Characteristics of Sloth Hind limb Muscles

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Sloths exhibit obligatory suspensory locomotion and posture. These abilities involve hanging for extended periods of time, and although their behaviors require both strength and endurance, the muscle mass of sloths is reduced, thus requiring modifications to muscle architecture for large torque. Based on our previous findings in sloth forelimbs, it was predicted that their hind limb muscles are specialized for sustaining force by a predominant expression of slow myosin heavy chain (MHC) fibers that rely on cheap/rapid ATP re-synthesis. This hypothesis was tested by determining MHC fiber type (%) and muscle metabolism in two-toed (*C. hoffmanni*, N=3) and three-toed (*B. variegatus*, N=5) sloths using gel electrophoresis, immunohistochemistry, and enzyme assays. A primary expression of the slow MHC-1 isoform as well as moderate amounts of fast MHC-2A fibers were found in both species. Slow MHC fiber type (%) was greater in the flexors of *B. variegatus*, whereas expression of fast MHC-2A was greater in the extensor groups of *C. hoffmanni*. MHC-1

fibers were larger than MHC-2A fibers and comprised the greatest % CSA in each muscle sampled from both species. Sloth hind limb muscles showed a reliance on elevated activity for anaerobic enzymes compared to moderately low activity for aerobic enzymes, especially in *B. variegatus*, and enzyme activities showed little dependence on body size. These findings are less uniform than those from sloth fore limbs but emphasize a role in stabilization for the hindlimbs during suspensory habits, most notably in three-toed sloths. They further indicate that two-toed sloths may be capable of greater power generation for arboreal maneuvering. Nevertheless, the intrinsic properties observed match well with locomotor requirements of both species, and these modifications may have further evolved in unison with low metabolism and body temperature, and slow movement patterns as means to conserve energy in tree sloths.

The Skull of *Tanystropheus* as Revealed by Synchrotron Microtomography and its Implications for Phylogeny and Functional Morphology

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Tanystropheus is one of the most iconic reptiles from the Triassic due to its unique morphology, epitomized by its extremely elongated neck. Although its postcranial anatomy is well-documented, the skull morphology has remained enigmatic due to compression of specimens and strong cranial ontogenetic variation in *Tanystropheus*. We synchrotron μCT-scanned a virtually complete adult skull, which allows for the first detailed cranial description of the taxon. Our findings differ strongly from previous studies. The external nares were very likely confluent and rimmed by an anteriorly well-rounded premaxilla, showing a convergence to certain crown-group Crocodylia. The dentition is profoundly specialized towards catching fast swimming prey, with large fang-like marginal teeth anteriorly, as well as a row of fang-like vomerine teeth. The postorbital region differs strongly from previous interpretations and includes a dorsoventrally tall squamosal that contacted the jugal anteroventrally. The very high resolution of the scan allows for description of the articulation of individual bones, including the squamosal-quadrate articulation, which indicates possible streptostyly in *Tanystropheus* with functional implications regarding jaw mobility and prey acquisition. Finally, the atlas-axis complex and the braincase are described in detail, the endocast including the inner ear is reconstructed, and a full skull reconstruction is provided. The results of this study have strong implications for phylogeny and paleobiology. *Tanystropheus* shows many derived features in comparison to other tanystropheids and “protorosaurs”, particularly in the braincase, postorbital region, and snout, indicating Tanystropheidae were a morphologically diverse group. Finally, the dentition and shape of the skull indicates *Tanystropheus* hunted in an aquatic environment, providing further evidence for an at least semi-aquatic lifestyle for *Tanystropheus*.

Ontogeny of the Bizarre: Extreme Asymmetry in the Priapium of Phallostethid Fishes

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Bilateral symmetry is the predominant way of body patterning in the Bilateria, yet asymmetry is often a solution to evolutionary challenges. Whilst subtle asymmetries develop from small stochastic fluctuations, extreme asymmetry indicates genetic or environmental cues triggering differential genetic programs at corresponding loci. The priapium of male phallostethid fishes is extremely asymmetric. It develops as a modification of the paired pelvic fin anlagen. Early development is typically bilateral, then one primordial fin becomes the priapium whilst the other recedes. The side which forms the priapium appears to be determined at random (antisymmetric) in most species. The priapium is composed of over a dozen skeletal elements, and is distinctively different between tribes. NanoCT-scanning and clearing and staining of developmental stages of antisymmetric *Neosthethus bicornis* and *Phenacostethus smithi*, revealed that the priapium forms from modified elements of the pelvic fin, but also includes neoformations without pelvic-fin homologue. To identify genetic cascades underlying establishment of asymmetry in *N. bicornis*, males were collected in Sungei Buloh, Singapore. RNAseq was performed on left and right pelvic fin anlagen in triplicate from four developmental stages; and differential expression between paired sides was evaluated. To further investigate the findings from the transcriptome sequencing, we visualized the development of the neurons and muscles of the priapium with confocal microscopy. We observed significant proliferation of nerve fibres on the side of the pelvic fin anlagen that are becoming dominant, particularly in the posterior area where the papillary bone develops and the sperm duct and seminal vesicle are housed. Interestingly, myological asymmetry is less pronounced than skeletal asymmetry, the muscles of the regressive, non-priapial side persist and become associated with the skeleton of the priapium. Supported by the Leverhulme Trust.

The Overt Thematic Collections Network: 3D-Anatomical Data for Nearly Every Living Vertebrate Genus

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The oVert (openVertebrate) Thematic Collections Network—funded by the US National Science Foundation—is a new collaborative initiative among museums across the U.S. that aims to CT-scan ~20,000 fluid-preserved vertebrate specimens, representing over 80% of the approximately 10,500 extant genera. This project is generating free, publicly available three-dimensional anatomical data housed in the online MorphoSource database. We will also generate contrast-enhanced scans to reveal soft tissues and organs for a majority of the living vertebrate families. Our network of leading U.S. vertebrate collections is developing best practices and guidelines for high-throughput CT-scanning, including efficient workflows, preferred resolutions, and archival formats that optimize the variety of downstream applications. Using digitized collections data via iDigBio, we are locating data-rich specimens (with geocoded locality data, associated tissues and/or media files) in U.S. museum collections representing type species of extant genera. We then loan relevant specimens to one of six participating institutions serving as imaging centers for the TCN. To date, we have CT-scanned >2,300 fluid-preserved specimens that represent more than 2,100 extant genera in 500 vertebrate extant families. These provide a rich resource for comparative and functional anatomy and reference libraries for identifying fossils and even prey preferences from scat. The oVert TCN will provide a collection of digital imagery and three-dimensional volumes that is open for exploration, download, and use by the neontological and paleontological communities.

Diversification of Dermal Armor in Squamates

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The order Squamata contains over 10,000 species, many of which are small-bodied and occupy a low trophic position. As a result, the group displays a remarkable diversity of anti-predation defenses, including camouflage, audible, visual and chemical warning displays, a broad range of fight/flight behaviors and —universally— armor. All squamates are protected by toughened, keratinized scales and in some lineages these scales are buttressed by osteoderms. These bony subdermal plates strengthen the integument, provide additional ornamentation in the form of spines or keels, and may play a role in calcium sequestration and thermoregulation. Osteoderms are found in several orders of fish, mammals, amphibians, archosaurs, turtles and in 13 extant families of squamates. This study employs comparative phylogenetic analyses of micro-computed tomography (μCT) data to quantify and investigate the diversity of dermal armor across Squamata, with deep sampling in the families that are known to possess osteoderms. Our analysis reveals multiple independent origins of osteoderms within the order, with three clades—Cordylidae, Anguidae and egerniine skinks—displaying increased rate-shifts in the distribution and extent of their armor. There are repeated losses and gains of ossified armor within these three lineages, and variations in the extent and distribution of osteoderms are shown to be correlated with microhabitat but not climate.

Segmentation of Oral Epithelium in the Cheek Region in Mice

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Different organs and systems are formed by general patterning processes. Tooth development is one of the practical models that can help us understand the formation of sequential organs in general. We focus on the segmentation of oral epithelium during the development of the mouse molar tooth germ to solve the question of its pattern formation. The cultivation *in vitro* of molar primordia cut in two parts (anterior and posterior parts) documented that the rudimentary (R2) signaling center actively competes with the first molar (M1) early signaling center during formation of the primary enamel knot (pEK) of a nascent functional tooth. When the anterior and posterior parts were separated at ED14.3, both parts formed a similarly sized tooth germ in 6 days. The signaling center of the anterior part was recovered after one day of cultivation *in vitro*. In the posterior part the *Shh* signaling appeared one day later. The intact controls formed a similarly sized M1 tooth germ as in the anterior part of the dissected molar tooth. The signaling centers of the second molar did not appear before the third day of cultivation. Compared to M2, the second tooth from the cultured segments was obviously larger. Thus we confirmed that if separated from the M1 germ, R2 is able to revive its *Shh* signaling center and give rise to a full-size tooth germ. We attribute this to the loss of the inhibition of a posteriorly located developing early M1 *Shh* signaling center, which is in the intact molar germ actively inhibiting the former signalization of R2. Financial support: This study was supported by the Czech Science Foundation (18-04859S).

The Evolution of the Dermal Skeleton in the Paired Fins of Tetrapodomorph Fishes

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The fin-to-limb transition involved both the evolution of endoskeletal patterning and the loss of the dermal fin skeleton. However, understanding of dermal skeletal evolution in the paired fins of tetrapodomorph fishes is limited due to its poor preservation and fin rays being prepped away to expose the endoskeleton beneath. Here, we present micro-computed tomography (μCT) data on the pectoral fins of *Sauripterus taylori* (Rhizodontidae) and *Tiktaalik roseae* (Elpistostegidae), which allow for analysis of how the spatial distribution and morphology of fin rays evolved in tetrapodomorphs. In both taxa, dermal fin rays cover a substantial portion of the dorsal surface of the fin endoskeleton, a feature likely widespread among tetrapodomorph fishes. Notably, in *Tiktaalik* the distribution of fin rays is dorsoventrally asymmetric, with hemitrichia on the ventral surface being restricted further distally, indicating that the musculature of the distal fin was also dorsoventrally asymmetric. Additionally, the dorsal fin rays of *Tiktaalik* differ from those on the ventral surface in their cross sectional size and geometry. We compare these data with μCT-scans of pectoral fins of a diverse sampling of extant fishes, including *Neoceratodus forsteri*, *Polypterus*, *Acipenser*, *Danio*, *Thunna*, and *Leucoraja erinacea*. Comparative analyses reveal that dorsoventral asymmetries in the dermal skeleton are widespread among osteichthyans, suggesting an unrecognized axis of diversification in paired fins, and we predict that the developmental and genetic mechanisms for the dorsoventral patterning in limbs are plesiomorphic to gnathostomes.

Functional Morphology of the Middle Ear of *Homo* and *Pan* – Implications for the Evolution of Human Hearing Capacities

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Comparing hearing capacities of humans and chimpanzees reveals distinct differences between the two species with humans possessing a number of derived auditory characteristics. The functional basis for these differences is not yet understood but morphological differences in the ear region of humans and chimpanzees are known. Our aim was thus to experimentally study the functional morphology of the outer and middle ear of non-human apes for the first time. We measured the middle ear transfer function (METF) on cadavers of two common chimpanzees, three bonobos and 15 humans and added results from simulations of the sound pressure gain of the external auditory canal (EAC). We recorded stapes footplate vibrations using Laser-Doppler Vibrometry after gaining access to the tympanic cavity. Middle ears were excited acoustically through the EAC and the investigated frequency bandwidth ranged between 0.1 and 10 kHz. We found a number of differences between the METF of *Homo* and *Pan*. In the low frequencies (<1 kHz), the magnitude of the METF of *Pan* is greater compared to that of humans. This likely relates to a lower stiffness of the larger eardrum of *Pan* and is seen in the context of acoustic properties and/or need for long distance communication in the forested habitats most chimpanzees occupy. Humans and both chimpanzee species show a decrease in magnitude of the METF after 1 kHz. While the METF in humans continuously decreases until the end of the measuring range, it slopes upwards around 4-5 kHz in *Pan* progressing above the human curve. However, after adding the pressure gain of the EAC, when compared to *Pan* the magnitude of the human METF increases around 4 kHz which is also seen as a characteristic of the human mid-frequency hearing range. Our experiments indicate that auditory capacities of *Homo* and *Pan* are related to ear morphology, opening up new avenues for studying the evolution of hearing in fossil hominins.

Navigating Phylogenetic Lines of Least Resistance: a Phylometric morphospace Approach

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Projections of phylogeny into morphospace, i.e., phylomorphospace allow evolutionary relatedness and morphological diversity to be visualized. Positioning tree topologies within spaces produce estimates of branch length measured in units of morphospace distance. Evolutionary relatedness between observations is a source of distance information that is available to most of the biological systems we study. We can use this information to calibrate our perception of morphospace. We present a novel extension of the phylomorphospace approach which uses calibration to improve empirical estimates of theoretical morphospace. Warping morphospace around an ultrametric phylogeny results in space that is increasingly traversable along phylogenetic lines of least resistance, i.e., phylometric morphospace. We explore the behavior of this method using simulation, particularly when internal nodes have been misspecified due to uncertainty in ancestral state reconstruction. Incorporating distance-based information about evolutionary relatedness into the construction of phylometricmorphospace improves the informativeness of distance measures within this space, amounting to a phylogenetic correction of regions between point estimates of morphospace occupancy. The sampling distribution of measurable forms contained in phylometricmorphospace is structured by the tree topology. We expect a calibrated empirical morphospace to better estimate the 'spectrum of possible forms' (*sensu* Raup) when signals of, e.g., convergence and constraint captured in the tree are attenuated by the noise of merely measurable forms in the uncalibrated condition.

Evolution of Brain Size in Birds

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Vertebrates show dramatic interspecific variation in the size of their brains. The complexity of brains is considered to be the key factor of evolutionary success in vertebrates, and therefore an evolutionary trend towards increasing brain size and complexity is assumed. Large and complex brains evolved independently in birds and mammals. Birds have brains that are comparable in their relative size to the brains of mammals. However, in stark contrast to mammals, there is no general trend towards an increase of brain size in birds. Relatively large brains have evolved independently in many avian lineages. Highly encephalized orders are parrots (Psittaciformes), woodpeckers and relatives (Piciformes), hornbills, hoopoe and wood hoopoes (Bucerotiformes), owls (Strigiformes), storks (Ciconiiformes) and several families of songbirds (Passeriformes), mainly bowerbirds (Ptilorhynchidae) and corvids (Corvidae). Other highly encephalized groups are non-parasitic cuckoos (genus *Centropus*, *Phaenicophaeus* and *Coua*) and family Diomeidea and genus *Pelecanus* belonging to the clade water birds. Less encephalized groups include the basal lineages such as paleognaths and fowl (Galloanserae), and also pigeons (Columbiformes) and swifts, treeswifts and hummingbirds (Apodiformes). We suggest that this pattern of evolution is a result of simultaneous acting of selective pressures on cognitive enhancement and constraints on brain size, which may stem from the constraints on body size imposed by active flight. In this context, it will be most interesting to learn whether increased encephalization goes hand in hand with increased neuronal densities.

No Small Feet: Investigating Mass Distribution and Heteropody in the Past and Present

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Why do some quadrupedal animals have different sized fore and hind feet? Could this be connected to the position of their centers of mass, as an attempt to equalize underfoot pressure? In the trace fossil record, where extreme heteropody is commonplace, could center of mass position and pressure equalization attempts account for phenomena such as manus-only sauropod trackways? We took several approaches to exploring this question. We used 2D-foot alpha shapes derived from CT-scans of 29 extant species (consisting of mammals, reptiles, birds and amphibians), to examine the relationship between skeletal and skin foot surface area, and whether it is possible to predict *in vivo* foot contact area from fossil foot remains, or vice versa from fossil footprints. Underfoot soft tissue area was found to be ~1.67 times that of skeletal surface area (~2 times for manus, ~1.6 times for pes) with a high degree of predictability. We then gathered a database of 58 extant, quadrupedal animal skeletons (representing mammals, crocodiles, and lepidosaurs), consisting of freely available laser scans, CT-scans, and specimens from the Liverpool World Museum digitized using photogrammetry. Several measurements of the feet of these animals were taken and used to calculate heteropody. Convex hulls of the skeletons were then used to calculate center of mass positions for each. With this data we attempted to answer the question of whether center of mass position was generally correlated with heteropody in extant animals. Most animals clustered around a center of mass of ~50-70% and a heteropody index of ~60-140 (manus is 0.6 to 1.4 times pes size). However, the lizards studied showed CoM of less than 25% and the majority of semi-aquatic species exhibited extreme heteropody. Semi-aquatic mammals were the only sub-group to show a strong correlation, with higher heteropody ratios associated with a more anterior center of mass.

Never Change a Winning Team: The Jurassic Skeletal Fossil Record of †Hybodontiformes Reveals New Insights into Taxonomic Diversity and Ecomorphological Disparity of Mesozoic Chondrichthyan Fishes

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Shark-like chondrichthyans of the extinct order Hybodontiformes, which form the supposed sister group to Elasmobranchii (sharks, skates, and rays) are characterized, inter alia, by rather robust bodies with two dorsal fins supported by spines displaying hook-like denticles arranged along the posterior midline. Their dentitions indicate diverse morpho-functional adaptations in relation to prey and feeding, ranging from crushing, grinding, clutching, tearing to even cutting. Hybodontiforms first occurred in the Late Devonian (~360 Ma), surviving two of the 'big five' Phanerozoic mass extinction events until they finally disappeared at the end of the Cretaceous (~66 Ma). They were abundant and widespread during the Triassic and Jurassic occurring in fully marine to continental depositional environments. From the Early Cretaceous onwards hybodontiforms apparently underwent a diversity decline and subsequent adaptation to freshwaters, probably in response to increasing competition with elasmobranchs, which rapidly diversified from the Early Jurassic onwards. However, much uncertainty still surrounds the taxonomy and systematics of Mesozoic hybodontiforms. This is mainly because most species are based on isolated teeth and/or fin spines only, commonly displaying morphological characters that are either ambiguous or broadly distributed among these shark-like chondrichthyans. Conversely, disarticulated or articulated skeletons, which provide important taxonomic but also ecomorphological features, remain extremely rare and restricted to a few localities only. We provide a review of the skeletal fossil record of Jurassic hybodontiforms including yet undescribed specimens from the world-famous Fossil Lagerstätten of Lyme Regis, England (Early Jurassic) and Solnhofen, Germany (Late Jurassic), and discuss their significance for better understanding Mesozoic chondrichthyan diversity and disparity patterns using qualitative and quantitative approaches.

Effective CRISPR/Cas9 Gene Editing in the European Sturgeon (*Acipenser ruthenus*) Offers New Possibilities for Evo-Devo Studies in Basal Fishes

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European sturgeon (*Acipenser ruthenus*) belongs to one of only few extant non-teleost (or basal) fishes and its phylogenetic position makes it a very interesting model in evolutionary research. As a species commercially bred in aquaculture, it also offers the opportunity to obtain large quantities of embryos that could be subjected to experimental manipulations necessary for the study of gene functions and developmental mechanisms. Here, we report successful high-efficiency production of F0 mutants using CRISPR/Cas9-mediated mutagenesis. We successfully mutated the gene coding for the protein Tyrosinase, required for melanin synthesis and known for its low

pleiotropy. The resulting phenotypes are usually perfectly healthy and easily screenable partial or complete albinos. Using mutations in other developmental genes, we further show more severe phenotypic effects on sturgeon embryos and also discuss challenges and pitfalls of the method. Our results show that CRISPR/Cas9 can be used as an effective tool in the study of sturgeon developmental mechanisms, opening up new possibilities in evo-devo research of basal fishes and vertebrates. The work was supported by the European Union's Horizon 2020 research and innovation program under the Marie Skłodowska-Curie grant agreement No 751066 (to DJ).

Altered Migratory Patterns of Cranial Neural Crest Cells in Non-Teleost Fishes

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Cranial neural crest (CNC) is a transient cell population emerging during the formation of the neural tube that extensively migrates throughout the embryo in discrete streams. In all vertebrates, CNC stereotypically follows a tripartite pattern of migration along the AP axis so that the most anterior (trigeminal) stream emerges first, followed by hyoid and branchial CNC streams. Although this pattern is considered highly conserved across vertebrates, we have found a major alteration in CNC emergence and its migratory pattern in the embryos of non-teleost fishes (bichirs, sturgeons, and gars). In bichir and gar embryos, emigration of the hyoid CNC stream is seemingly accelerated when compared to the trigeminal stream. Interestingly, this heterochronic shift is developmentally associated with the early formation of their key larval adaptive structures of hyoid arch origin, namely the external gills (bichir) and the large operculum (gar). In sturgeon, the hyoid and branchial CNC cells initially constitute a single hyobranchial sheet, which becomes separated only later in concert with the second pharyngeal pouch morphogenesis. Moreover, in all non-teleost fish embryos, the trigeminal CNC cells interact with the preoral gut (POG) forming a conspicuous anteriormost endodermal structure. Thus, the POG provides a key patterning influence on the trigeminal CNC cells, identical to the pharyngeal pouches on the more posterior CNC streams.

Morphology and Function of the Avian Furcula

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The diversification of bird flight involved substantial changes to the pectoral girdle and musculature, including modification of the furcula, a synapomorphy of theropod dinosaurs. The furcula articulates with the scapulo-coracoid complex medially to the glenoid and is the rostral-most attachment of the m. pectoralis, the primary down stroke muscle in flying birds. As a result, furcula morphology has been used to infer flight behavior in extinct avialans. However, furcula morphology only modestly correlates with flight style in extant birds, and some volant birds lack furculae. While furcular morphology has often been considered in isolation – under the assumption that the functional signal of the element resides primarily in its gross shape – the bone's anatomical orientation, structural properties, and relation to adjacent pectoral muscles remain unexplored in most extant avians. We collected contrast imaging, dissection, and morphometric data of the musculoskeletal system of a sample of passerines (Passeriformes) and parrots (Psittaciformes), groups with disparate furcula morphology but similar flight styles. Generally, passerines possess more robust and rostrocaudally-curved furculae than do parrots, whose furculae are reduced to ligamentous bands in some taxa. We examined pectoral muscle architecture, muscle resultants, and mechanical properties of the furcula as correlates of flight style and furcular morphology. In volant parrots with reduced or absent furculae, modified pectoral muscle architecture and morphology may functionally replace a bony furcula. Whereas earlier studies found that lateral and anterior shape of the furcula may covary with flight style among all avians, we find that these trends may not hold at higher taxonomic resolution. Our data suggest that the question of furcula function, and thus of avian pectoral evolution, depends substantially on taxonomic level.

Similarities and Differences of Tympanic Membrane Development in Mammals and Diapsids

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One of the most fascinating craniofacial evolutionary changes in mammals is the acquisition of the mammalian-specific middle ear. In mammals, a novel jaw joint was formed and the original jaw joint (primary jaw joint) was incorporated into the auditory apparatus, resulting in three ossicles in the middle ear. On the other hand, diapsids (modern reptiles and birds) evolved only one ossicle in the middle ear. To understand developmental bases behind the evolution of the different morphology of the middle ear, we have focused on development of the tympanic membrane (TM) in mammals and diapsids. The TM is a thin layer that originates from the ectoderm (the external auditory meatus), endoderm (the first pharyngeal pouch), and mesenchyme in pharyngeal arches. We performed comparative developmental analysis of TM formation in mice and chickens. We revealed that the TM evolved independently in the mammalian and diapsid lineages, and the relative positions of the primary jaw joint and first pharyngeal pouch led to the coupling of TM formation with the lower jaw in mammals, but with the upper jaw in diapsids (Kitazawa et al., 2015, Nat. Commun. 6: 6853). We also examined TM development focusing on patterning of the pharyngeal arches along the anterior-posterior axis in mouse and chicken

embryos. We found that the first pharyngeal arch plays an important role in the mouse TM formation, but the second pharyngeal arch is indispensable for the development of the chicken TM (Furutera et al., 2017, Development 144: 3315-3324). We are currently trying to find molecular mechanisms of TM formation in mammals and diapsids. We have compared gene expression profiles by microarray, qPCR, and *in situ* hybridization analyses in the middle ear forming region of embryos between the wild-type and the TM-deficient (*Gsc*$^{-/-}$) mouse, and found several candidate genes for TM development in mice. Further analyses will shed light on understanding similarities and differences in developmental mechanisms of the TM in mammals and diapsids.

When Marsupials Can't Run – Variation in Hind Limb Morphology and Implications for Escape Locomotion in Marsupials

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Australian animals have suffered exceptionally high rates of extinction over the last 200 years, with the greatest impact seen in 'critical weight range' (CWR; 35g–5.5kg) terrestrial mammals. These declines are probably driven by introduced eutherian predators as CWR species fall within the preferred prey size of feral cats and red foxes. The predation impact of these introduced predators in Australia is more than double that of native predators, likely due to the lack of co-evolution between predator and prey. Marsupials show marked diversity in how they move during escape (e.g., 'outrun' or 'outmaneuver'), which could make some species more vulnerable to the hunting strategies of eutherian predators than others. This study investigates the effect of morphological variation between CWR species on their locomotor performance during escape. We present a comparative analysis of hind limb myology in nine species of CWR marsupials with representatives of quadrupedal and bipedal taxa. We predicted that differences in muscle morphology would be reflected in locomotor performance (i.e., speed, acceleration, agility). To quantify hind limb morphology, we measured muscle architectural properties including mass, fascicle length and physiological cross-sectional areas (PCSA) of key muscles, as well as distribution of functional groups and differences in muscle attachments. We compared this muscle data to preliminary escape locomotion data collected from these same species. Differences in both hind limb morphology and escape locomotion between species were found, with species which showed a propensity for jinking ('outmaneuver') separating from species that fled in a straight line with a burst of speed ('outrun'). This preliminary analysis gives us an integrated view of morphology and locomotor behavior to better understand the mechanistic basis of escape performance in CWR marsupials.

Masticatory Covariation in *Macaca fascicularis*: Integrating Dental Wear, Craniofacial Morphology, and Pathology

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Dental and craniofacial morphologies have been a frequent focus in comparative studies but have not often been linked to one another and/or to pathologies. As a result, the ways in which these different components of the masticatory apparatus influence one another, both in non-pathological and pathological conditions, are unclear. Here, we examine a sample of *Macaca fascicularis* (49 females, 60 males) to evaluate how these often disparate lines of evidence covary. We collected surface scans of the cranium and mandible and high-resolution scans of the maxillary and mandibular dentition. For each specimen we evaluated temporomandibular joint (TMJ) osteoarthritis (OA), antemortem tooth loss (AMTL), and other craniofacial and dental trauma and pathologies. Dental relief and a measure of wear asymmetry was calculated for upper and lower first and second molars. Results indicate that TMJ-shape varies significantly in relation to TMJOA, pulp cavity exposure, and periapical abscesses. No significant relationships were found between overall cranial or mandibular shape and pathology. Further, we observed no significant correlations between any pathology and dental relief or between craniofacial/TMJ morphology and dental relief. There was a significant positive correlation between wear asymmetry and the presence of teeth with exposed pulp cavities. These results suggest that certain pathological conditions may be more likely to be linked to changes in bony morphology and patterns of dental wear. Further analyses will focus on how these pathologies vary across species and in relation to dietary patterns.

Modularity and Diversity of the Bird's Neck: A 3D-Geometric Morphometric Approach of Cervical Vertebrae

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The neck makes the connection between the head and the trunk, being the key structure allowing all the head movements. The bird's neck morphology is the most variable among current tetrapods, with significant differences in the number and the shape of cervical vertebrae. Until now, three functional regions have been identified along the neck but only few quantitative studies searching for modules have been performed and no consensus exists. Consequently, a major question arises: what is the structure of the morphological diversity in the neck of birds? Based on 195 cervical vertebrae, belonging to 17 species with various ecology, we performed a morphological study of the vertebrae using 3D-surface geometric morphometrics. We used a without a priori clustering approach to identify modules along the neck. Phylogeny influence was also tested. Each module was modeled and its postural characteristics were studied. We characterized nine modules: seven of them are transspecific, shared by at least three and up to 16 species. Two modules were more specific to one or two species with particularly long necks. The postures and the positions of the modules along the neck correspond to the three already identified regions of the typical birds' S-shaped neck, but we have also found subdivisions of these regions. Therefore, the bird neck's morphology seems to be constrained by the posture, more than by phylogeny or ecology. This work was granted by Avineck ANR 16 CE33-0025.

Five Fingers - Pentadactyli in *Metoposaurus krasiejowensis* (Temnospondyli, Metoposauridae)

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The Late Triassic Krasiejów locality in the southwest of Poland is well known for its great preservation of fossil bones. The most commonly occurring fossil remains belong to the temnospondyl amphibian *Metoposaurus krasiejowensis*. However, most bones, as in a concentrate Lagerstätte, are disarticulated finds. The rare exception is an articulation of the shoulder girdle, a humerus with an ulna and radius, as well as an articulated manus. The specialty is that the manus contains five metacarpals, yet only four preserved digits. The preserved phalanx formula is 1-1-3-3-0, the reconstructed formula may be 2-2-3-3-2. Pentadactyly is an extremely rare character among Temnospondyli, having been recorded to date yet only for *Paracyclotosaurus davidi*, however not commonly believed because of the poor preservation of the manus material. The articulated specimen provides new information about a possible ossification sequence of the manus in large Temnospondyli and places metoposaurids between two known patterns: the reduction or late ossification of the first digit is shared with the amniote-frog system; the early development of the second and third digit corresponds to a salamander-like pattern (including *Apateon*). This finding is in contrast to the findings of *Dutuitosaurus*, a close relative of *Metoposaurus* which had only four digits and leaves some questions unanswered e.g., why both characters occur in the family of Metoposauridae. A closer look at the entire group of Temnospondyli does not show a clear trend with respect to pentadactyly. It is therefore likely that the number of fingers, similar to today's amphibians is not a phylogenetic signal. Therefore future studies in the field of biology concerning recent amphibians might provide possible answers.

New Basicranium of *Micropternodus cf. M. morgani* (Micropternodontidae, Eulipotyphla), from the Turtle Cove Member of the John Day Formation, Oregon

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A partial skull (JODA 6211), from the Turtle Cove Member (unit E1) at John Day Fossil Beds National Monument is referred to *Micropternodus cf. M. morgani*, a species previously known only from an incomplete skull lacking the basicranium, and an associated incomplete left dentary. The site is dated between 29.586–31.356 Ma in age (Oligocene), referable to either the Whitneyan or early Arikareean (Ar1) NALMA, based on recent radiometric dates of tuff units. JODA 6211 includes a partial skull and articulated dentaries, with the teeth in occlusion. CT-imaging and reconstruction allows identification of the dentition to *Micropternodus cf. M. morgani*. There is damage to the anterior dentition, but P3–M3 are complete. Both M1s show slight erosion at the buccal side near the roots. P1 and P2 are absent and lack alveoli. The upper canines are less sectorial and the P3 metastylar cusp is less well developed than in the holotype, UCMP 60801. In the dentary i1-3, p2–4 and m1–3 are preserved. The lower molars lack cingulids, and the paraconids appear somewhat more labially positioned than in UCMP 60801. The rostrum is well preserved, with portions of the cranial roof and basicranium present. The basicranial bones are fused. CT-reconstruction shows the petrosals and bony labyrinths are preserved on both sides, with the malleus and incus preserved on the left side, and the incus on the right. The cochlea is relatively compact with two and a half turns. Additional comparative work should help to clarify the phylogenetic relationships of *Micropternodus*. Although *Micropternodus* is known from earlier deposits in Montana, Wyoming, Nebraska, Utah, and Saskatchewan, JODA 6211 likely represents the earliest occurrence of a eulipotyphlan in the Pacific Northwest. Unit E1 is interpreted as representing a relatively open habitat based on paleosol evidence, and it also records the first clear open habitat specialist in the region, the burrowing beaver, *Palaeocastor peninsulatus*.

Vertebral Centrum Homology in Lissamphibians – A Frog Perspective

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Very few detailed accounts on vertebral development in extant amphibians are currently available and conflicting interpretations on centrum homology have prevented utilization of this character for inferences of their systematic affinities with early tetrapods. However, recent advances in paleontology revealed opposing patterns of inter- and pleurocentrum formation in temnospondyl tetrapods, the putative stem group of lissamphibians. Based on these results we investigated vertebral development and centrum formation in *Xenopus laevis* and *Bombina orientalis*. Our results show that the centra in both frogs develop as cartilaginous structures dorsolateral to the notochord, where they subsequently become replaced by endochondral bone. In *X. laevis*, two separate ossification centers emerge in lateral aspects of the cartilaginous centra. During ontogeny, the paired bony centra fuse to form the adult solitary centrum dorsal to the notochord. The situation in *B. orientalis* is very similar, with the notable exception that its bony centra arise as unpaired elements. No bony centra were found ventral to the notochord. The observed pattern of centrum formation in both archaeobatrachian frogs is highly similar to the formation of pleurocentra in temnospondyls like *Eryops*, *Lydekkerina* and *Dissorophous* as described by Danto et al. (2017, J. Morphol. 278:1262–1283). Our results support the homology of the solitary centrum in adult frogs with temnospondyl pleurocentra. We argue that the loss of intercentra potentially constitutes a synapomorphy of amphibamids and lissamphibians. Additionally, sequences of axial chondrification and ossification were assessed. While the general pattern of development agrees with the existing dataset for other frogs, some obvious deviations include a very early chondrification of transverse processes in *B. orientalis* and a comparatively late onset of hypochord chondrification in metamorphic stages of *X. laevis*.

Significance of Hip Kinematics for Interpreting Articular Soft Tissue Function in *Alligator mississippiensis*: Evolutionary and Biomechanical Implications for Archosauria

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Archosaurs (birds, crocodylians, and their extinct relatives) evolved a wide diversity of hind limb skeletal morphologies, suggesting highly divergent articular soft tissue anatomies. Recent studies have shed light on the soft tissue anatomy of the archosaur hip joint, but the general lack of understanding of the dynamic interaction between joint soft tissues has hampered further functional and evolutionary inferences. Here, we use contrast-enhanced computed tomography to generate 3D-models of the pelves, femora, and joint soft tissues of the American alligator, an extant archosaur. The hips were then animated using marker-based XROMM to visualize soft tissue articulation and hip kinematics during terrestrial locomotion. The anatomical femoral head of the alligator travels beyond the cranial extent of the acetabulum and does not act as a pivot as has been suggested for some extinct archosaurs. Additionally, the fibrocartilaginous surfaces of the alligator's antitrochanter and femoral neck maintain engagement during hip flexion and extension, similar to the articulation between homologous structures in birds. Lastly, the fovea capitis of the femur remains in close proximity to the membrane-bound inner acetabular foramen, suggesting that the ligamentum capitis remains within this unossified portion of the acetabulum. Our results illustrate the utility of XROMM for studying joint kinematics in light of articular soft tissue interactions. These results also allow us to propose functional hypotheses for crocodylian hip joint soft tissues, which expand our knowledge on the role of joint soft tissues in vertebrate locomotor behavior. Finally, because the pelves and femora of fossil archosaurs possess osteological correlates for hip joint soft tissues, these new data improve our ability to reconstruct hip articulation in archosaurs, and form the basis for further studies on the evolutionary relationship between joint anatomy, locomotor posture and body size transitions.

The Enigma of the Sturgeon Skull: A Transformational Approach

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Sturgeons and paddlefishes are classified in two families (Acipenseridae and Polyodontidae), which together with fossil relatives constitute the crown-group Acipenseriformes. It is generally agreed that Acipenseriformes are the sister-group of Neopterygii, and along with Cladistia represent the most basal taxa of the extant ray-finned fishes. Based on their position on the cladogram, acipenseriforms could be a valuable link to the early radiation of the actinopterygians. This perspective, however, is only partially realized due to the highly derived morphology and unresolved homologies of the snout and jaws in acipenseriforms. In contrast to all other actinopterygians, they lack the articulation of the upper jaw with the ethmoid region, while their palatoquadrates form a syndesmosal symphysis beneath the cranial base. Accordingly, the whole snout is preoral in position and does not participate in the roof of the mouth cavity. Here, I present the results of a comparative anatomical analysis of the skull in sturgeons. Homologies of the jaws and ethmoid region are established, and an evolutionary scenario is proposed to explain the transformations of the skull during the presumed transition from the palaeoniscoid ancestors to Acipenseriformes. It is shown that these transformations were triggered by paedomorphosis, which caused, inter alia, the underdevelopment of the lower jaw. This underdevelopment resulted in the caudal shift of the oral margin and an exclusion of the ventral side of the snout and the anterior ends of the upper jaw rami from the mouth cavity. Having been released from the functional limitations inherent to biting jaws, the rostral ends of the palatoquadrates became transformed into the skeletal elements of the sensory barbels, while the rest of the palatoquadrates turned midward to keep the occlusion with the mandibles. In this way, the upper jaw symphysis was formed. The study was supported by the Russian Foundation for Basic Research, grants № 17-04-01215 and № 18-04-00928.

Fin-fold Formation in Paddlefish and Catshark: Insights into the Evolution of Limb Specific Morphologies

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The evolutionary origin of the autopod involved a loss of the fin-fold and associated dermal skeleton with a concomitant elaboration of the distal endoskeleton to form a wrist and digits. The developmental mechanisms underpinning this anatomical conversion, however, remain poorly understood. Developmental studies, primarily from teleosts and amniotes, suggest a heterochrony-based model for appendage evolution in which a delay in the AER-to-fin-fold conversion fueled endoskeletal expansion by prolonging the function of AER-mediated regulatory networks. Here, we take a broadly comparative approach to explore predictions of this model using zebrafish (a teleost), paddlefish (a nonteleost actinopterygian), and catshark (a chondrichtyan), each with different fin-fold morphologies. Our data demonstrate that in both basal gnathostomes, the autopod marker HoxA13 co-localizes with the dermoskeleton component And1 to mark the position of the fin-fold. These data provide phylogenetic context for recent functional analyses in zebrafish supporting a deep homology between the autopod and fin-fold. Additionally, we show that in paddlefish, the proximal fin and fin-fold mesenchyme share a common mesodermal origin, and components of the Shh/LIM/Gremlin/Fgf transcriptional network critical for autopod outgrowth and patterning, also function in the fin-fold with a profile similar to that of tetrapods. Finally, we integrate these data with previous analyses showing a role for migratory somitic cells in mediating the AER-to-fin fold conversion. Collectively, these data highlight the complex nature of fin-fold ontogeny and suggest that limb specific morphologies arose through evolutionary changes in the differentiation outcome of deeply conserved early distal patterning compartments.

The Origin and Evolution of the Tiger Shark Genus *Galeocerdo* (Elasmobranchii, Carcharhiniformes) Revisited

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The evolutionary history of the unique tiger shark genus always was ambiguous due to the vast amount of fossil species that were described based on highly similar teeth. Over the past two centuries, more than sixty extinct ancestors and relatives of the sole extant tiger shark *Galeocerdo cuvier* were recorded. Several attempts to revise the seemingly complex fossil record of *Galeocerdo* resulted in a reduction to about twenty valid species of this genus. However, there are still many controversies and unresolved questions about the origin and age of both the genus and the respective species, as well as about the number of actual extinct relatives of *Galeocerdo cuvier*. We gathered several hundred teeth of different tiger shark species, both extinct and extant, and compared them using geometric morphometrics. With this quantitative approach we were able to determine morphological variabilites as well as similarities within the sample and as a result were able to reinterpret the fossil record of tiger sharks. The morphospace analysis revealed that morphometric characters of the teeth are well-suited to distinguish different species of *Galeocerdo*. Several formally ambiguous species consequently can be reassigned to other species or even genera, hence the number of valid tiger shark taxa has to be reduced to less than ten species. Moreover, the evolutionary history of some species was re-adjusted, including that of the extant *Galeocerdo cuvier*, whose origin dates back much further than previously assumed. The results of this study clarify many questions and controversies regarding the possible date of origin and fossil record of the iconic tiger shark genus and furthermore procure new information about the history of *Galeocerdo cuvier* and its extinct relatives.

New Type of Development of Olfactory Rosette of Bushymouth Catfish *Ancistrus dolichopterus* (Teleostei: Loricariidae)

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The form of the olfactory rosette and morphology of the olfactory lamellae affect the ability of fish to perceive an odorant. In ontogeny, the olfactory organ of fish goes through such developmental stages as the olfactory placode, olfactory pit, and olfactory chamber with olfactory rosette. However, the mechanism of development of the olfactory rosettes remains unclear. So far, little attention has been paid to the particularities of formation of the central raphe in the olfactory rosettes, and the appearance of new lamellae in different species of teleosts. To study the development of the bilateral olfactory rosette, bushymouth catfish, *A. dolichopterus*, were cultured, and the larvae were serially sectioned. In *A. dolichopterus*, formation of the olfactory rosette goes through four stages: (i) the first lamella appears in the central part of the olfactory chamber and becomes elongated towards its rostral wall; (ii) the first lateral and medial lamellae start to form; (iii) the fourth lamella appears from the medial side of the central raphe; (iv) initially, the extension of the lamellae takes place, symmetrical to the central raphe; then, when it comes to new paired lamellae, the lateral lamellae become more rostral than the medial ones. The central raphe develops from the first central lamella, which elongates with the increase in length of the olfactory chamber. The thickening of the raphe is possible due to attaching of new pairs of olfactory lamellae to it, in the rostral part of the olfactory chamber. The distal end of the central lamella moves laterally and loses its axial position. The bilateral olfactory rosette of *A. dolichopterus* acquires its definitive state due to addition of new lamellae, more rostrally than already formed lamellae. During the formation of the fourth lamella, the symmetry is broken, as lamellae are being formed only from one side of the central raphe. All next lamellae are formed in pairs.

The Tri-layered Keratinous Sheath on the Upper Beak Bone of Chicken and its Relevance to the Form and Growth Orientation of the Beak

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The structure and growth pattern of the keratinous cover that overlies the beak bone are yet to be understood in birds. We analyzed the microstructure of the rhinotheca, the keratinous sheath on the upper beak, using the combination of thin section and scanning electron microscopy observations, and small-angle X-ray scattering analysis in post-hatching chicken specimens up to ~80 days old. We found three different layers in the rhinotheca—outer, intermediate, and inner layers—throughout its growth. Unlike the outer layer that covers a wide area of the dorsal surface of the rostral bone, the intermediate and inner layers arise from the distal portion of the beak bone. Micro-layers composing the outer and inner layers are bedded nearly parallel to the rostral bone at the base. The micro-layers in the outer layer are more anteverted at the distal portion. The micro-layers of the intermediate layer are bedded nearly perpendicular to those of the outer and inner layers on the median plane. The distal appositional growth of the intermediate layer contributes to the distal growth of the rhinotheca, which causes the difference in profiles between the beak bone and the rhinotheca in the distal portion of the beak. The outer layer is dragged distally by the growth of the intermediate layer because the outer and intermediate layers are closely packed with each other at the boundaries. The limited distribution of the intermediate and inner

layers is consistent with the portion on the beak which is frequently worn out. Understanding the layer-structure of the rhinotheca among the extant beaked taxa will lead us to a more reliable reconstruction of the form of the keratinous beak in extinct taxa.

Shoulder-blade Runners: Utility of the Scapula Fossa Ratio to Investigate Locomotor Evolution in Equids (Mammalia: Perissodactyla)

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The scapula fossa ratio (SFR) has been used in recent years to demonstrate functional locomotor differences in perissodactyls. The SFR describes the relative attachment areas of the lateral shoulder muscles: supraspinatus (extensor/stabilizer) and infraspinatus (lateral collateral stabilizer). Here, we use the SFR to investigate deep scapula muscle attachment sites of equids (Perissodactyla: Equidae), and whether any variation observed between extinct and extant species can be explained by habitat variation. 3D-surface models of scapulae were obtained via laser scanning and photogrammetry. Areas of the supraspinous and infraspinous fossae were calculated for 14 species of equids. We also included 9 cervid (Artiodactyla: Cervidae) and 3 alcelaphine (Artiodactyla: Bovidae) genera to test whether extinct equid SFRs are comparable to modern ungulates living in forested habitats (cervids) or open-grassland habitats (monodactyl equids; alcelaphines). Our results demonstrate that extinct tridactyl (three-toed) equid SFRs exhibit significant differences to modern monodactyl (one-toed) species. The infraspinous fossa is relatively larger in cervids and tridactyl equids compared to monodactyl equids; cervid and tridactyl equid SFRs could not be statistically separated. We interpret that the infraspinatus muscle is relatively more important for shoulder stability in tridactyl equids (and cervids) than in monodactyl equids. As monodactyl equids possess an advanced passive stay apparatus (muscle-tendon mechanism locking the shoulder to enable standing in open terrain with minimal energetic input), it is possible that the infraspinatus has become less integral for shoulder support during stance. Without such a mechanism, tridactyl equids still required shoulder support from the infraspinatus to exploit open habitats. This study demonstrates the utility of the SFR as a tool for investigating links between the musculoskeletal system and habitat use through equid evolution.

Relating Trapeziometacarpal Joint Morphology to Functional Capabilities in the Primate Thumb

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The high dexterity of modern humans is associated with a highly mobile thumb. This high mobility is a result of its relatively long length, the saddle-shaped configuration of the trapeziometacarpal (TMC) joint and the well-developed thenar musculature. Complex manual tasks are, however, also observed in non-human primates, e.g., during food manipulation and tool use. To investigate evolutionary form-function relations of the primate thumb, we relate the 3D-geometry of the TMC joint to the functional capabilities of the thumb in primate species with a distinct thumb function and/or morphology; humans with a saddle-shaped TMC joint and highly mobile thumb; bonobos, with a similar TMC-joint and thumb use during climbing and manipulation, and gibbons, with a ball-and-socket-shaped TMC joint and thumb use mainly during climbing. We use a CT-based kinematic analysis to quantify the 3D-movement of the first metacarpal during principal movements of the thumb (flexion-extension and abduction-adduction). In addition, we determine the position and orientation of the trapezium within the wrist/carpal complex as well as the curvature of the articular facets of the TMC joint. Our results show overall similarities between humans and bonobos, both in TMC-morphology and in functional capabilities. Humans, however, display an increased capability of thumb extension compared to bonobos. The gibbon TMC morphology allows for high mobility as thumb range of motion exceeds that of humans and bonobos, most notably in the flexion-extension plane. Furthermore, our study shows that the functional capabilities of the thumb cannot be related to bone morphology alone. Other factors, such as ligaments, also play an important role in determining thumb mobility. Our study has important implications for the study of not only the evolutionary development of the thumb, but also of various joint systems, as we show that functional capabilities of a joint are influenced by multiple morphological factors.

(How) Does Primate Wrist Morphology Relate to Wrist Mobility?

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The primate wrist is a highly complex structure as it is a combination of different articulations that together constitute the overall wrist mobility. In addition, there is a reduction of the distal ulna in the hominoid lineage, which has been linked to a greater ulnar deviation. However, the precise contribution of the different joints in radioulnar deviation and the link with ulnar morphology remains unclear. In our study, we want to quantify wrist morphology and the contribution of the different joints to overall radioulnar deviation across primate taxa of different locomotor groups. We CT-scanned each cadaver specimen in neutral and maximal radioulnar deviation using a rig to standardize wrist positions. Afterwards, we performed detailed dissections of the extrinsic hand muscles. We created 3D-bone models of the carpal bones, third metacarpal (MC3), ulna and radius. The range of motion (ROM) of the MC3 relative to the radius is measured using an in-house developed Python code. We include 5 hylobatid and 2 macaque cadavers and compare the ROM with data from 15 human volunteers. The ROM during radioulnar deviation is highest in hylobatids (71,8 ± 8,32°) and lowest in macaques (43,2 ± 4,9°), while humans are intermediate (62,2 ± 8,32°) and overlap with hylobatids. However, analysis of the extrinsic hand musculature shows that force-generating capacity (PCSA) of the radioulnar deviators is higher in humans than in gibbons (resp. 35% and 25% of total forelimb muscle PCSA). This suggests that observed differences in ROM during radioulnar

deviation are likely related to joint geometry rather than muscle PCSA. It has indeed been proposed that the lower ROM in macaques is due to flatter midcarpal joint facets, while the unique ball-and-socket wrist joint of gibbons enhances ulnar deviation. However, the precise contribution of the mobility and 3D-geometry of the carpal bones to overall wrist mobility remains unclear and will be the focus of future studies of our group. Ethical statement: Human specimens were obtained via the Human Body Donation Program of the University of Leuven.

Osteology and Life History: the Formation of the Skeleton in the Asian Narrow-Mouthed Frogs (Anura: Microhylidae) Depends upon Tadpole Ecology

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The morphology of the amphibian skeleton is known to be influenced by a set of heterochronic processes, mostly related to paedomorphosis. Certain paedomorphic underdevelopments, such as reduction of some cranial and postcranial bones, are believed to accompany the trend of body miniaturization. At the same time, the role of reproductive mode and life history in the skeletal development in amphibians is also widely recognized. The anuran family Microhylidae is a speciose and diverse taxon encompassing frogs of various sizes, from rather large to extremely miniature, and with various reproductive modes. Thus, microhylids represent a good model system to study diversification of skeletal morphology and development. Using ontogenetic series of larvae, metamorphs, and adults, we compared osteology in frogs from the genera *Glyphoglossus*, *Microhyla*, *Kalophrynus*, and *Kaloula* from Southeast Asia (Vietnam). To estimate the impact of miniaturization, skeletal structure and development were compared in the most large- and small-sized species. In the latter, adult osteology was revealed to be affected by the pattern of larval development rather than miniaturization *per se*. As compared with typical pond-breeders, in hole-breeding *Microhyla arboricola* with oophagous tadpoles, reduction of cranial elements (columella, quadratojugal) and vertebrae count (6 presacral vertebrae instead of 8) presumably results from the heterochronic shift in the timing of bone formation. Abbreviated larval development in the medium-sized *Kalophrynus interlineatus*, which breeds in ephemeral pools, accounts for the underdevelopment of the skeleton in metamorphs and loss of some bones in adults (palatine, sphenethmoid). These findings suggest that the ecology of reproduction and life history traits play a key role in the formation of the skeleton in frogs.

Ossification of the Sternum in a Flighted Paleognath and the Evolution of the Keel in Modern and Extinct Carinatae

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The keeled sternum of modern flying birds is considered homologous to that of the earliest Carinatae such as *Ichthyornis*. Current knowledge prescribes that in modern birds, the main body of the sternum including the keel develops from a single midline ossification center. In paleognath birds that have lost flight ("ratites"), the sternum lost the keel and develops from paired ossification centers, as in non-avian dinosaurs. The fact that enantiornithes independently evolved a keel that also developed from a medial ossification center has led to the notion that the evolution of the keel requires a single medial ossification center, and suggests a possible reversion in ratites. Here, we report the development of the sternum for the first time in a flighted and keeled paleognath, the Chilean tinamou *Nothoprocta perdicaria*. It presents a pattern that is completely different to that reported so far in other keeled birds. The main body of the sternum develops as in non-avian dinosaurs, from paired ossification centers. The keel begins ossification from a separate center, previously undescribed, which is formed in the midline, anterior to the sternum. It forms the anterior part of the keel and then grows towards posterior, merging with the main body of the sternum. We propose that this pattern corresponds to the ancestral mode of development present in early Carinatae. The ratites have lost the keel, but their pattern of paired ossifications would not represent a reversal. In turn, the development of both the main body of the sternum and keel from a single medial ossification centre, as reported in Galliformes and Psittaciformes, would be a derived pattern. Research funded by grant Anillo ACT172099, Conicet, Government of Chile.

The Hands and Feet Musculature of Hominoid Primates

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The hands and feet of primates interact closely with the support and are likely to show adaptations to their specific locomotor behavior. While the foot and hand bones have been studied rigorously in a diverse range of primates, the characteristics of the hand and foot musculature remain rather elusive. In our study, we focus on the hominoids, who are closely related but display distinct locomotor behaviors. It is expected that these different locomotor behaviors are associated with differences in hand and foot musculature. We obtained anatomical data from a large series of hominoids, based on dissections and on literature. For all specimens, the extrinsic hand and foot musculature was quantified, in a subset we were also able to quantify the intrinsic musculature. Ratios were calculated per specimen and averaged per species to evaluate functional differences in musculature. In extrinsic foot musculature, the mass ratios are very similar between African great apes and hylobatids, with a somewhat higher percentage of digital flexors in hylobatids. Orangutans are distinct with larger digital flexors and dorsiflexors than the other apes, which could be related to their quadrumanous clambering behavior. For the intrinsic foot musculature, we find a high proportion of hallucal and low proportion of fifth digit muscles in hylobatids compared to the great apes. This could be associated with a different grasp type compared to the great apes. In the extrinsic hand musculature, we observe relatively well-developed thumb muscles in bonobos (5.7%) compared to humans (8%), and a weaker development in hylobatids and chimpanzees (resp. 4.4% and 3.7%). The forearm flexors are much larger than the extensors in all studied apes (ratio of 1.8 to 4.4), in contrast with humans where flexor and extensors are equal in size. These unique anatomical data should be integrated with kinematic data to obtain a complete understanding of the functional adaptations of the primate extremities.

Development of the Embryonic Anatomy of the Madagascar Ground Gecko

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The embryonic development of the muscles, skeleton, nerves or other soft tissues of non-avian reptiles has been historically neglected in the literature. Romer (1942, J. Morphol., 71: 251-298; 1944, J. Morphol. 74: 1-41) and Walker (1947, J. Morphol. 80: 195-249) described the development of the limb muscles of *Lacerta* and *Chrysemys*, respectively, but other examples are scarce. Here, we present a detailed study of the embryology of muscles, nerves and early skeletal tissues during the first half of the embryonic developmental period of the Madagascar Ground Gecko (*Paroedura pictus*), a promising new model of lizard for developmental biology and anatomical embryology. We followed the development of different tissues by means of immunofluorescence and confocal microscopy which allows for observing the embryonic anatomy in great detail and studied its 3D-morphology and the spatial relationships of different tissues with respect to each other. The development of complex anatomical regions such as the chondrocranium, the pectoral gridle or the hand and foot can be studied and reconstructed at different stages of development, and can shed new light on what we know about the anatomy and evolution of reptiles. Studies like this, especially if combined with other kinds of methods like high contrast CT-scanning, have the potential to provide understanding of the development of the whole anatomy of non-model organisms as never before. Comparison with other species of lizards or vertebrates could also provide new insight into the development, evolution and homology of many anatomical structures and the history of land vertebrates.

Locomotion of the Snake-eyed Skink *Ablepharus kitaibelii* (Squamata: Scincidae) on Different Substrates

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Ablepharus kitaibelii (Bibron & Bory de Saint-Vincent, 1833) is a small scincid lizard with a slender body and a long tail but short legs. The species is thought to be adapted to a semi-fossorial lifestyle and is often found in leaf litter, short grass, and sometimes rocky terrain. This species is of interest as it represents a transitional phase in the evolution of limblessness and it often moves in a snake-like fashion without using its legs. However, the kinematics of locomotion have not been quantified to date. We used high-speed video recordings (at 1000 or 500 frames/second) to film animals in dorsal (and in few instances lateral) view while moving on diverse substrates. We used glass (smooth surface), fine sand (0-0.2 mm), small rocks (0.5 mm), and asphalt shingles (imitating hard rocky surface). We additionally tested movement within glass tubes of three diameters to emulate concealed and narrow spaces. We further created a complex 3D-landscape to simulate tall-grass. Furthermore, we tested individuals with both intact and regrown tails, and then repeated the experiments after removing a part of the tail. We filmed over 800 movements of 22 individuals (7 juveniles and 15 adults). Preliminary results revealed that high-speed movements were achieved by strong whole-body undulations, with the active use of the limbs. During slow movements, the lizards maintained an almost straight body, at times employing only the front legs to generate thrust. The tail is involved in some movements, but in general does not actively participate in the locomotion. We also obtained microCT-scans of two individuals that reveal the bone and muscle structures employed in locomotion. Funds were provided by project № M11/12 of the National Scientific Research Fund, Bulgaria.

How to Grow a Backbone: Ancestral Ossification Patterns in the Vertebral Column of Amniotes

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Ossification in the axial skeleton of amniotes displays a great diversity with regard to timing and patterns. Unfortunately, due to the infrequent preservation of ontogenetic sequences in the fossil record and to limited research interest, the evolutionary history of these patterns remains poorly understood. In this study, thanks to several exceptionally well-preserved specimens of the early Permian mesosaurid *Stereosternum tumidum*, we were able to observe mineralization gradients along the spine and retrace the ossification sequences of several vertebral elements. We focused our attention on three major traits for which we performed ancestral state reconstructions: the number of loci from which neural arches ossify, the direction of this ossification sequence, and the spreading direction of neurocentral suture fusion. For all three examined traits, it appears that the condition in *Stereosternum* represents the plesiomorphic state not only for reptiles but for amniotes in general. Neural arch ossification first occurs in one atlantal locus and progresses posteriorly along the spine. Similarly, fusion of initially paired neural arch elements first occurs in the anteriormost cervicals and then follows a “zipper-like” cranio-caudal gradient. Conversely, closure of the neurocentral sutures begins in the last caudal vertebrae and then proceeds anteriorly from that point. These patterns seem to constitute a major difference between the reptilian and the synapsid lineages, the latter being more diverse with regard to the number of loci and direction of ossifications. Modes of neurocentral suture closure appear to vary substantially within the reptilian lineage, with marked differences between major clades, suggesting that this character may bear more evolutionary importance than previously thought. However, further research is necessary to refine our more detailed and deep-time understanding of the evolutionary history of these traits.

Cranial Ecomorphology of Odontocetes: a 3D-Evolutionary Approach

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The cranial morphology of toothed whales (Odontoceti) evolved under strong selective pressures. Extant odontocete species exhibit differences in feeding strategies, body size, diving adaptations, echolocation and brain size. These factors likely contributed to morphological diversification of the odontocete skull. Previous studies and experimental work on toothed whales confirmed that cranial anatomical features such as the number of teeth and mandibular bluntness correlate with feeding strategy, diet, and diving adaptations. Nevertheless, how overall skull size and shape vary between species in relation to feeding ecology and biosonar mode have yet to be tested in a phylogenetic context. In this study, we generated 3D-cranial models by using photogrammetry of 111 specimens representative of 60 (out of 72) odontocete species. We addressed the following questions: 1) what is the link between morphological variation and ecological adaptation in extant toothed whales? 2) Does morphological variation exhibit a strong phylogenetic signal? And 3) to what extent does such signal obscure our ability to detect ecomorphological adaptations? We found that skull morphology shows a significant phylogenetic signal, which is much stronger in terms of size than shape. After accounting for phylogeny, significant associations occur only between skull size and biosonar mode as well as other size parameters including body length and mass. Skull shape is only influenced by evolutionary allometry and no association with ecological parameters could be identified, suggesting that ecomorphological adaptations occur within major clades, which obscures functional anatomical adaptations across the entire Odontoceti clade.

Predicting Cochlear Frequencies Using Mechanical Properties of the Basilar Membrane

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Obtaining audiograms for most marine mammal species is not practical. Here, we show that audiograms can be estimated using measurements on post-mortem tissue combined with auditory models. A custom force probe was used to measure the mechanical stiffness at multiple points along the length of the basilar membrane in three land and five cetacean species (humans, gerbils, chinchilla, porpoises, dolphins, and beaked and baleen whales). Probe derived width and stiffness measurements were used to compute the center frequency of the measured location on the basilar membrane. The estimates were compared to known audiograms and basilar membrane frequency maps where available. The results from a diverse group of marine and terrestrial mammals suggest that mechanical measurements of the basilar membrane can be used to estimate the hearing range for species where a behavioral audiogram is not available, such as in mysticete whales.

Insight into the Development of the Avian Shoulder Girdle from a New Clade of Basal Pygostylian Birds

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Stemward Pygostylia (birds with a short tail ended in a compound bone pygostyle) are critical for understanding how the modern avian Bauplan evolved from the long-tailed most basal bird *Archaeopteryx*. However, the known diversity of early-branching pygostylians is obscured by limited fossil records. Recently, we described a new basal pygostylian *Jinguofortis perplexus* from the Early Cretaceous of China. Phylogenetic analysis recovers a clade uniting *Jinguofortis* and the enigmatic basal avialan *Chongmingia*, here named Jinguofortisidae, representing the second earliest diverging group of the Pygostylia. Jinguofortisids preserve a mosaic combination of plesiomorphic non-avian theropod features such as a fused scapulocoracoid and more derived flight-related morphologies including the earliest evidence of reduction in manual digits among birds. A fused scapulocoracoid in adult individuals independently evolved in Jinguofortisidae and Confuciusornithiformes. Its presence may relate to an accelerated osteogenic process during chondrogenesis. This, in turn, could be the result of a heterochronic process of peramorphosis by which these basal taxa retain the scapulocoracoid of the non-avian theropod ancestors, with the addition of flight-related modifications. With wings having a low aspect ratio and wing loading, *Jinguofortis* may have been adapted particularly to a dense forest environment. The discovery of *Jinguofortis* increases the known ecomorphological diversity of basal pygostylians, and highlights the importance of developmental plasticity for understanding the mosaic evolution in basal birds.

Components and Construction of the Thorax and Vertebral Column in Anthropoid Primates: Implications for Hominoid Evolution

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Primates exhibit perhaps the greatest diversity of positional repertoires among mammals, and the evolution of locomotor specializations is intertwined with the evolution of primate clades. Among extant anthropoids, thoracic shape varies with locomotor adaptation, which

has implications for interpreting hominoid evolution and hominin origins. Locomotor signals from skeletal elements thought to reflect thoracic form have dramatically influenced reconstructions of positional repertoire for several Miocene ape genera (e.g., *Ekembo*, *Nacholapithecus*, *Sivapithecus*, *Pierolapithecus*), despite being drawn from only a handful of vertebrae, ribs, pelves, and sterna. The impact and utility of these inferences rely on the accuracy with which reconstruction of overall thoracic form can be made from isolated bones. We quantified and compared morphology of the intact bony thorax with that of individual thoracolumbar vertebrae, sterna, and ribs. Landmarks and semilandmarks collected from 3D-reconstructions made from CT-data of 59 anthropoid cadavers were used to characterize thoracic shape. Landmark coordinate data from an additional 160 anthropoid skeletons were collected from thoracolumbar vertebrae and the pelvis, and metrics reflecting rib size and curvature were measured from calibrated photographs. Data were compared among taxa using standard 2D- and 3D-geometric morphometric approaches. Our results reveal that each bone associated with the thorax provides different information about overall thoracic shape, and that different bones may provide complementary signals, but not in all cases. Elements often covary in different patterns across taxa, even along the vertebral column and throughout the rib cage. Rib and vertebral morphology each contribute to thoracic shape, although in different and often complementary ways. Results from this research provide a basis for accurately interpreting thoracic form, behavioral reconstruction, and locomotor evolution in fossil hominoids.

Clade-specific Ontogeny Biases Evolutionary Diversification in the Avian Limb Skeleton

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The evolutionary diversification of birds has been facilitated by specializations for various locomotor modes, with which the proportion of the limb skeleton is closely associated. However, recent studies have identified phylogenetic signals in this system, suggesting the presence of historical factors that have affected its evolutionary variability. Previous empirical data suggest that variability of organismal form/shape could reflect the covariation pattern of the period when ontogenetic form/shape change is most pronounced. As different clades of birds are known to have distinct ontogenetic trajectories in limb proportions, evolutionary variability may also differ in a clade-specific manner. In order to investigate this hypothesis, this study examined evolutionary diversification patterns of limb proportions in six avian families (Anatidae, Procellariidae, Ardeidae, Phalacrocoracidae, Laridae, and Alcidae), and compared them to the postnatal ontogenetic trajectories in those taxa, based on measurement of 2641 museum specimens and recently collected ontogenetic series, supplemented by published data. Morphometric analyses of lengths of six limb bones (humerus, ulna, carpometacarpus, femur, tibiotarsus, and tarsometatarsus) demonstrated that: (1) ontogenetic trajectories are diverse among the families; (2) evolutionary diversification is significantly anisotropic; and, most importantly, (3) major axes of evolutionary diversification are correlated with clade-specific ontogenetic major axes in the shape space. These results imply that the evolutionary variability of the avian limbs has been biased along the clade-specific ontogenetic trajectories. It may explain peculiar diversification patterns characteristic to some avian groups, including the long-leggedness in Ardeidae and tendency for flightlessness in Anatidae.

Distinguishing Pattern from Chaos: Superficial Neuromast Receptor Organs of the Lateral Line System in Fishes

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The mechanosensory lateral line system (LL) of fishes is comprised of two types of neuromast organs that mediate the detection of low frequency water flows of biotic or abiotic origin. In bony fishes, canal neuromasts (CNs) are found in pored canals located in a conserved subset of dermatocranial bones and in the LL scales. Superficial neuromasts (SNs) occur singly ("pit organs"), in lines ("pit lines"), or in clusters on the skin of the head, trunk and caudal fin. Several methods have been used to visualize neuromasts including whole mount staining (e.g., methylene blue), SEM, histology, and high-resolution µCT-imaging, but these methods are time consuming, expensive, and/or destructive. Recently, *in vivo* staining using fluorescent mitochondrial stains (e.g., 4-di-2-ASP) has revolutionized our ability to simultaneously image the distribution of all CNs and SNs on the head, trunk and tail (including dramatic proliferations of 100's - 1000's of SNs). Here, we report on SN proliferations in neon tetras and allies (Fam. Characidae), and explore SN proliferations in two genera of gobies (Fam. Gobiidae) using 4-di-2-ASP to map SN distributions and SEM to determine the size, shape and axis of best physiological sensitivity of SNs. We also surveyed recent papers that document SN distributions using 4-di-2-ASP and/or SEM in diverse taxa (e.g., Ostariophysi, Salmoniformes, Stomiiformes, Gobiiformes, Pleuronectiformes). We used these data to reveal the "rules" that define variation in SN morphology and the structural (and functional) organization of the lines, clusters, and large dense fields (patches) of SNs among fishes. Collectively, these data demonstrate that the number and distribution of SNs has been underestimated among fishes and require a new context in which to address the role of SNs in flow sensing. Funded by the URI Office of Undergraduate Research & Innovation (EJM) and NSF Grant #1459224 (JFW).

First Occurrence of Distal Caudal Pneumaticity in an Apatosaurine Sauropod Suggests Homoplasy of Distal Pneumatic Diverticula Throughout Neosauropoda

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Proximal caudal vertebrae of many diplodocid, rebbachisaurid, brachiosaurid, and saltasaurid sauropod dinosaurs show osteological correlates of pneumatic diverticula extending into the tail. Pneumatic invasion of the caudal vertebrae is often serially discontinuous and bilaterally asymmetrical. Caudal vertebrae from new locality OMNH V1694 in the Jurassic Morrison Formation of Oklahoma, representing at least three individuals of an apatosaurine sauropod, all exhibit a high degree of caudal pneumaticity. Pneumatic features include symmetrical left and right lateral pneumatic fossae on the centra, a midline ventral fossa, and camerae in all the centra. Neural spines are preserved on at least three vertebrae, and these bear bilateral pneumatic fossae for most of their length. Most significant are two distal caudal vertebrae of the largest individual. Pneumatization has not previously been documented distal to caudal vertebra 13 in Apatosaurinae. Nonsequential vertebrae OMNH V79226 and OMNH79227, probably representing caudals 20 and 22, however, have bilateral and ventral pneumatic fossae, a central camera, and bilateral pneumatic fossae along the neural spines. Diverticula extending into the distal tail are known in the diplodocines *Diplodocus* and *Barosaurus* and in the titanosauriforms *Giraffatitan* and *Saltasaurus*. Distal caudal pneumaticity in the Oklahoma apatosaurine may mean that pneumatic invasion of the distal tail evolved convergently in multiple macronarian and diplodocoid lineages. Alternatively, caudal pneumatic diverticula may have been widespread in sauropods, but remain undetected because sufficient study of the distal caudal vertebrae of mature individuals of many taxa remains to be done. Pneumatic lightening of the neck has been identified as a crucial adaptation in the evolution of sauropods, and pneumaticity may have served a similar function in the tail.

3D-Intra-oral Prey Trajectories Indicate Distinct Phases in how Channel Catfish (*Ictalurus punctatus*, Siluriformes: Ictaluridae) Swallow Food

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Most predatory ray-finned fishes swallow their prey whole; given that prey items can be half as large as the predators themselves, this can pose a serious challenge. How do fishes transport captured prey from the mouth to the stomach? Prior work indicates that fishes use a combination of directed water flows and pharyngeal manipulation, but understanding how these manipulations transport prey requires tracking the prey itself through the mouth and esophagus. We used X-Ray Reconstruction of Moving Morphology (XROMM) to track prey transport in channel catfish (*Ictalurus punctatus*, *n* = 3). We marked the prey and seven bones on the left side of the head, recording 25 feeding events. By reconstructing the 3D-motions of both the prey and the catfish, we were able to track how the fish move prey through the head and into the stomach. Prey enters the oral cavity at high velocities as a continuation of suction and stops at the approximate location of the pharyngeal basket (~55% of head length) before moving in a much slower, more complex path toward the esophagus. This slow phase coincides with little motion in the head and no substantial mouth opening or hyoid depression. Although we did not mark the pharyngeal jaws, the lateral X-ray videos show them repeatedly opening and clamping down on the food during this phase, suggesting pharyngeal manipulation. Once the prey is in the esophagus, however, its transport is surprisingly tightly correlated with gulping motions (hyoid depression, cleithrum retraction, and mouth opening) of the head. Although the transport mechanism itself remains unknown, to our knowledge, this is the first description of synchrony between cranial expansion and esophageal prey transport in a fish. Our results provide direct evidence of prey transport to the esophagus and suggest that peristalsis may not be the sole mechanism of esophageal transport in fishes.

The Role of Muscles in the Evolutionary Transformation of Limbs and Body Axis: A Case Study in Australian Lizards

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Within several lineages of squamate reptiles there is a transition from a quadrupedal pentadactyl morphology to a limbless, elongated body type. However, studies on the relationship between bones and muscles during such a dramatic change in body plan have so far been limited. Here, we focus on the Australian lizard genus *Lerista*, in which limb reduction and body elongation occurred multiple times independently, and investigate how the pectoral region was evolutionarily affected during limb reduction. We examined 30 species of *Lerista*, covering all different types of limb and phalangeal reductions that are known for the genus, as well as two quadrupedal, pentadactyl outgroup taxa. We applied iodine-staining ("diceCT") to visualize muscle tissues using micro-computed tomography. We were able to assign species into 8 different configuration types depending on the presence of pectoral bones, limb bones and the number of phalangeal bones within each digit present. By considering the number of presacral vertebrae and using linear regression analyses, we also determined the relationship between body elongation and limb reduction for all configuration types. We found evidence for sexual dimorphism in the phalangeal count of some species, and each configuration type appears to display specific patterns of pectoral muscle morphology, e.g., species possessing reduced limbs tend to have a smaller amount of muscles in the ventral part of the pectoral region. Our findings indicate that, even when limbs are reduced or lost, pectoral muscles are not lost accordingly but retained and restructured. We predict a correlation between the ventral thickness of the pectoral muscle layer and the presence and number of digit bones, as previous results indicate that the more digits are lost, the thinner this layer becomes. Based on our findings we aim to test if each configuration type follows similar reduction patterns independent of phylogeny.

Quantification of Skull Ontogeny across Therian Mammals in a Comparative Framework

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Phenotypic variation across mammals is vast and reflects their ecological diversification into a remarkable range of habitats on every continent and in every ocean. The skull is a structure performing many functions, from prey acquisition, feeding, sensory capture to brain protection. Diversity of function is reflected in its complex and highly variable morphology, making it one of the best suited skeletal elements in developmental and evolutionary analyses. Phenotypic variation across species is generally only studied at a fully mature 'adult' state, with limited comparison on how such variation develops. The lack of comparative developmental data is striking considering the intrinsic link between evolution and development. There has been little quantitative analysis of ontogenetic morphology as it relates to cranial diversity, with the exception of heterochrony and allometry studies. As part of a larger study of development and morphology of cranial sutures and cranial shape, we here quantify skull ontogeny in a comparative framework, with microCT-scans spanning late prenatal fetuses to adult stages for 10 mammalian species representing all therian superorders. With 3D-geometric morphometric data, we quantify ontogenetic trajectories across mammals, with the view to making comparisons with a developmental series of transgenic mice (cFos -/-) and WT littermates. cFos -/- have defects in bone remodeling and suture abnormalities. Pilot results show the greatest cranial variation between mutant and WT skulls was in cranial height (PC1=37%) and width (PC2=31%). c-Fos -/- represented the negative extreme of both PCs with a heightened and widened skull morphology. Phenotypic trajectory analysis was significant for strain type (P<0.001) and developmental stage (P<0.001) and attributed to significant variation in orientation (P=0.002). The ultimate goal of such comparisons centers on understanding how diversity in developmental patterns generate adult skull disparity.

A 3D-Neuromechanical Study of Disturbed Locomotion in Rats

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One of the major questions in locomotion science is how mammals compensate disruptions during running. This question has mostly been addressed using either externally applied markers or, if the focus is on skeletal movements, X-ray videography. In our research, we are interested in not only tracking motion patterns, but also which muscles are involved in the different points in time during a disturbance. To that end, we combine biplanar X-ray videography with surgically implanted radiopaque beads for calculation of 3D-joint kinematics, with electromyography of flexors and extensors and measurements of GRF. The combination of neurobiological and mechanical methods in one animal provide a global view of the compensation, which has not been possible before. Our data will offer a baseline for an artificial network for robotic applications.

Functional Morphology of the Palate in *Varanus exanthematicus* (Squamata: Varanidae) and Its Significance for the Evolution of Cranial Kinesis

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Although many species of vertebrates evolved feeding behaviors that employ cranial kinesis, little is known about the loading environment of the palate and other parts of the suspensory apparatus responsible for this movement. Additionally, the role protractor muscles play in controlling palatal excursion or insulating the braincase and sensory capsules via palatocranial joints is challenging to test *in vivo* and equally unclear. We explored the morphology of jaw musculature, kinetic joints, and cranial bones using diffusible iodine-contrast CT and histology of *Varanus exanthematicus*, a modestly kinetic anguimorph lepidosaur. DiceCT-imaging and fiber tracking analysis shed new light on the muscular anatomy and architecture of these muscles. Finite Element Modeling was employed to test the effects of muscle activation and joint material properties on the loading environment of the palate, braincase, and skull. We found different joint material properties have only minor effects on the loading environment of the skull. Complex interactions between *m. levator pterygoideus* and *m. protractor pterygoideus* work to stabilize the palate about the palatocranial joints and ultimately diminish the strains experienced by the braincase. The tubular cross-section and second moment properties of the pterygoid bone reflect the bending and torsional environment developed during biting. These data will inform future studies of cranial function and illustrate how morphological complexity of cranial bones, joints, and muscles evolve in different lineages of lepidosaurs and reptiles in general. New understanding of the biomechanics of the jaw muscles, bony linkages, and connecting joints reveals a better understanding of skeletal adaptation, physiology, and evolution.

Chewing in Musteloid Carnivorans: The Effect of Anatomical Constraints on Variation in Jaw Kinematics

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The carnivoran superfamily Musteloidea consists of over 80 extant species exhibiting diets ranging from carnivory to strict herbivory and frugivory. This dietary diversity is reflected in the morphology of the feeding apparatus, with carnivores displaying the classic features of a well-developed carnassial and hinge-like temporomandibular joint (TMJ). In contrast, the more omnivorous species have expanded crushing areas on the carnassial, whereas frugivorous carnivorans have relatively broad, flat occlusal surfaces. Here, we investigate the extent to which these morphological differences in occlusal morphology, and to a lesser extent the TMJ, impact the ability to alter jaw movements during chewing. We used marker-based XROMM to characterize jaw movements and occlusal dynamics in 4 species of musteloids representing the group's dietary and morphological diversity: carnivorous ferrets (*Mustela putorius furo*), omnivorous raccoons (*Procyon lotor*) and skunks (*Mephitis mephitis*), and frugivorous kinkajous (*Potos flavus*). All animals were fed hard/tough and soft foods during experiments. Compared to soft foods, hard/tough foods elicit longer yet less variable power strokes in all species. Hard/tough foods are also associated with more jaw rotation about a vertical axis (i.e., jaw yaw) and larger mesiodistal and buccolingual occlusal displacements during the power stroke, reflecting an increased emphasis on grinding. Differences between foods tend to be most pronounced in raccoons and least pronounced in ferrets, suggesting that occlusion of the blade-like carnassial coupled with a hinged TMJ may limit variation in jaw movements in response to different foods. This project was supported by National Science Foundation (USA) grants DBI-0922988 and IOS-1456810.

Untangling the Effects of Internal and External Abrasives on Dental Microwear

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In dental wear research, there is an ongoing debate which ingesta are responsible for observed wear patterns. Internal amorphous silica bodies (phytoliths) in plant tissue are softer than enamel, but have been shown to act as abrasives. External silicate particles, such as dust and grit, are harder than enamel and thus wear teeth. Plant forages often comprise both, internal and external abrasives. It remains unclear which of the two abrasives predominantly causes tooth wear, and whether their respective influence can be identified. To address this question, we performed controlled feeding experiments with guinea pigs (in groups of 6) which either received a natural (plant) feed free of external abrasives in fresh and dried state, or a pelleted feed with addition of different external abrasives (volcanic ash, quartz sand, loess, kaolin). We chose plant forages with increasing phytolith content (lucerne, grass, bamboo: 0.4-3.2%) and mineral abrasives (1-8%) with different mean particle sizes (4-166 μm) and geometry (rounded *vs* angular). As a measure of tooth wear we are using dental microwear texture analysis employing 46 ISO, SSFA and other surface texture parameters. In the natural diet groups, enamel surface roughness increases with phytolith content, but for grass also depends on hydration state. Fresh grass leads to surface textures with low roughness similar to those of lucerne groups, while dry grass is significantly more abrasive. In the external abrasive groups, surface roughness is found to increase with particle size. Surface complexity is not significantly affected by particle size, but by particle geometry. Angular volcanic ash (96 μm) results in higher complexity as compared to natural feeds, while rounded quartz fine sand (166 μm) results in higher roughness values. This is the first direct evidence of wear parameters quantifying textures caused by coarse-grained external abrasives, thus untangling their effects from internal abrasives.

3D-Visualizations of the Hearing Apparatus in Teleost Fish

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A number of teleost fish exhibit a special connection between swim bladder and the statoacoustic organ (i.e., labyrinth) enabling an excellent hearing capacity. Since the 19th century, various anatomical details of hearing organs have been described, e.g., in clupeids and especially the Weberian apparatus in Otophysi. Corresponding schematic drawings have been circulated among the scientific literature ever since. However, clear 3D-visualizations of this immensely important organ system are still rare. Here, we present 3D-visualizations of the hearing apparatus in three species: Atlantic herring (*Clupea harengus*), common minnow (*Phoxinus phoxinus*) and stone loach (*Barbatula barbatula*) based on X-Ray tomography. This will be complemented by data on the Northern pike (*Esox lucius*) as representative of the great majority of fish not possessing such structural connection of swim bladder and labyrinth.

Bone Without Minerals in Atlantic Salmon (Salmo salar): Growth, Function and Retention of the Capacity to Mineralize

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Calcium and phosphorus are the main bone minerals. Tetrapods depend on dietary calcium for the mineralization of their skeleton. Calcium intake via the gills makes teleosts independent from intestinal calcium uptake, but dietary phosphorus is required for bone mineralization (Witten & Huysseune, 2009, Biol. Rev. 84: 315-346). We fed Atlantic salmon a diet with a low phosphorus content for 7 or 16 weeks. These fish developed bone completely devoid of minerals (Witten et al., 2019, J. Exp. Biol. doi: 10.1242/jeb.188763). The growth of the vertebral bodies was not interrupted and bone structures remained regular. Mechanical testing showed vertebral bodies that are highly compressible but not malformed. Interestingly, the large amounts of non-mineralized bone that developed during the time of the experiment retain the capacity to mineralize. The bone mineral content could be restored by feeding animals diets with sufficient P content. Late mineralization can also restore the mechanical properties of the vertebral bodies. It is commonly accepted that osteoblasts produce the bone matrix and actively mineralize the bone. Therefore a surprising result of this study was that late mineralization did not start in the vicinity of the osteoblasts. Instead, mineralization resumed deep inside the bone matrix, continuous with the last mineralized areas. The large distance between the osteoblasts on the bone surface and the mineralization front suggests that osteoblasts do not actively contribute to late mineralization. It is, however, evident that despite the lack of minerals, osteoblasts produce a matrix that is capable to mineralize. Our experiments show decoupling between bone matrix formation and mineralization.

Limb Bone Diversification in Sciuromorph Rodents in Light of Scaling, Lifestyle, Homoplasy, and Macroevolutionary Modeling

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Sciuromorph rodents are a monophyletic group of more than 300 extant species. Arboreal locomotion is the most likely ancestral condition, whereas an aerial lifestyle was acquired once and a fossorial lifestyle three times independently. Each lifestyle includes species with a body mass range spanning two orders of magnitude. First, we asked how the morphology of the most proximal fore- and hind limb bones, i.e., scapula and femur, depends on scaling and lifestyle. Various traits were investigated, respectively, representing length-, robustness-, and muscular properties of 180 species. Ornstein-Uhlenbeck (OU) modeling was applied to assess the phylogenetic inertia of all traits, which was found to be low. Thus, ordinary regressions were used, including an interaction effect to test whether scaling depends on lifestyle. Then, it was evaluated whether independent acquisitions of a fossorial lifestyle are reflected in morphological homoplasy of these appendicular bone traits. The influence of body mass on trait homoplasy was accounted for by using regression residuals. The likelihood of OU models differing in whether fossorial groups do or do not share a common trait optimum was compared using Monte Carlo simulation. Only a few traits of each bone displayed a distinct allometric pattern and/or a difference in scaling among lifestyles. The low phylogenetic inertia indicates that it might have been advantageous to maintain the isometric scaling pattern of the arboreal ancestor for most of the traits during sciuromorph diversification. Model comparison suggests that homoplasy is found more likely in the scapular- than in the femoral traits. We hypothesize that digging imposes strong functional constraints on the scapular morphology, limiting the diversity of morphological solutions. The hind limb appears to be less constrained in its functional role, reflected by an absence of trait homoplasy.

The Fibrous Musculo-Hydrostatic System of Sea Lampreys (*Petromyzon marinus*; Agnatha)

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As a result of over 500 million years of independent evolution, the skeleto-muscular system of the trunk of the jawless lamprey differs in several aspects from that of jawed vertebrates. Its fibroskeleton comprises the dermis, hypodermis, dorsal longitudinal ligament, perimysial lamellae, deep fascia (periaxial and perivisceral fasciae), and the myosepta, but lacks the horizontal skeletogenous septum and the zigzag configuration of the myosepta of piscine gnathostomes. Nevertheless, lampreys are capable of a wide range of motions, from a more anguilliform swimming mode to extreme flexions and torsions performed in building nests from stones. To understand how the mobility of lampreys depends on the morphology of the skeleto-muscular system, its three-dimensional configuration was investigated through microdissection, histology, MRI, and 3D-modeling. Radial and longitudinal fibers create a scaffolding that encases the muscle blocks within the myomeres and anchors the skin to the axis of the body (i.e., notochord, fat column, and dorsal vertical septum). Radial fibers pass from the basement membrane through the dermis, cross the hypodermis, become part of the perimysial lamellae, and merge with the deep fascia. Myosepta are formed by radial fibers from the permysial lamellae and by tendon fibers that interconnect muscle fibers of adjacent myomeres. Some of these tendon fibers dive medially and merge with myosepta. Fibers from the myosepta, dorsal vertical septum, and hypodermis interbraid with the fiber bundles of the dorsal longitudinal ligament. Forces generated by contracting muscle fibers are transmitted across the myosepta and to the deep fascia. The radial expansion of the shortening muscle fibers is resisted by the dermis and perimysial lamellae while the turgidity of the trunk increases. Hence, the fibroskeleton functions as a hydrostatic system that can modulate forces for swimming and moving stones depending on the number of muscle fibers involved.

Tibia Osteohistology Reveals Non-Annual Vascular Cortical Rings in *Maiasaura* (Dinosauria: Hadrosauridae) Young of the Year

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The annual pause in tetrapod bone apposition is recorded in the cortex as a hypermineralized "line of arrested growth" (LAG). One histology study utilized LAG periodicity to quantify ontogenetic ages and growth rates in a dataset of fifty tibiae from the hadrosaurid dinosaur *Maiasaura*. Prior to the first LAG in the tibiae, cortical rings resulting from localized changes in vascular diameter were also noted, but not investigated further. Here, the composition, frequency, and cortical extent of localized vascular changes (LVCs) in the fifty *Maiasaura* tibiae are documented to investigate potential cause(s) and enable eventual comparisons to LVCs in other taxa. Results show the *Maiasaura* LVC is made of laminae forming a ring of primary osteon vascular canals with diameters uniformly larger or smaller than those in the adjacent cortex. With one exception, *Maiasaura* LVCs are only present prior to the first LAG. However, LVC frequency is variable: some tibiae had no LVCs and others had as many as five before the first LAG. Because LVC frequency is variable, and LVCs are restricted to cortex formed during the first year of growth, LVCs likely do not have an annual periodicity in *Maiasaura*. Instead, LVCs may signal temporary, stressful events. *Maiasaura* growth rates were highest during the first year, as were mortality rates, which suggests *Maiasaura* were especially susceptible to physiological stresses during that time. One subadult tibia with a pathologic outgrowth is the only specimen within the sample to have LVCs throughout the cortex, which supports the association of LVCs and stresses on growth. Unfortunately, the presence and cause(s) of LVCs in extant taxa is under-explored, so the physiologic implications of *Maiasaura* LVCs is unresolved. As LVCs may provide yet another histological method for interpreting extinct vertebrate biology, foundational investigations of LVCs in extant vertebrates should be pursued.

Predicting Muscular Architecture of the Early Mammalian Hind limb by Comparing Extant Species with Different Locomotor Ecologies

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Early mammals are often portrayed as small, non-cursorial quadrupeds capable of navigating various three-dimensional environments, such as the ground of the forest floor or understory. Compared to their larger "sprawling" ancestors, early mammals had limbs adducted underneath the body, increasing speed and mechanical efficiency for locomotion. However, locomotion also depends on the underlying musculature, which has not been reconstructed in the limbs of early mammals. Here, we compare hind limb muscular architecture in a small, quadrupedal mammal - the short-tailed opossum - to seven other extant mammal species in order to infer the musculature of early mammals. These species can be broadly separated into larger, more cursorial (horse, greyhound, cat, hare) and smaller, non-cursorial (opossum, mouse, rat, guinea pig) forms. By comparing muscle architectural properties, we demonstrate that hind limb musculature in the opossum is not significantly different from other small, non-cursorial mammals but is very different from larger, more cursorial mammals. The more cursorial species have larger, longer, and more pennate muscles with shorter fibers and larger physiological cross-sectional area (PCSA). Larger PCSAs may provide the force production necessary to maintain high speeds during cursorial locomotion. Longer muscle fibers in small, non-cursorial forms may instead reflect faster muscle contraction through larger joint ranges of motion, improving postural maintenance to navigate more complex environments. Given that the earliest mammals are described as small, non-cursorial quadrupeds, they likely faced similar biomechanical challenges to extant, small-bodied species. The muscular architecture of the early mammalian hind limb may thus have been similar to the short-tailed opossum and other small, extant mammals.

Contrasting Musculoskeletal Structure of the Turtle (Reptilia: Testudines) Pectoral Apparatus in Paddling *vs* Flapping Species

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Despite a conservative body plan, the structural diversity of turtle limbs is considerable. Few studies have examined how variation in the structure of the pectoral girdle and its muscle, tendon, and ligament systems relates to differences in locomotor function across turtle species. We compared pectoral musculoskeletal structure between a species that swims by paddling (the river cooter, *Pseudemys concinna*) *versus* one that swims via forelimb-based flapping (the loggerhead sea turtle *Caretta caretta*). In both species, the pectoral girdle is tri-radiate. The scapula extends dorsally from the glenoid, but has a ventromedial acromion process that arises roughly orthogonal to the scapular blade. A large procoracoid also extends posteromedially from the glenoid, nearly parallel to the plastron and adjacent to the collagenous coelomic wall. Pectoral muscles support the procoracoid. In cooters, the scapula is the longest element. It articulates dorsally via a short suprascapular cartilage with the lateral aspects of the 1st or 2nd trunk vertebrae, attaching via ligaments and portions of the origins of three scapular muscles. Ventrally, the acromion attaches loosely to the entoplastron and is roughly as long as the procoracoid. In the loggerhead, the acromion is short and the scapula and procoracoid are nearly equal in length. The scapula articulates dorsally, by a flexible suprascapular cartilage, to the dorsolateral aspect of the 1st trunk vertebra, with ligaments extending from the suprascapular cartilage to the ventral aspect of the neural bone. The dorsal scapula is supported by four muscle origins that also extend to the carapace. The girdle articulates ventrally via strong ligaments to the entoplastron, by muscle insertions to the epiplastra, and fibrous connective tissue of the plastron's gular rim. Anteroposterior rotation of the pectoral girdle is greater in cooters but limited in sea turtles and functionally linked to the acromion-plastron attachments.

Ontogenetic Changes of Trabecular Bone in the Femoral Head of Pigeon

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Trabecular bone is typically localized in the proximal and distal ends of limb bones, provides strength and transfers external load away from the joint to the cortical bone. It is more sensitive to variations in magnitude and direction of load throughout life, and may more clearly reflect function and biomechanical characteristics of bone. Using microCT and 3D-bone analysis software, femur specimens of 30 healthy pigeons *(Columba livia)*, aged from 4 to 336 days, were studied to identify and evaluate three-dimensional microstructural changes during post-hatching growth. A series of structural parameters were quantified in spherical volumes of interest positioned in the center of the femoral head. With increasing body mass during ontogeny, trabecular bone volume (BV/TV) was found to grow continuously until reaching 28.99% by week 8; trabecular number (Tb.N) persisted with a rapid increase before fledging at four weeks, and then remained stable; trabecular thickness (Tb.Th) grew rapidly and constantly in the early postnatal development, reaching a maximum value at week 16; the trabeculae changed from rod-shaped to plate-shaped from 4 days to 4 weeks; the fabric anisotropy (DA) of the spatial arrangement of trabeculae presented two rapid growth stages, during the nesting period (4 days-4 weeks) and post-fledging period into sexual maturity (8-24 weeks), respectively. Pearson correlation test showed that BV/TV, Tb. Th, DA were positively correlated with age. Taken together, the growth of trabeculae in the femoral head was dominated by both the increase in bone density and trabecular anisotropy during nesting period, and a sustained improvement in trabecular spatial arrangement before maturity. These features were associated with the attainment and enhancement of locomotor ability, and further revealed different strategies in response to the change of the external load.

Quantifying Enamel Complexity and Thickness in Early Pleistocene African Suids

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Plio-Pleistocene African suids, such as *Notochoerus* and *Metridiochoerus*, rely heavily on their third molars for processing grasses. They followed similar trajectories in their evolution, with increasingly higher crowns with more pillars in the M3s. Previous studies also suggested increased number of shearing crests and decreased enamel thickness. However, they have never been confirmed quantitatively. In the early Pleistocene, the dispersal of *Metridiochoerus* coincided with the decline of *Notochoerus* in the fossil record. This has been attributed to abiotic factors such as habitat changes, despite the observations that their stable isotope records have significant overlaps. To further explore the functional implications of suid dental morphology, we developed quantitative measurements for enamel complexity and thickness with dental wear controlled for, so that occlusal morphology of different species can be properly compared. We selected third molars of contemporary *Notochoerus* and *Metridiochoerus* specimens from the Turkana Basin, northern Kenya, which are dated between 2.1 and 1.8 Ma. We used occlusal photographs and microCT-scans of selected specimens to generate the measurements. When controlling for wear, *Notochoerus* has consistently higher complexity than *Metridiochoerus*. As tooth wear progresses, enamel thickness in *Notochoerus* also decreases less rapidly than in *Metridiochoerus*. These results imply that *Notochoerus* likely have better food processing ability than *Metridiochoerus*. We suggest that other aspects in physiology or ecology may better explain the decline of *Notochoerus* and thriving of *Metridiochoerus* in the early Pleistocene. The next step is to expand the time scale of our investigation and test hypotheses regarding the evolutionary trends in suid dental morphology.

A Tale of Two Extremes: Palate Length Predicts Vomeronasal Morphology

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Mammalian social chemical cues are primarily detected in the vomeronasal system. While vomerolfaction is well conserved due to its role in fitness-related behaviors, several mammalian groups have lost function, including Old World primates, some aquatic mammals, and most bats. Furthermore, there is extensive variation in both size and shape of vomeronasal morphology in both the nasal cavity and brain. These losses and vestigializations might relate to ecological variation, such as circadian rhythm, social system, or habitat specialization, but it has never been considered that loss may be due to selective pressures on the skull. We predicted that skulls that exhibit extreme palate lengths, either exceptionally long or short, had a higher probability of rudimentary or absent vomeronasal morphology. Using Bayesian hierarchical models, we estimated the probability of palate length and the response of vomeronasal morphology in mammals. We discovered that intermediate palate sizes had a higher probability of having intact vomeronasal morphology, after accounting for clade-specific variation. This may indicate that selection is stronger for skull and palate specialization than for maintaining two nasal chemosensory systems. Our study opens up a new hypothesis for the many instances of vomeronasal loss observed in mammals and sheds light on new mechanisms leading to vestigialization and trait loss.

Intracranial Soft Tissue Adaptations in the Land-to-Sea Transition: Shifts in Marine Crocodylomorph (Crocodylomorpha: Thalattosuchia) Vasculature and Paratympanic Sinus Systems

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From an osteological perspective, the secondary aquatic adaptations of vertebrates are well understood; from a soft tissue one, less so. Here, we use an ancient group of crocodylomorphs, Thalattosuchia, as an exemplar of the land-to-sea transition. During the Jurassic, thalattosuchians transitioned from shallow marine to open ocean habitats, with the subclade Metriorhynchidae convergently evolving osteological adaptations seen in other Mesozoic marine reptile groups (e.g., hydrofoil-like forelimbs, hypocercal tail). However, the soft tissue adaptations underpinning the success of Thalattosuchia remain obscure. Our team microCT-scanned and digitally segmented the cranial endocasts of extinct and extant crocodylomorphs. All thalattosuchians share the same profound shifts in intracranial vasculature and pneumaticity (although metriorhynchids adapted these systems further). There was hypertrophy of the carotid-orbital system, temporoorbital system, transverse sinuses and possibly the cavernous sinus. Based on the blood flow patterns of extant species, thalattosuchians would have had far greater blood flow entering and exiting the orbital and nasal regions. This increase corresponds with their proportionally large eyes, and suggests that the nasal salt glands of Metriorhynchidae evolved at the base of Thalattosuchia. In thalattosuchians, invasion of the cranium by the paratympanic sinus systems was less extensive than those of sphenosuchians, protosuchians and extant species. The recessus epitubaricum, otoccipital diverticula and vestigial infundibular diverticula were confluent with the tympanic cavity (rather than discrete diverticula), while the intertympanic, prootic and quadrate diverticula were absent. Our results suggest that at least some of the major soft tissue adaptations that underpinned the metriorhynchid radiation into the pelagic realm occurred much earlier in thalattosuchian evolution, and occurred prior to their osteological and locomotory adaptations.

Comparative Limb Bone Scaling in Turtles: Phylogenetic Transitions with Changes in Functional Demands?

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Several terrestrial vertebrate clades include lineages that have evolved nearly exclusive use of aquatic habitats. Such transitions are often associated with the evolution of flattened limbs that are used to swim via dorsoventral flapping. Studies on limb bone loading in turtles found that torsion is high relative to bending loads on land, but reduced compared to bending during aquatic rowing. Release from torsion among rowers could have facilitated the evolution of flattened limbs among aquatic species, conferring hydrodynamic advantages. Because rowing is regarded as an intermediate locomotor stage between walking and flapping, rowing species might show limb bone flattening intermediate between the tubular shapes of walkers and the flattened shapes of flappers. We collected measurements of humeri and femora from specimens representing four functionally divergent turtle clades: sea turtles (marine flappers), softshells (specialized freshwater rowers), emydids (generalist semi-aquatic rowers) and tortoises (terrestrial walkers). Patterns of limb bone scaling with size were compared across lineages using phylogenetic comparative methods. Rowing taxa did not show the intermediate scaling patterns we anticipated, but our data provide other functional insights. For example, sea turtle humeral flattening was associated with positive allometry (relative to body mass) for the limb bone diameter perpendicular to the flexion-extension plane of the elbow. Softshell limb bones exhibit positive allometry of femoral diameters relative to body mass, potentially helping them maintain benthic positions in water by providing additional weight to compensate for shell reduction. Tortoise limb bones showed positive allometry of diameters, as well as long humeri, relative to body mass, potentially reflecting specializations for resisting loads associated with digging. Overall, scaling patterns of many turtle lineages appear to correlate with distinctive behaviors or locomotor habits.

Variability in the Postcranial Skeleton of the European Dabbling Ducks (Aves, Anatidae): Identifying Nodes of Strong and Relaxed Selection

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It is commonly believed that variation is poorly pronounced in the skeleton of birds, which in turn is usually explained by strong flight adaptations. And, although general size variability of some skeletal elements has been extensively studied, differences in variation for various elements and within element variability have never been assessed for the bird skeleton. I have studied variability of linear measurements and ratios of the main postcranial bones in 7 species of European dabbling ducks (*Anas* s.l.). The main result is that various measurements and ratios showed distinctly uneven variability. Total length of the wing bones varied the least, whereas the shaft width of all bones (and especially hind limb) was found to be the most variable. Several nodes of notably increased variation have been detected, which include some measurements of the coracoid, distal width of the ulna, and proximal width of the femur. Most studied indexes were found to be very stable, especially for the humerus: i.e., the width/total length index of the humerus equals 0.22-0.23±0.01 in all studied specimens (more than 200). I interpret the observed difference in variability as an indication of stronger and relaxed selection as applied to various functional units within the body. This study was supported by the grant from RFBR, project 17-04-01162.

Cell and Tissue Interactions in Head and Heart Development and Evolution

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All vertebrates begin their development from a zygote and the processes from this cell to a complex organism are often complicated and include many gene regulatory networks, cell migration, cell differentiation, communication between cells and between tissues, etc. Earliest mis-regulations in those processes lead almost always to the demise of the developing embryo. This is because the most complex processes related to body plan formation happen during the earliest phase of embryonic development. For example, in humans at the end of the first month (28 days after fertilization), the head and heart regions are clearly distinguishable: the heart is beating, u-shaped and atria and ventricles are aligned; the pharyngeal arches are present, as are eye and ear anlagen (placodes), in the brain several regions are distinct, including forebrain, midbrain, and hindbrain. There are many research groups all over the world studying one or the other system (brain, cardiovascular, craniofacial), but only few groups study the interactions between all tissues (ectoderm, mesoderm, endoderm – neural crest as special tissue derived from ectoderm). Even less studied is the evolution of cell and tissue interaction during early head and heart development. However, understanding precisely those interactions will help us to understand the evolutionary development of our most complex body parts, head and heart. Additionally, this knowledge can contribute to a better understanding of human syndromes where often craniofacial and cardiac abnormalities occur in the same individual. Therefore, I aim to present here a summary of what is currently known about the evolutionary and developmental processes important for the early stages of head and heart development in vertebrates.

3D-Quantitative Morphometrics in Craniofacial Development by X-ray Computed Microtomography

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X-ray computed tomography is a widely used technique not only in medicine, but it has found its application also in industry and scientific fields including developmental biology. X-ray computed microtomography (microCT) allows to extract quantitative 3D-information about various objects with resolution down to 1 micrometer, and it is used for non-destructive testing, materials characterization and dimensional metrology. We have exploited these possibilities and applied them in craniofacial research. Modern developmental biology requires both qualitative and quantitative 3D-information about the studied objects, which is not provided by conventional 2D-imaging methods. Besides, the complexity of biological structures often requires a comprehensive methodology to compare shapes and sizes. Our approach is to apply procedures and analysis routinely used or developed for industrial microCT to address scientific questions in craniofacial research. This approach is based on the long-term experience of the CEITEC BUT microCT-research team in both, industrial and scientific applications. The connection of material and life sciences brings new possibilities in imaging, data processing and evaluation of 3D-biological models. In this work, we present 3D-structures that were analyzed by different approaches on selected examples from craniofacial research conducted on mouse embryos; e.g., wall thickness analysis of facial cartilage, shape comparisons of mouse heads, volume determination of ossification centers etc. A complete procedure consisting of staining, microCT-measurement and subsequent data processing is discussed. This research was carried out under the project Czech Science Foundation GACR 17-14886S and CEITEC 2020 (LQ1601) with financial support from the Ministry of Education, Youth and Sports of the Czech Republic under the National Sustainability Programme II and CEITEC Nano Research Infrastructure (MEYS CR, 2016–2019).

Frugivorous Adaptations in the Feeding Apparatus of *Calyptomena* (Aves, Passeriformes, Eurylaimides)

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Our morphofunctional study of the feeding apparatus (both the jaw and hyoid) of the frugivorous broadbills *Calyptomena* - a genus of the small archaic group Eurylaimides (suboscine passerines of the Old World) - revealed a number of peculiar features, interpreted here as adaptations for the frugivorous diet. For example, *Calyptomena* broadbills have morphological features that prevent passive protraction of the upper jaw when the bird tears off an attached fruit. These birds can successfully consume fruits that differ significantly in both size and hardness, including very large fruits with a large seed, comparable to the bird head in size. *Calyptomena* broadbills swallow the fruit entirely since the construction of their small and gracile but very wide bill does not allow any significant mechanical processing of the object before swallowing. The branches of their lower jaw are arranged as wide as possible for this skull structure, but when the bird swallows the fruit, they are able to move apart passively, further expanding the gap. This movement may activate a special mechanism for locking of the jaw joint. This mechanism generates a peculiar force action of the jaws onto the object, which allows them to increase the force pushing the fruit down the throat with jerks. Active retraction of the *Calyptomena* tongue also helps push the fruit down the throat. These birds can mash soft fruits and squeeze the nourishing juice from them, pressing the fruit with a wide tongue to the specifically fortified arch of the oral cavity. Their movable tongue also helps the birds to perform complex manipulations in the bill with relatively small objects. Some of these specific details and mechanisms are reported in other fruit-eating birds (for example, hornbills, Asian barbets, mousebirds, etc.), but only in *Calyptomena* all of them are present within one feeding apparatus.