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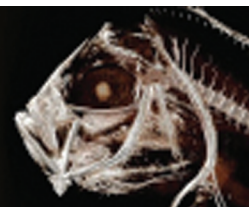
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Abstracts of the International Congress of Vertebrate Morphology 14 Virtual Meeting: 07.-10. August 2025

Abstracts

Note FROM THE President

On behalf of the International Society of Vertebrate Morphologists, I'm pleased to introduce this abstract volume for the 14th International Congress of Vertebrate Morphology, our first ever online virtual conference, to be held from 7 to 10 August, 2025. It is vital that we publish our abstracts in an actual journal even though we are online-only this time, for the scientific record and because many attendees have institutions or careers that mandate or benefit strongly from such formal publications. We have continued our longstanding partnership between the ISVM/ICVM and the Journal of Morphology, and once again Editor Matthias Starck has been a tremendously valuable ally in inviting and editing this volume – many thanks to him from ISVM.

ISVM is an INTERNATIONAL celebration of vertebrate morphology in all its guises. And we are proud to be a unique conference. ICVM is key for disseminating research in progress, from original methods to new datasets and novel expertise to all the kinds of vital biological insights, ideas and discoveries that the dynamic, highly interdisciplinary field of morphology is. We do, and must continue to, seek to maintain and improve on our inherent global inclusiveness. This striving is particularly important in these times of political, social and economical challenges to science itself in many countries around the world. We need togetherness and the strength that comes with it. That internationality was intended to be promoted by this “experimental” online conference. We hope, and see signs that we have succeeded, to be more inclusive in terms of welcoming those who have a harder time attending our in-person meetings, for various reasons such as financial and disability and the privilege to travel at all. We also hope that this is an ethical shift in these times of obvious and dreadful global climate change, and the disproportionate contributions of global travel to that climate change that are caused by scientists in more wealthy countries (like other people who travel). Our global reach is also demonstrated by our prior conference locations:

Previous ICVM meetings:

1. Giessen, 1983 (ca. 300 participants)
2. Wien, Austria, 1986 (ca. 350 participants)
3. Antwerp, Belgium, 1989 (ca. 430 participants)
4. Chicago, USA, 1994 (ca. 450 participants)
5. Bristol, UK, 1997 (ca. 450 participants)
6. Jena, Germany, 2001 (ca. 700 participants)
7. Boca Raton, USA, 2004 (ca. 470 participants)
8. Paris, France, 2007 (ca. 600 participants)
9. Punta del Este, Uruguay, 2010 (315 participants)
10. Barcelona, Spain, 2013 (450 participants)
11. Washington DC, USA, 2016 (650 participants)
12. Prague, Czech Republic (ca. 750 participants)
13. Cairns, Australia (ca. 450 participants)

At this writing, we have > 250 people registered for ICVM14, which is certain to increase substantially over the next > 2 months, and > 200 abstract submissions now that the deadline has passed. We will be particularly interested in scrutinising the demographic data for these participants before the conference, so we can report on success of ICVM14 in ISVM's business/members' meeting.

And we look forward to returning to an in-person meeting in Halifax, Nova Scotia, Canada in 2027 for ICVM15. Members then will vote on how to proceed with future online/in-person conferences.

We should be proud of our international inclusiveness to date, and creative about how we encourage its expansion with future ICVMs. This inclusiveness extends to ICVM's other benefits to attendees, including as a social outlet for enjoyment with like-minded scientists but also as for continuing and creating collaborations. And other institutions such as businesses that rely on us as customers form pivotal interfaces with ICVM, including as sponsors, such as these for ICVM14: The Anatomical Record and University of Chicago Press, at this writing (with more pending).

I finish this note to our community with broad thanks to individual morphologists. ICVM conferences cannot happen without many efforts of those who are passionate about ISVM, and we cherish the fact that these people volunteer their valuable time in service to ISVM and ICVM. ICVM14 has benefitted from the service of:

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ABSTRACTS

Plenary Speakers

Alida Bailleul (*Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China*)

Anne-Claire Fabre (*Institute of Ecology and Evolution, University of Bern and Naturhistorisches Museum Bern, Switzerland*)

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Tiana Kohlsdorf (*Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Brazil*)

Regular Talks

The Postural Stability of the Birds, a Passive Tensegrity System

Abourachid A¹, Pelletan I¹, Vimbert R², Chevallereau C², Porez M²; ¹Muséum National d'Histoire Naturelle, CNRS – Mecadev, ³Nantes Université, LS2N, CNRS, UMR 6004 (anick. abourachid@mnhn.fr)

Birds stand on one or two feet when resting or sleeping. The fact that they can sleep while standing suggests that this posture involves minimal energy expenditure. We hypothesise that postural stability is passive and involves a tensegrity system, whereby rigid elements are passively stabilised by cables under tension due to gravity. The skeleton corresponds to the rigid elements, while the musculature corresponds to the cables. The bodies of birds in a resting position were modelled with five rods and one cable stretched from the pelvis to the foot. The model was positioned as the pelvic skeleton is when standing up, with gravity applied to the centre of mass of the body. We used an iterative method to determine the minimum features required to achieve stable equilibrium. We found that the shape of the joints enables the cables to stretch the legs. A single cable is insufficient to stabilise the system. Depending on body shape, four to six cables are required. The size of the pulleys and the stiffness of the cables ensure stability, positioning the centre of mass above the foot in the resting position and enabling the system to return to this position after small disturbances. Synapomorphies of bird anatomy, such as the iliofibularis ligamentous loop or calcified tendons, are involved in this process.

Functional Consequences of Neuromast Size and Shape Variation In Fishes

Aggarwal I¹, Webb J², Onck P¹, Kottapalli A¹; ¹University of Groningen, ²University of Rhode Island (jacqueline_webb@uri.edu)

The mechanosensory lateral line system is composed of neuromast sense organs located on the skin and in lateral line canals. The apical ciliary bundles of all the mechanosensory hair cells within a neuromast project into a gelatinous cupula whose size and shape mirrors that of the neuromast. Cupula displacement by flows stimulates the hair cells allowing fishes to respond to water flows generated by prey, predators, and conspecifics (e.g., communication), and to orient and navigate in their aquatic habitats. Known morphological variation in the lateral line system among fishes is striking. Functional correlates have been examined with respect to differences in cranial canal morphology (e.g., narrow vs. widened), but the functional significance of variation in neuromast morphology has largely been the subject of speculation. Here we report on a new computational model that uses cupula size and shape as a proxy for superficial neuromast size and shape to explore the effects of these parameters on the ability to detect biologically relevant water flow stimuli that vary in velocity (amplitude) and direction (relative to the major axis of the neuromast). This model presents a powerful predictive platform that can be used to probe the functional consequences of this unexplored aspect of the evolutionary diversification of the lateral line system among fishes.

Shouldering the Burden: Functional Morphology of the Therian Mammal Scapula

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The therian mammal scapula presents a particularly interesting, if challenging, opportunity to relate anatomical form to biomechanical function, being both biomechanically complex and highly variable in its morphology. Previous research in constrained taxonomic groups has demonstrated links between scapular morphology and factors including evolutionary history, size and locomotion, but no single large-scale study has explored scapular variation across therians. This study aims to investigate particularly the links between scapular morphology and locomotion behavior across therians, including associations with size variation, evolutionary history, and clavicle presence/absence. To address this, we landmarked the scapulae of 201 extant therians, representing 73% of families and subfamilies, using a combination of true landmarks and semilandmark curves which capture the overall shape and key anatomical features of the scapula. We also used a novel methodology for quantifying locomotion behavior using ability scoring, which captures behavioral profiles in higher resolution than traditional categorization. Our results demonstrate that scapular morphology in therians is influenced by a complex mosaic of factors and interactions, but we are able to identify influences of key locomotion abilities across the data set, particularly running and digging, and how these behaviors are related to scapular morphology. These results advance our understanding of the interplay between shape, function and evolutionary history in the therian scapula, providing insights

which may contribute to a broad range of research, including biomechanics and paleontology.

Morphological Predictors of Locomotion and Distribution in Fossorial Lizards

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Fossoriality is a key force involved with phenotypic diversification in Squamata. The occupation of subterranean habitats is associated with the evolution of elongated and limb-reduced forms in several lizard lineages. Snake-like bodies facilitate locomotion through the soil, and fossorial lizards often use their heads to perforate the substrate. The correspondence between head shape and burrowing substrate is remarkable among these animals, and specialization to some types of soils likely influences distribution patterns in several lizard lineages. We investigated the morphological predictors of locomotion and distribution in fossorial lizards using three approaches. First, we modelled phenotypic evolution to characterize ecomorphological associations between head shape and soil. Sand-swimming lizards exhibit wedge-shaped snouts, while leaf-litter dwellers evolved bullet-shaped heads. Then, we evaluated the resistance of different substrates to distinct shapes. We simulated headfirst burrowing in three different soils using 3D-printed skull models of six lizard species. Wedge-shaped heads tend to outperform bullet-shaped forms in all conditions tested. Finally, we investigated the morphological correlates of distribution range in fossorial lizards. Head shape explains distribution better than other morphological components, including body size. Altogether, our results suggest that highly specialized traits mediate geographical distribution by affecting lineages' abilities to disperse. Fossorial lizards adapted to specific soils are likely isolated from their surroundings, suggesting a complex interplay between evolution, ecology and the capabilities of organisms to cope with fast environmental changes.

You Should Look a Gifted Ungulate In the Mouth: Using 2D Occlusal Cheek Tooth Morphology to Study the Evolution of Molarization In Hoofed Mammals

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Cheek teeth are filled to the cusp with information about mammalian evolution. Most work is focused on individual cheek tooth loci as opposed to considering the premolars and molars as serial homologues. This focus on individual tooth loci has left the exploration of interregional phenomena behind. One such phenomenon is the molarization of premolars across hoofed mammals; some have simple unicuspid premolars while others have premolar crowns that are equal in complexity to their molars. We studied 2D occlusal morphology across the upper and lower premolar-molar boundary in artiodactyl and perissodactyl taxa to study the evolution of molarization. We developed a landmarking scheme for the upper and lower premolar-molar boundaries to capture the morphology across this important identity boundary. Shape data were analyzed through phylogenetically informed modularity analyses to understand the covariation structure at the upper and lower

premolar-molar boundaries. Artiodactyl results showed support for modularity across the premolar-molar boundary, and that relationship was consistent between the upper and lower dentition. Perissodactyl results showed support for modularity across the premolar-molar boundary but showed differences between the upper and lower dentition. Both groups showed limited differentiation of proposed molarization mechanisms based on current dental development understandings. Our results lead us to hypothesize that multiple pathways to molarization in mammalian cheek teeth obstruct any deep homology signals present in 2D occlusal crown morphology.

An Exceptional Network of Diploic Veins In Pangolins: Implications for Brain Drainage and Placental Mammal Phylogeny

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Endocranial veins are critical for cerebral drainage, yet their macroevolutionary patterns are largely unexplored. This knowledge gap is especially pronounced for diploic veins, which are integrated within endocranial venous networks and run between the inner and outer tables of the calvarium. Their diversity, in particular their size, course, or connections, remains virtually unknown in most placental mammals. Here, we employed μ CT-scans and histology to investigate the morphological variation of the diploic venous system across a broad range of placental species. Our analysis confirms the largely endocranial venous drainage of the cerebral hemispheres as the prevailing pattern in placentals, associated with generally modest development of the diploic veins. We demonstrate that pangolins deviate from this pattern, displaying an extraordinarily dense network of diploic venous channels throughout the cranial vault. Furthermore, we observe a similar, albeit less pronounced, pattern in carnivorans and their extinct relatives. These findings establish diploic veins as a potentially powerful phylogenetic marker, providing a distinctive signature for Pholidota and adding a long-sought synapomorphy for the molecularly supported Ferae clade. The discovery of this extensive diploic venous network is also remarkable due to its remote similarity to the human diploic veins, thereby offering new insights into their potential function for cerebral drainage. We propose that this network provides an alternative drainage pathway in pangolins, echoing human cases with superior sagittal sinus hypoplasia.

Miniature Giants: Investigating Limb Long Bone Structure in Dwarf Proboscideans

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Terrestrial vertebrates rely on their skeleton to provide structural support and allow movement. Graviportal taxa, such as extant elephants, exhibit numerous adaptive features in their bone anatomy, enabling them to withstand their immense weight. Conversely, dwarfing events impose novel biomechanical constraints on the skeleton. The case of dwarf elephants raises questions regarding the adaptation of graviportal animals to drastic size reduction. In this study, we examine the morphology and microanatomy of the six long bones in two fossil species of dwarf elephants, *Palaeoloxodon tiliensis* (adults) and *P. falconeri* (juveniles), using both quantitative and qualitative approaches. Our results show that in *P. tiliensis*, the reduction in body mass is reflected in the morphology and microanatomy of the bones, suggesting a more flexed limb posture and a reduced parasagittal orientation compared to fully graviportal proboscideans. Despite this shift, several key graviportal adaptations are retained in *P. tiliensis*. Additionally, comparisons with early, non-graviportal proboscideans indicate that dwarf elephants exhibit a partial reversion to ancestral limb traits, while maintaining essential weight-bearing features. Finally, adult *P. tiliensis* and juvenile *P. falconeri* specimens exhibit a medullary area filled with trabecular bone, similar to that of extant elephants. Dwarf elephants are thus not scaled-down versions of their mainland ancestors, but instead display a combination of juvenile, graviportal and ancestral traits reflecting the impact of dwarfism on their evolutionary trajectory.

Innovation in Jaw Musculature Drives the Evolution of Temporal Fenestration Patterns of the Amniote Skull

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Evolutionary innovation in the musculoskeletal system is behind some of the major body plan transformations in vertebrate history. The temporal region of the skull is central in the macroevolution of amniotes, since major clades (e.g., anapsids, synapsids, diapsids) are traditionally defined by the number of temporal bars and fenestrae. The diversity of fenestration patterns is thought to reflect variation in muscle attachment, size, orientation and physiology, since the temporal region houses the jaw adductor musculature, although this has been scarcely explored. Lepidosaurs showcase outstanding variation in the structure of the temporal region and the arrangement of jaw musculature, representing an ideal case to test these hypotheses. Here, we quantitatively explore the evolutionary relationship between temporal region morphology and jaw muscle anatomy and physiology using 3D geometric morphometrics and phylogenetic comparative methods in 149 extant lepidosaurs, and musculoskeletal modelling of the skull in 13 species spanning morphospace. We find significant co-variation and correlation signals between jaw muscle properties (mass, fibre length and PCSA) and skull and temporal shape, and accelerated evolutionary rates in clades with high temporal region variation. Loss of temporal bars is associated with expanded external adductors, less vertical fibre orientation and relatively shorter in-levers. Our findings suggest that the evolution of temporal fenestration patterns is driven by innovation in jaw musculature arrangement and function, associated with diversification of feeding mechanics and diets.

Morphological Adaptations of the Olfactory System of Subterranean Lizards

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Convergent evolution, a central concept in evolutionary biology, illustrates how distinct lineages independently develop similar morphological adaptations due to shared environmental pressures. Subterranean lizards, facing unique ecological challenges, often evolve morphological adaptations, such as elongated bodies and reduced limbs, that enhance their burrowing ability. Although substantial research has focused on the visual systems of subterranean vertebrates, frequently showing reduced vision, comparatively little attention has been given to their olfactory capabilities. It is likely that these animals rely heavily on olfaction for critical behaviors such as foraging and mating, potentially driving the evolution of specialized olfactory structures to offset diminished visual input. Given the independent transitions to subterranean lifestyles across reptile lineages, our project investigates variation in olfactory organ morphology along the squamate phylogeny. We explore how ecology influences these adaptations in a convergent framework, using diceCT data to compare subterranean squamates with their terrestrial relatives. Our data set includes roughly 20 independently evolved subterranean lineages and related surface-dwelling species. We assess potential olfactory adaptations by measuring the relative volume of the olfactory bulb and vomeronasal organ. Some lineages show marked increases in these structures, suggesting enhanced olfactory function; however, convergence is incomplete across the phylogeny. Notably, we observe significant morphological diversity in the olfactory system of lizards. Ongoing histological analyses aim to deepen our understanding of these intriguing evolutionary patterns.

The Oropharyngeal Structure of the Marini's Grenardier *Coelorinchus marinii* Hubbs, 1934 (Teleostei, Gadiformes, Macrouridae)

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Macrouridae includes 370 valid species in 27 genera, typical inhabitants of the deep sea, for which morphological and biological information is scarce. An interesting anatomical feature to study is the oropharyngeal cavity to increase our knowledge of prey capture mechanisms that has direct links to different aspects of the species' biology. Specimens of *Coelorinchus marinii* were collected during expeditions onboard the RV Alpha Crucis on the Southern Brazilian continental slope, providing the opportunity to cast light on the morphological aspects of their feeding apparatus. Two specimens were dissected, one was cleared and stained for skeleton (250.5mm SL), and another (243.9mm SL) only stained for musculature. The most interesting features are the presence of a relatively large pseudobranch medial to the interhyal, which serves for oxygenation of the well-developed eye, a subventral protrusible mouth with many small villiform teeth, an extra point of origin of the adductor *mandibulae pars rictalis* in the interopercle, as well as a series of gill rakers transformed into conical teeth along ceratobranchial 1 and two series along the remaining ceratobranchials possibly correlated

to the carnivorous habits of the species. In the literature, this species was suggested to be carnivorous with some seasonality, eating prey such as infaunal polychaetes, small crustaceans and mesopelagic fishes.

Forelimb Muscle Architecture Reveals Functional Specializations in Large Dasyurids

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The three largest dasyurids (the Tasmanian devil, the spotted-tailed quoll, and the Eastern quoll) are the largest living Australian marsupial carnivores and engage in specialised feeding and locomotory behaviours such as terrestrial carcass scavenging (Tasmanian devils) or arboreal prey hunting (spotted-tailed quolls). As these species vary in their forelimb use during feeding and engage with different substrates in locomotion, we hypothesised that forelimb muscle proportions would reflect the emphasis on localised force generation to perform these behaviours. Here we provide the first modern descriptions of the muscle topology of all three species from direct dissection of fresh-frozen forelimbs, quantified muscle architecture (muscle-tendon unit lengths, masses, fibre lengths, and pennation angles translated to physiological cross-sectional area [PCSA]), and the outcomes of diffusible iodine-based contrast-enhanced computed tomography (diceCT) to three-dimensionally visualise the muscular anatomy and extract muscle volumes. Our results support that the muscle proportions and quantified variables across these three species reflect the observed differences in forelimb feeding and locomotory behaviours. This is observed particularly in an emphasis on shoulder muscles in the spotted-tailed quoll and brachial muscles in Tasmanian devils, indicative of arboreality and prey-processing adaptations, respectively. The study highlights the role of muscle architecture in revealing behavioural adaptations in dasyurid species and future directions in interpreting extinct dasyurid feeding and locomotory adaptations.

Sharkbait: Shark Community Assemblage of Batesford Quarry

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Due to anthropogenic global warming, temperatures will continue to rise until the climate becomes similar to the Miocene Epoch (23.03 – 5.33 Ma), which may negatively impact shark populations. Consequently, studying the Miocene elasmobranch fossil record can help infer the future of shark populations. Here we study the elasmobranch fossil record in the Batesford Limestone (Victoria, Australia) as it is important for discovering the origins of the local elasmobranch population and for examining potential effects of warming. Describing fossil tooth shape patterns can facilitate identification at the species level. In addition to the ~2600 museum specimens, fossils were collected by screenwashing sediment. Tooth shape analysis was conducted using 3D geometric morphometrics on 331 teeth. Our findings have increased our understanding of the Australian elasmobranch fossil record, with 15 species recorded in

the Batesford Limestone for the first time, most of which are still present off the south Victorian coast. Following global warming, elasmobranch population distributions may return to how they were in the Miocene. Tooth shape analysis demonstrated differences between modern species, and along the tooth row, increasing the ability to identify fossils. This provides a point of comparison for elasmobranch populations between the warm Miocene and the predicted future climate. Thorough identification of fossil species can help predict the impacts of warming on modern shark populations.

Regeneration Research Beyond the Model Organism Axolotl: Evolution and Diversity of Regenerative Abilities of Salamanders

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Regeneration research has advanced significantly in biomedicine and molecular biology, deepening our understanding of its molecular regulation, medical potential, and evolution of vertebrate regenerative capacities, including organ, limb, and tail regeneration. The Mexican axolotl (*Ambystoma mexicanum*) has been the primary model organism in this field. Although the axolotl will undoubtedly remain an essential subject for regeneration studies, incorporating data from non-model organisms is increasingly crucial for revealing shared and divergent regenerative mechanisms and broadening evolutionary perspectives. Moving beyond the axolotl, our research highlights the value of alternative research organisms and studying regeneration in natural conditions. This approach provides initial insights into shared and divergent regenerative traits across salamander taxa, expanding the taxonomic and evolutionary scope of regeneration research and identifying future directions. Here we present the tiger salamander as a promising alternative model organism to the axolotl for fracture healing and regenerative biology research of body appendages, especially due to its metamorphic life history pattern, and we demonstrate regenerative capacities in plethodontid salamanders to investigate the effects of life history strategies and habitats on limb regeneration.

Evolutionary Transformations in the Morphology and Biomechanics of Vertebrate Respiratory Pumps

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The evolution of costal aspiration breathing has lacked a complete, plausible scenario for the intermediate steps and selective pressures that led to the transformation from buccal pump breathing in anamniotes to the use of ribs and intercostal muscles for aspiration breathing in amniotes. Problems have included the selective pressure that would have produced such a profound change from a head pump to a body pump, the adoption of costal aspiration despite some kind of diaphragmatic solution arguably being more plausible, and the possibility that the transition may have been abrupt, without a prolonged period of buccal pumping and costal aspiration being used together. The advent of XROMM for studying the role of ribs and intercostal muscles in lung ventilation and

locomotion is yielding new insights into this transformation. In this talk I'll synthesize new and existing data on the biomechanics of lung ventilation to propose a plausible, but as yet untested, set of intermediate steps and selective pressures that could have produced this great evolutionary transformation.

Early Evolution of the Lungfish Fin Skeleton

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Although lungfish are the closest living fish relatives of tetrapods, their skeleton has drastically reduced mineralisation and modern taxa remain essentially cartilaginous. As a stem lungfish, the Devonian porolepiform *Glyptolepis groenlandica* is essential for shedding light on the early stages of lungfish skeletal evolution. Using synchrotron microtomography, the pectoral fins of *G. groenlandica* and *Protopterus* sp. were imaged. Three-dimensional models of the fin skeleton of *G. groenlandica* revealed the presence of longitudinal trabeculae densely located at the distal and proximal ends of each mesomere and surrounding an empty cavity. As in tetrapod long-bones, this suggests that the appendicular skeleton of lungfish formed and grew through endochondral ossification, i.e. by replacement of cartilage with bone. This means that the process of elongation through endochondral ossification was already established in stem lungfish. In *G. groenlandica*, the core of the mesomere was free of trabeculae but filled with sediment around short vascular canals preserved in three dimensions. This infilling sediment probably replaced a non-mineralised tissue (such as cartilage) that did not fossilise with time. Surprisingly, this indicates that the inhibition of ossification in the lungfish fin may have started in the core of the fin segment, i.e. where endochondral ossification is supposedly initiated. This study provides a first glimpse to our understanding of the evolutionary pathways that led to the derived condition of the lungfish appendicular skeleton.

Evolution of the Hymen In Mammals: Phylogenetic Distribution, Diversity and Function

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Despite its broad cultural significance and medical importance in humans, little work has been done on the evolution of the mammalian hymen. This includes its presence or absence in different mammalian groups, its development, its ontogeny, and potential function. We reviewed the literature on mammalian reproductive tracts to evaluate the hymen's presence or absence, its hypothesized function, and phylogenetic distribution. We found that the hymen has been reported as present in 12/17 orders of placental mammals, absent in one, with data missing from four. The hymen is absent in Monotremes, suggesting that the hymen is an ancestral trait of placental mammals. This hypothesis is supported by hymen development, which occurs early in the embryo when the mullerian ducts encounter the tissue of the vaginal floor. It is unlikely that the hymen serves an adaptive function in most clades, but rather it is a byproduct of the development of the mammalian vaginal canal.

Based on histological descriptions, we suggest that vaginal closure membranes found in some mammalian groups are co-opted from the hymen, and serve the function of protecting the reproductive tract in immature individuals from superfluous copulation and/or pathogenic agents. Due to the paucity of data on hymens in the vast majority of mammalian families, a fuller picture of hymen evolution can only be described once further work is done on the hymen in mammals.

Polydactyl Precursors: Insights for Early Tetrapod Terrestrial Locomotion from Polydactyl Alligators

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Several of the earliest taxa of tetrapod vertebrates exhibited polydactyl hands and feet, with seven or eight digits rather than the typical five or fewer seen in extant lineages. How such digit arrangements might have been used during terrestrial locomotion is unclear, given the dearth of living models in which their performance can be studied today and limited evidence from fossil trackways. However, polydactyly occasionally appears in natural populations of American alligators (*Alligator mississippiensis*), animals with body plans that broadly resemble those of early tetrapods. To test how polydactyly like that seen in early tetrapods might have functioned on land, we used high-speed video and an EMED-ST pressure mat to measure the limb movements and foot pressures of three polydactyl alligators (~1.5 m in length) during walking. Our data did not indicate significant pressures from supernumerary digits in many cases, but a few trials showed their limited use in some instances. This indicates that polydactyly might not contribute substantially to terrestrial propulsion, providing context for the evolutionary loss of these structures as tetrapods became more terrestrial and potentially helping to explain the lack of examples of polydactyly in fossil trackways. Our results also imply that extra digit usage does not impede terrestrial locomotion. Thus, polydactyl digits might not be strongly selected against, potentially enabling the reappearance of this trait in extant populations.

Homology and Evolution of Caudal Auricularis Muscles in Bats

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Extant bats are classified into three major groups: pteropodoids, rhinolophoids, and yangochiropterans. During echolocation, bats are known to routinely move their pinna. In mammals, pinna movements are typically controlled by the caudal auricular muscles (*m. cervicoauricularis* and *m. cervicoscutularis*), which are innervated by the retroauricularis nerve. However, the anatomy and diversity of these muscles in bats remain largely unknown. Here we

examined the muscles innervated by the retroauricularis nerve and attaching to the pinna in representative bats from each group—*Cynopterus sphinx* (pteropodoid), *Coelopus fritthi* (rhinolophoid), and *Vespertilio sinensis* (yangochiropteran), using 3D reconstructions of immunohistochemically stained fetal sections and diffusible iodine-based contrast-enhanced computed tomography for adults. Our results and literature review indicate that bats possess unique caudal auricular muscle morphologies compared to other mammals. Bats were commonly found to have four caudal auricular muscles attached to the pinna, while non-bat mammals have three caudal auricular muscles. Specifically, the pinna of pteropodoids and rhinolophoids is attached by four cervicoauricularis muscles, while that of yangochiropterans is attached by three cervicoauricularis and one cervicoscutularis muscles. Given the innervation patterns, we hypothesize that the common ancestor of bats first acquired an additional cervicoscutularis muscle connected to the pinna. Then, pteropodoids and rhinolophoids converted the additional cervicoscutularis into a new cervicoauricularis, while yangochiropterans retained the ancestral trait.

Finescale 3D Characterization of Shark Fin Structure: Critical Design Features of a Biological Hydrofoil

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The stiffness of shark fins is correlated with species' ecology and the extent of skeletal support (fin radials) at the base of fins. The distal fin, however, is not supported by radials and instead contains collagenous, needle-like structures called ceratotrichia. Though ceratotrichia seem to offer a combination of structural support and flexibility to fins, there is little known about their functional morphology. We characterised the internal anatomy of fins from three carcharhiniform species with focus on anatomical features of ceratotrichia; their interaction with other fin tissues; and their finescale architecture. Ceratotrichia are slender gel-like rods organized in dorsal and ventral layers relative to the fin's bending plane, attached to the skin by a loose connective tissue. Extracted ceratotrichia are broad at the base with tapering tips, with radii ranging from few micrometres in small species (pacific spadenose) to 1 mm in large species (blue sharks). Regardless of animal size, our Dice- μ CT and SEM results reveal ceratotrichia in three size classes of different cross-sectional radii (e.g. < 10 μ m, 10 – 100 μ m, > 100 μ m in Pacific spadenose). The radii classes are stacked hierarchically, like wood in a pile, suggesting this arrangement may play a role in controlling dynamic flexibility. By correlating finescale fin structure with mechanical properties, we provide insights for biomimetic hydrofoil design.

Predictive Simulation of Jumping Biomechanics in the Late Triassic Dinosaur *Coelophysis Bauri* and the Evolution of Tail Usage In Theropoda

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Theropod dinosaurs dramatically reduced the size of their tails on the lineage leading to birds. This reduction altered terrestrial

locomotion in many ways due to reduction of a key hip extensor muscle and cranial shift of the body's centre of mass (CoM). However, tail reduction also may have influenced other, less studied behaviours, with potentially different impacts on ecology and other aspects of palaeobiology. Using optimal control simulations, we predict the vertical jumping performance of the Late Triassic theropod dinosaur *Coelophysis bauri* (with a more plesiomorphic large tail) and compare it to that of the extant tinamou *Eudromia elegans* (with a derived, very reduced tail). We find similar relative performance abilities but important differences in jumping dynamics. Our simulations indicated that maximal jumping height in *Coelophysis* depended strongly on tail form and mobility. Jumping performance increased with a heavier, more mobile (proximal) tail as this allowed for larger CoM displacement during ground contact, increasing net CoM work. This mechanism was different to that in *Eudromia*, which used greater body pitch to raise its CoM. These differences support the inference that, as tail size reduced on the line to birds, jumping performance shifted from a reliance on tail dorsiflexion (strong dorsiflexor muscles and mobile proximal joints) to pelvic/trunk dorsiflexion (strong hip – and ankle – extensors).

A Hawaiian “Kiwi”: Evidence of a Nocturnal Foraging Niche in the Extinct Ibis, *Apteribis*

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Evolution on islands often generates specialized sensory ecologies that are rarely seen in continental species. The Hawaiian Islands are among the most isolated archipelagos on Earth and host a unique and diverse assemblage of endemic taxa. Most of the endemic Hawaiian vertebrates became extinct following human colonization. One such example is *Apteribis* (Threskiornitidae), an extinct genus of flightless ibises from Maui, Moloka'i, and Lāna'i. Despite being first described 49 years ago and with a rich fossil record, there is little information on its behaviour or ecology. We provide a quantitative analysis of its sensory system, combining comparative osteology and microCT scanning. We integrate data from its skull, mandibles, nerves, and brain (endocast) anatomy to infer foraging behaviour, activity pattern, and lifestyle. While its olfactory and somatosensory systems are comparable in size and anatomy to those of other ibises, *Apteribis* has a strikingly reduced visual system. Its orbits, optic nerves and optic lobes are half the size than in extant ibises. These reductions suggest a nocturnal lifestyle, an unprecedented trait among ibises, which otherwise lack nocturnal or even crepuscular species. Overall, our data suggest that *Apteribis* occupies a niche somewhat similar to that of New Zealand kiwi: a nocturnal, flightless, and tactile feeding lifestyle. This partial convergence between *Apteribis* and kiwi emphasizes the remarkable diversity of avian ecologies that have been lost due to human impact.

Development of Educational Material of Fish Neuroanatomy: Integrating Anatomical Specimens and 3D Models

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Despite its relevance to understanding evolutionary and behavioral aspects, the complexity of the nervous system creates challenges for both teachers and students in the study of vertebrate neuroanatomy. These difficulties are amplified when studying fish anatomy, as their morphological differences from human neuroanatomy make it harder to understand their nervous structures. Additionally, the lack of educational materials addressing fish neuroanatomy makes teaching this topic even more challenging. The use of anatomical specimens and 3D models, virtual or printed, enhances anatomy and zoology education by facilitating the identification and comparison of anatomical structures among groups. Thus, we developed educational material on fish neuroanatomy using dissected specimens and 3D brain models. We selected species from different orders and behaviors (trophic levels and lifestyles), dissected them, and exposed their brains. The main regions and structures were identified based on the literature, revealing variations that may reflect evolutionary patterns and environmental adaptations. After dissection, brains were photographed and 3D models were generated via photogrammetry. Ten brain models from different species were made available online, allowing users to interact with and explore labeled structures. In addition, the dissected specimens will be accompanied by anatomical sheets, to be used as educational material for the Animal Anatomy and Ichthyology courses at the University of Brasília. We believe the material will provide students with an educational and interactive tool for studying fish neuroanatomy.

Bone Conduction Hearing In Mysticetes: Vibroacoustic Validation

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The largest mammals are filter-feeding mysticetes. They generate sounds underwater with wavelengths longer than their bodies, but each ear is approximately the size of a human fist. How do they hear long wavelength sounds with relatively small ears? Cranford and Krysl (2015), constructed a computational finite element model (FEM) to simulate low-frequency hearing in a fin whale. That study predicted a bone conduction hearing mechanism, involving the enormous skull. Physical, vibroacoustic experiments with gray whale skulls show that long wavelength incident sounds excite the skull. Skull vibrations are transferred to each bony ear complex. The tympanoperiotic complexes contain dynamic components: flexible pedicles, dense tympanic bullae and middle ear ossicles. The anatomic geometry of the dynamic components mechanically amplify the skull vibrations and deliver them to the cochlea through the stapes footplate. At the oval window, mechanical vibrations are necessarily transformed into hydrodynamic fluid displacement within the inner ear. These results validate the bone conduction hypothesis (Morris et al., 2025). This mechanism of sound reception by the skull and amplification within the bony ear complexes is key to understanding mysticete natural history and low-frequency hearing. We now have FEM evidence that the bone conduction mechanism is at work in other rorquals, including minke and humpback whales. The bone conduction hearing mechanism is likely functional in all mysticetes due to commonalities of anatomic geometry and functional morphology.

Protocol for 3D Photogrammetry and Morphological Digitization of Complex Skulls

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Understanding the anatomical foundations of mammalian biodiversity and disparity requires accurate and comparable morphological data across a wide range of taxa, including species with highly complex cranial structures. Here, we present a standardized and cost-effective protocol for the 3D digitization of mammalian skulls using photogrammetry, with a particular focus on specimens bearing challenging features such as antlers, horns, and tusks. These traits, which play key roles in species ecology, behavior, and sexual selection, are often underrepresented in digital datasets due to technical difficulties in capturing and reconstructing them. Our method outlines optimized procedures for image acquisition—including specimen positioning, camera setup, and lighting—and subsequent image processing to generate high-fidelity 3D models. We also provide guidelines for extracting geometric morphometric data and performing shape analyses. By enabling the digitization of morphologically diverse and delicate specimens, this protocol facilitates comparative anatomical studies and supports broader efforts to document and interpret the evolutionary and functional basis of cranial diversity in mammals.

Transition from Occasional to Habitual Theropod Flyers: Origin of Regular Flight Use in Early Birds and Their Close Relatives

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Habitual flight behavior enabled modern birds to shape global ecosystems. However, it is unclear when and how their habitual flight was achieved. To address this, we re-assessed species of early birds and close relatives with the potential for powered flight and then evaluated their ability to sustain powered flight using two criteria: (1) available muscle power output and maximum flight performance; (2) energetic cost of flight. The Late Jurassic early-diverging bird *Anchiornis* - probably the oldest known bird - was found to fail both criteria. Thus, it was unlikely that *Anchiornis* was volant at all, clarifying their pre-existing 'borderline' flight status. Instead, its wing-assisted locomotion was confined to terrestrial behaviours such as leap assist, running or wing-assisted incline running. In contrast, iconic Late Jurassic bird *Archaeopteryx* and Early Cretaceous early-diverging dromaeosaurid *Microraptor* met both criteria for flight habituality, suggesting that they were not just occasional functionally flapping flyers as previously proposed. We find that later birds then built upon this early flight habituality by evolving greater flight performance with lower energetic costs, as expected using their more derived flight systems. Thus, flight habituality appeared by at least the Late Jurassic and had a complex and nonlinear pattern that set the stage for the rise of modern birds.

Variation in Cortical Bone Geometry In Primates and Consequences for Ecological and Biomechanical Inferences

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The distribution and geometry of bony tissues is the most important determinant of gross biomechanical performance of bones in the body. Bone cross-sectional geometry using beam-bending theory is one approach to quantifying bone function, and has been used extensively across vertebrates to infer biological and biomechanical adaptation. The universal approach in long bones has been to measure cross-sectional geometry at midshaft and infer whole bone performance. This is based on the prediction under beam bending that under compression loads, the midshaft experiences the highest forces, and is therefore most biomechanically informative. Here we demonstrate that numerous assumptions of beam bending theory are violated in long bones, calling into question the validity of midshaft measurements. We find that diaphyses of primate humeri are neither homogeneous in cross-section nor evenly curved - both of which are required under beam bending theory to be valid. Comprehensive analyses find that midshaft is the least ecologically informative site for sampling, and that proximal, distal or ideally whole-diaphyseal sampling are the most ecologically informative approaches with highest predictive accuracy. These results demonstrate that current assumptions about bone loading are oversimplified and outdated. Whole-diaphysis variation in bone geometry and curvature suggest ecologically driven adaptations to non-compressive loading regimes and that the adoption of a new standard of comprehensive analyses will provide greater insight into the functional evolution of limb bones.

Diet isn't Everything, Intestinal Length Differences In "Spiny" Mammals (*Setifer Setosus*, *Atelerix Albiventris*, *Erinaceus Europaesus*)

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There is a link between diet and intestinal length in mammals. Herbivorous species tend to have longer intestines, while faunivorous species have shorter ones. However, some exceptions to this rule exist. For instance, despite having similar insectivorous diets and at comparable body masses, the greater hedgehog tenrec (*Setifer setosus*), African hedgehog (*Atelerix albiventris*), and European hedgehog (*Erinaceus europaeus*) differ markedly in intestinal length, with the European hedgehog having three times the length of the African hedgehog and six times that of the tenrec. To investigate the anatomical and molecular basis of intestinal length across these species, we

combined gross and histological measurements with transcriptomics from eight sections of the intestine of these species. The histological features of the intestine show that tenrecs generally have the highest surface enlargement factor, indicating a highly developed microabsorptive anatomy. However, the overall absorptive area is markedly higher in *E. europaeus* due to its considerably longer intestinal tract. Transcriptomic analyses further reveal conserved anterior-posterior identity and an expansion of the small intestine in the European hedgehog, which suggests higher physiological demands in that species, in line with its long hibernation and short gestation period. These findings highlight that, within dietary niches, differences in length can be linked to other selective pressures, such as metabolic and energetic demands or taxonomic contingency.

Of Sheaths and Cores: Modeling Horn Shape with the Power Cascade

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Horns are a particularly striking feature of many vertebrates, especially within Bovidae, where they exhibit dramatic variation in shape. However, most attempts to describe this variation have been inconsistent, qualitative, or disconnected from underlying biological structure. Bovid horns are composed of two distinct components—a bony core and a keratinous sheath—yet there is no standardised framework for describing their shapes or comparing them meaningfully. Here, we apply the Power Cascade, a geometric model based on a power law between radius and distance from the tip, to quantify horn shape across a broad sample of adult Bovidae. CT scans were used to segment the core and sheath of each horn, and both components were measured independently. Each structure was modelled using Power Cascade parameters and plotted in a morphospace defined by slope and aspect ratio. Both cores and sheaths showed strong fit to the model (median $R^2 > 0.98$). Sheaths generally had higher aspect ratios than their corresponding cores, while slope values were more variable. Despite substantial morphological diversity, no clustering by subfamily was observed. This framework enables direct, quantitative comparison of horn shapes across taxa and between tissues. It provides a foundation for future work on horn classification, growth, and reconstruction, particularly in fossil taxa where only the core is preserved.

Palatal Foramina and Their Connection to Baleen in Extinct and Extant Cetacea

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Lateral palatal foramina (LPF) and their associated canals within the maxilla of living mysticetes (baleen whales) transmit neurovascular structures that support baleen. Presence of LPF has been used to reconstruct baleen in extinct mysticetes when

baleen is not preserved. Some early toothed mysticetes, including the Oligocene-aged Aetiocetidae, possessed LPF on the maxilla medial to the toothrow, suggesting a co-occurrence of teeth and baleen. However, the reported presence of superficially similar palatal foramina in living odontocetes and terrestrial artiodactyls weakens this hypothesis. Therefore, we assess the homology of palatal foramina across marine and terrestrial artiodactyls to determine if the structures observed in Mysticeti are unique to that clade. Computed tomography (CT) reveals that the LPF of extant mysticetes and extinct aetiocetids connect internally to the infraorbital (IOC) and superior alveolar canals (SAC). In contrast, all maxillary palatal foramina in the terrestrial artiodactyls and odontocetes we examined, including in odontocetes with edentulous maxillae, connected internally to the greater palatine canals (GPC) rather than to the IOC or SAC. Thus, the palatal foramina of odontocetes and terrestrial species are not homologs of LPF in extinct and extant mysticetes. Optimization of LPF on mysticete phylogeny at the ancestor of Kinetometa, or Aetiocetidae plus all edentulous mysticetes, supports evolution of baleen (or proto-baleen) before tooth-loss in Mysticeti.

Do Head and Skull Tell the Same Story? Determinants of Bite Force Sexual Dimorphism

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Identification of morphological associations with performance is a crucial step towards understanding the evolution of biological structures. The vertebrate head shape is highly associated with bite performance, and both external (head) and internal (skull) traits have been used to identify functional associations, although they are not always analyzed together. In this study, we integrate and compare two morphological datasets - external head shape and skull morphology - to identify the best predictors of bite force in each sex of the sexually dimorphic lizard *Tropidurus catalanensis*. We measured bite force for 78 lizards and took linear measurements on their external head shape and on 3D skull images from CT scans. In both sexes, head measurements explained bite force slightly better than skull morphology, and the closing in-lever, a biomechanical trait associated with jaw-closing muscles, was the strongest predictor among head traits. For skull measurements, closing in-lever remained the strongest predictor in females, while the supratemporal fossa width was the best predictor in males, which, for a given skull width, presented wider heads than females. These findings reinforce that, although lever mechanics are broadly predictive across sexes, bite performance in male lizards may rely more on jaw muscle mass than on isolated osteological components. Comparing head and skull traits helped to elucidate sex differences and the evolution of form-function sexual dimorphism in lizard heads.

3D Network Analysis of Stingray Jaw Trabeculae

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Sharks and rays possess cartilaginous skeletons reinforced by a cortex of mineralized tiles (tesserae) encasing an unmineralized core, providing compressive stiffness to skeletal elements. In stingrays that feed on hard prey, additional reinforcement exists as hollow mineralized trabeculae, which course through the cartilage like structural beams. Using high-resolution micro-CT imaging and quantitative network analyses, we characterized the trabecular network in cownose rays (*Rhinoptera*). Trabeculae are highly aligned toward the occlusion surface, thickest near their origins on the non-occlusal side of the jaw, and branch into thinner struts beneath the teeth. They are more mineralized under functional teeth, while those beneath forming teeth appear thinner and less defined in micro-CT scans. The upright, branching morphology resembles staghorn coral, with finer branches near the teeth suggesting that trabeculae may compartmentalize unmineralized cartilage in addition to providing compressive reinforcement. The interaction between trabeculae and the jaw cortex is notably complex. Trabeculae are formed by individual tesserae and exposed externally via pores in the cortex. These pores may represent growth sites where cortical tissue invaginates into the cartilage, enabling trabecular development. This mechanism suggests trabeculae offer a novel model for understanding cartilage mineralization, growth, and mechanics, with potential insights into how skeletal adaptations arise in response to functional demands.

How Do Embryonic Muscle Forces and Changes In the Biomechanical Environment of the Developing Avian Hallux (Digit I) Relate to its Evolution from Theropod Dinosaurs?

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The hallux opposability in the avian foot is acquired during embryonic development by embryonic muscular activity (EMA) and involves torsion of metatarsal bone I (MT I). In birds, the hallux articulates with metatarsal bone II (MT II) via MT I on its medioventral surface and in distal positions, unlike in basal theropods, where the hallux was non-opposable, MT I was not twisted, and articulated in medial positions with MT II. Embryonic paralysis leads to a non-opposable hallux with a non-twisted MT I, similar to that of ancestral theropods. Despite this, how these forces act on development and on the MT I morphology is not understood. Using immunofluorescence, radiopaque staining, microscopy and microCT, we generated 3D reconstructions of the musculoskeletal components of the foot to describe the effect and magnitude of EMA on MT I during development. Muscular forces associated with the hallux (FHL, FHB and EHL) were estimated through segmentation and PCSA, and biomechanical simulations were generated at different embryonic stages, with Finite Element Analysis. Empirical results show asymmetric changes in muscular forces, and the simulations show displacement and deformation

patterns in MT I that recreate the morphological changes during development, a product of these asymmetric forces. This suggests the importance of the asymmetry of muscular forces in the development of this trait to explain the morphological changes observed in the dinosaur-bird transition.

The Cranial Microanatomy and the Relation to the Anuran Clade Pipoidea

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Anurans are vertebrates known for their ability to live in diverse environments, a trait that reflects their extensive evolutionary history. We determined whether the microanatomical structures of cranial bones display not only an ecological signal but also a clade-specific range of values within the Pipoidea clade, characterized by its unique structure and lifestyle. Micro-CT scans of the skulls of eight extant and extinct Pipoidea were compared with four phylogenetically distant aquatic species. The scans focused on the frontoparietal and maxilla bones, from which, the overall compactness, cross sectional area, and thickness were extracted and analyzed. Statistical analysis, which tested means among the taxa, revealed clear differences in the microanatomical values. The results showed significant differences between the different groups when observing the thickness and cross-sectional area. However, the compactness presented no statistically significant difference between the extant and extinct Pipoidea specimens. These findings suggest the potential for a significant clade-specific signal, as well as an environmental signal, in skull bone compactness, which could be considered in future phylogenetic analyses. However, further examination with more taxa is needed to confirm these findings and to gain a deeper understanding of the microanatomical features of anurans and their evolutionary implications.

Finite Element Modeling Reveals the Effect of Jaw Muscles on Intramandibular Joint Flexibility and Strain in Taxa with Differently Built Mandibles

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The reptilian intramandibular joint (IMJ) separates the rostral and caudal mandibular bones and creates a potentially flexible “weak spot” constraining mandibular performance. Many nonavian theropod dinosaurs possessed superficially “hinge-like” IMJs and are hypothesized to have used isometric contraction of their *pterygoideus ventralis* (mPTv) and *intramandibularis* (mIM) muscles to limit IMJ excursion. We built 3D finite element models of *Tyrannosaurus rex* (putatively akinetic), *Majungasaurus crenatissimus* (putatively kinetic), and extant *Alligator mississippiensis* (akinetic) to determine whether/how differential muscle contraction affected their mandibular performance. *T. rex* and *Alligator* showed minimal joint excursion, while *Majungasaurus* displayed modest (~10°) excursion associated with pathologically high bone and IMJ ligament strains. mPTv and mIM had a greater influence

on bone and joint ligament strain in *Majungasaurus* and *T. rex* than in *Alligator*, but mPTv contributed very little to overall bite force in either *T. rex* or *Majungasaurus*. Moreover, contralateral activation of mPTv best reduced bone and joint strain during unilateral bites. Our results indicate that mPTv in nonavian theropods helped maintain IMJ coherence by controlling long axis rotation, whereas mIM primarily increased bite force and was not effective at controlling joint excursion as previously hypothesized. Moreover, *Majungasaurus*’ pathologically high bone and joint ligament strains suggest that additional recruitment of the cranio-cervical musculature or specialized feeding behaviors were necessary to maintain IMJ coherence during feeding.

Being Plastic is Fantastic? How Climate Influences Morphology Across Developmental Strategies in European Salamanders and Newts

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Climate is a key driver of morphological variation, especially in ectotherms like amphibians, which rely on environmental temperatures to regulate physiology. Salamanders and newts are highly sensitive to climate due to their permeable skin and need for moist habitats. Morphological changes, such as body size or shape, can influence gas exchange and survival under hot or dry conditions. This study examines how climatic variables—temperature, precipitation, humidity, and seasonality—affect external and skeletal morphologies across populations of two widespread European salamanders: the alpine newt (*Ichthyosaura alpestris*) and the fire salamander (*Salamanca salamandra*). Both species show facultative life cycles, either complex (with distinct aquatic and terrestrial stages) or simple (paedomorphic or pueriparous, remaining aquatic or bypassing larval stages in water). Complex life cycles may enable greater phenotypic plasticity, allowing individuals to adapt more easily to variable environments. We hypothesize that these populations exhibit stronger climate-related morphological responses than those with simpler life cycles. Using linear and geometric morphometric data from 1600 individuals across 150 populations, we investigate links between life cycle strategy, climate, and morphology. Preliminary results show that seasonality and humidity significantly influence morphology, with distinct patterns between life cycle types. These findings emphasize the role of environmental and developmental factors in shaping amphibian morphology and highlight the potential vulnerability of these species to climate change.

New Perspectives on the Development of the Ocular Skeleton

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The ocular skeleton is present in almost all reptiles and birds, and can be present in bony fish. It typically consists of a cartilage and a bony element; however, these two structures develop independently from one another. The development of both elements is intriguing and not well understood. Using both avian and teleost models in a comparative context, we have gained a deeper understanding of the development of the ocular skeleton as well as where homology likely exists. By inhibiting embryonic development of the eye at critical time points, we have uncovered several key genes involved in the development of the bony elements (the scleral ossicles) and how these genes interact with one another. In larval fish, a similar approach has revealed the pattern of scleral cartilage development. This presentation will summarize the current state of our understanding of the development of the ocular skeleton (namely the scleral ossicles and the scleral cartilage), including the timing of development, the underlying cellular and genetic mechanisms and tissue dynamics.

To the Necessity of Having the Assistance of Deep Learning for Landmark Positioning

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Geometric morphometrics has become a widespread approach of quantitative morphology in diverse biological fields. It relies on precisely placed anatomical landmarks. However, manual landmarking is tedious, time-consuming and prone to intra- and inter-observer variation. This bottleneck has spurred efforts to automate landmarking, often through deformable registration of 3D images, surfaces, or point sets. While these methods capture overall shape well, they introduce biases in landmark localization and in the structure of the variances and covariances. This study aims at correcting these biases with a deep learning (DL) approach, trained on variable skeletal elements. Our pipeline begins with approximate landmark predictions from a simple rigid registration. These predictions define local 3D surface regions, which are then parameterized into 2D and enhanced with colorization based on differential geometry and lighting. These generic bone structure representations are used to train Transformer and Convolutional Neural Network (CNN) architectures. Using a data set of mouse skull 3D models with manually labelled landmarks as a case study, we predicted the positions of ten distinct landmarks. We compared our DL predictions with those from the mainstream global registration approach, ALPACA, assessing both distance accuracy to the manual ground truth and shape conservation. This study establishes methodological guidelines for DL model architectures and parameterization. Our approach outperforms the standard deformable registration method, particularly in mitigating biases in shape conservation.

Cranial Lacertid Biomechanics Through the Application of Nanoindentation

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The genus *Gallotia*, endemic to the Canary Islands, includes both living and extinct species with marked variation in body size. Using nanoindentation, we quantified Young's Modulus (E) across cranial regions in *G. stehlini*, *G. galloti*, and *G. atlantica*. Our findings indicate a relatively homogeneous distribution of mechanical properties throughout the skull and mandible. Notably, E values were inversely correlated with body size, suggesting that larger individuals possess more elastic (less stiff) cranial bone. This size-dependent pattern permits estimation of E values in extinct large-bodied species, such as *G. goliath* and *G. auaritae*, offering new opportunities for reconstructing their cranial biomechanics. To test the functional significance of material properties, we incorporated measured E values into Finite Element Analysis (FEA) models of biting. The results showed minimal influence of local stiffness variation on overall mechanical performance, validating the assumption of using homogeneous Young Modulus' values in FEA simulations. These results enhance our understanding of biomechanical adaptation in insular lizards and support a link between cranial elasticity and ecological factors. Smaller species, like *G. atlantica*, exhibit stiffer skulls, while larger species display greater elasticity—potentially reflecting a shift towards herbivory and reduced predation pressure in giant forms.

Impact of Laryngeal Aspiration on the Lungs in Infant Mammals

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The evolution of the pharynx in mammals produced pathways of respiration and swallowing that cross the same space. This morphology creates the potential for aspiration, the movement of liquid into the respiratory system. Such aspiration is common in infant mammals but could cause damage to the lungs. We determined the link between laryngeal aspiration and damage to the lungs by recording six pigs over infancy with two synchronized fluoroscopes. We measured the aspiration of milk containing barium at (1) the pharynx and larynx in lateral view and (2) the trachea and lungs in dorsal/ventral view. We quantified laryngeal aspiration using the validated IMPAS scale and size of bolus. We measured the greyscale of aspirated barium/milk in the lungs using ImageJ software. Finally, we assessed the pathophysiology of lung tissue at the end of the experiments. The results show that only half of feeding/meals with laryngeal aspiration resulted in milk in the lungs. Average numbers of laryngeal aspiration events did predict the grey scale in the lungs in a feeding session. While the incidence of aspiration did not increase over an individual's development, there was a cumulative effect of aspiration in lungs of some animals. These data suggest that not all aspiration is problematic for infants, although the impact of sustained aspiration may have a negative impact on lung development.

Osteohistology of Wild and Captive Black Bears (*Ursus Americanus*) Reveals Life History and Regional Bone Remodeling

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Black bears (*Ursus americanus*) remain inactive during hibernation without experiencing cortical bone loss observed in other mammals. However, the skeletal response of axial bones like ribs remains understudied. This study compares midshaft femoral and rib histology in four individuals—three wild (two females, one male) and one captive female—to assess skeletal responses to hibernation, growth, and stress. Femora exhibit a laminar-plexiform fibrolamellar complex, with increasing parallel-fibered bone toward the periosteal surface. Each zone is bounded by parallel-fibered bone preceding a Line of Arrested Growth (LAG). Skeletal maturity was indicated in the captive bear by an Outer Circumferential Layer after the sixth LAG. One wild bear showed unusually thick parallel-fibered bands, suggestive of stress linked to hibernation with mange. Except for narrower bands of parallel-fibered bone, the femoral histology of the possibly non-hibernating captive bear is not markedly different from that of the wild hibernators, suggesting conserved growth dynamics. Relative Cortical Area was higher in femora (avg. 61.6%) than in ribs (avg. 46.5%), reflecting greater structural demands. Femoral remodeling was localized around the linea aspera, while all ribs were heavily remodeled and osteoporotic. Only the subadult's ribs retained primary tissue, suggesting age-related remodeling and that ribs function as dynamic calcium reservoirs during hibernation. Overall, bears appear to employ a region-specific skeletal strategy, maintaining cortical bone in weight-bearing limbs, while remodeling axial elements like ribs for calcium mobilization.

Elaboration of Ventral Body Wall Layers in the Limbless Tetrapod *Python bivittatus* and Homologies Across Tetrapoda

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Here we analyze the axial musculature and innervation patterns of the Burmese python (*Python bivittatus*) to establish muscle homologies with other vertebrates. We traced all individual muscle slips to identify each muscle and its respective dorsal or ventral ramus. We observed an interconnected musculature system with discrete epaxial and hypaxial muscle groups, consistent with previous research. The *semispinalis et spinalis*, *longissimus dorsi*, *retractor costae*, and *retractor costae biceps* (components of iliocostalis) were identified and verified to have

dorsal ramus innervation. Additionally, we confirmed dorsal ramus innervation to muscles including *multifidus*, *interarticular superior*, *interarticular inferior*, and *supracostalis dorsalis*, defining them as epaxial. We newly described the innervation of *interarticular superior*, and *intervertebralis*. We confirmed ventral ramus innervation to *levator costae*, *supracostalis lateralis superior*, *supracostalis lateralis inferior*, *costocutanei superior*, *costocutanei inferior*, *transversus dorsalis*, *costales interni superiores*, *costales interni inferiores*, *costovertebrocostalis*, *intercostales proprius*, *intercartilaginosi*, *transversus abdominis*, and *obliquus abdominis internus* defining them as hypaxial. Standard, limbed tetrapods generally exhibit three distinct muscle layers in the ventrolateral body wall. Here we suggest that while the snake body wall has more numbers of muscles due to complex locomotory adaptations, these muscles still conform to three distinct muscle layers, with a neurovascular bundle exiting between the deepest and middle layers, conforming to the pattern seen in other tetrapods.

Vitamin D Elicits Tissue-Specific Expression of Myofibrillar Protein Isoforms in Atlantic Salmon Muscle

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Accounting for isoforms is likely key to understanding muscle transcriptomic divergence. Muscles offer classic examples of tissues where changes in isoforms alter function and structure in response to stimuli like increased exercise or novel nutrient regimes. To determine how an essential micronutrient alters muscle isoform production, we examined how vitamin D supplementation influences transcription at multiple hierarchical levels across four Atlantic salmon (*Salmo salar*) muscle tissues. We will discuss our findings that myofibrillar genes, that compose the repeating units involved in muscle contraction, are impacted by vitamin D at all levels of gene regulation in different ways across muscle tissue types. This study demonstrates that vitamin D directly impacts many structural proteins that are involved in striated muscle contractions.

The Ecological Radiation of Therian Mammals Began Before the Extinction of Non-Avian Dinosaurs

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It is often hypothesized that the Cretaceous-Paleogene (K-Pg) mass extinction triggered a mammalian diversification by opening ecological space that was rapidly filled by surviving mammals. We test this hypothesis using a comparative approach that, unlike most previous studies on the topic, incorporates both paleontological and neontological data in a phylogenetic context. We produced a sample of time-calibrated meta-phylogenies ('metatrees') comprising over 3000 species of trechnotherians (the group including Eutheria + Metatheria

and close relatives) from the Mesozoic and Cenozoic Eras, based on 115 published character matrices and a molecular phylogeny. Fossil ecological diversity was quantified using jaw lengths (as a proxy for body size) and a jaw correlate of diet for 430 extinct and extant species. We fit a suite of evolutionary models to the data and metatrees, including models that allow for shifts in the mode of evolution at varying points in time. For both body size and diet metrics, we consistently find strong evidence that mammals began a rapid ecological radiation in the latest Cretaceous. Specifically, there was a shift from a constrained mode of evolution to an 'early burst' mode of evolution at ca. 74–72 Ma. These results suggest that the ecological diversification of therian mammals began before the K-Pg mass extinction event, challenging the view that the opening of ecological space by the extinction of non-avian dinosaurs was a requisite for mammalian diversification.

Ontogenetic Skull Shape Variation In *Chamaeleo Calypttratus*: Are Veiled Chameleons Sexually Dimorphic?

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Due to their color changing ability and ballistic tongue, chameleons are very emblematic lizards, but we know little about skull shape variation outside *Bradypodion*. Here we investigate ontogenetic shape changes and sexual dimorphism in the skull of the veiled chameleon (*Chamaeleo calypttratus*) using 3D geometric morphometrics methods. Both sex and skull size had a significant effect on skull shape, but growth-associated shape changes accounted for most variation within our sample. As in other lizards, growth is associated with orbits and naris becoming relatively smaller, the snout relatively lengthening and narrowing, and the posterior skull expanding laterally. The most dramatic changes reflect the formation of their characteristic casque: the hatchling's crescent-shaped parietal with a posteroventrally oriented crest compactifies as the crest lengthens and shifts anterodorsally and the lateral processes become buttress-like structures to support it. While sexual dimorphism in skull shape (ShSD) was present in the overall sample, it was not recovered within any age class. Ontogenetic trajectories suggest that ShSD only appears after males become larger than females, as their faster growth rates and longer lifespans contribute to creating peramorphic morphologies in older males. Many growth-related shape changes can be linked to functional changes in their masticatory system (with larger specimens presenting more robust skulls and larger muscle attachment sites) and support a dietary range expansion as chameleons grow and increased effectiveness in conspecific communication.

Heterochrony Structured Theropod Wing for Flight and Influenced its Evolution

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Forelimb length generally changed in an opposing trend to body size as theropods evolved. Birds and their close dromaeosaurid and troodontid paravian relatives underwent miniaturisation with associated forelimb lengthening attributed to heterochrony. Heterochronic shifts can involve changes in developmental timing and/or rate. These shifts played a key role in theropod skull evolution, but their proposed role in wing evolution has never been strictly tested. Using phylogenetic analysis of growth series shape change, we detected a peramorphic event (developmental trajectory extension) in the branch leading to paravians as an immature wing resembling adult early theropods. Coinciding development of pennaceous feathers, longer wings and a mobile shoulder in the common ancestor of paravians demonstrates major forelimb reorganisation just before flight appeared. Once flight evolved, peramorphism continued influencing wing evolution, including early continuous flapping flyers, but pedomorphism (developmental trajectory truncation) also impacted certain early birds. This suggests that heterochronic shifts also influenced the rapid early diversification of avian flight styles. Our study extends the influence of heterochrony to theropod wings, playing a central role in flight evolution.

Face to Face: Comparing the New *Homotherium* Cub Tissue Depths to *Smilodon fatalis*

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Smilodon fatalis, known as the saber-toothed cat, represents a fossil species without any direct living relatives. Recently, researchers discovered a mummified cub identified as *Homotherium latidens* in the permafrost of Siberia. This specimen was compared to a 3-week-old cub of the modern lion, *Panthera leo*. The mummy showcased distinctive features: a rounder head, a shortened muzzle, a larger mouth, more ventrally rounded ear pinnae, and a more robust neck and shoulder region. These differences emphasize the considerable variation in appearance compared to any extant conical-toothed cats. This new information suggests that the craniofacial shape of *Smilodon* should be reassessed. Forensic anthropological methods, which involve measuring soft tissue depths at specific locations on skulls and mandibles, have been successfully applied to accurately reconstruct craniofacial features in humans. In our study, we used tissue depth measurements from the skulls of three specimens of *Felis catus*. These measurements are homologous to those typically analyzed by anthropologists. We mapped the soft tissue depths onto corresponding points of the skull of *S. fatalis* and created a new facial reconstruction.

Cartilage Bonding to Bone: Unveiling the Osteochondral Interface Architecture

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The attachment of articular calcified cartilage (ACC) to subchondral bone (SCB) is integral to joint function, yet a complete understanding of this bonding remains elusive. Here, we investigate osteochondral interface architecture and bonding, especially the role played by the collagen type-I and -II fibrils. Collagen-I/-II colocalisation was investigated at the osteochondral cement line (OCL) in equine and bovine samples through confocal microscopy. In equine samples, distance between two collagen fibrils was investigated using transmission electron microscopy. The molecular crosslinking between collagen chains was evaluated using co-immunoprecipitation in-vitro. Equine osteoclasts were cultured in-vitro on cortical bone and ACC (with side-on and end-on collagen fibrils) to determine whether osteoclasts resorb tissues differentially. Collagen-I/-II overlapped over a distance of up to 5 μm , with millions of colocalising complexes per μm^3 of OCL; equine samples had significantly more colocalising complexes than bovine. Collagen fibrils were measured within 4 nm of each other, indicating at least partial collagen fibril overlap. In in-vitro experiments, osteoclastic resorption pits were significantly deeper and rougher on ACC versus bone, with the greatest depth and roughness in sections presenting end-on collagen fibrils. Our results demonstrate that collagen fibrils from bone and cartilage interact at OCL, with notable variation across sites and between species. Additionally, we show that osteoclast resorption is dependent upon substrate type (bone vs ACC) and orientation of collagen fibrils (end-on vs side-on).

Secondary Flightlessness In Waterfowl: Mallards, Indian Runner Ducks, and Their Hybrid Offspring

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Developing wings play an important role in the locomotion of immature birds. Though this has been a focus of studies on rudimentary wing function, rudimentary flight apparatuses also occur in secondarily flightless birds and birds that are temporarily flightless due to molt or injury. Here we explore anatomical and functional attributes of secondary flightlessness in waterfowl. We hypothesized that the loss of flight is associated with increases in leg investment and performance that at least partially compensate for reduced wing investment and performance, particularly in late ontogeny when flight capabilities develop. To test this idea, we measured the development of wing and leg musculoskeletal investment and performance during multiple behaviors in Mallards (*Anas platyrhynchos*), Indian Runner Ducks (a domesticated, flightless derivative of Mallards), and their hybrid offspring. As in previous studies, all three groups show evidence of tradeoffs: leg investment and performance decline with the onset of rapid wing development. For their size, Mallards have the highest wing investment and performance and Runner Ducks have the lowest. However, the declines in leg investment and performance are the most extreme in Mallards, partially because hybrids and especially Runner Ducks regain some leg muscle after wing growth slows. Coupled with other changes, this may suggest that the loss of

flight freed Runner Ducks to invest more in their legs and leg-dependent locomotion.

At the Heart of the Head-Trunk Interface: A Key to the Evolution of Cardiac Innervation and Coronary Arteries

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Our mammalian heart is maintained through dual vagal innervation of the inflow and outflow tracts, as well as well-developed coronary arteries. These systems are essential in mammals but absent in cyclostomes such as lampreys. How did such complexity in the heart system evolve? I compared embryonic development in lampreys and jawed vertebrates, including chondrichthyans and mammals. I found that jawed vertebrates develop a cardiac branch of the vagus nerve that innervates the sinus venosus, whereas lampreys never form such a branch. Considering the position of the hypoglossal nerve, I propose that the mesenchymal interface between head and trunk lies anterior to the heart in lampreys, but shifted caudally in jawed vertebrates. I also examined the evolution of cardiac arteries. In non-amniote jawed vertebrates, arteries branching from the pharyngeal arches supply the ventricle. In amniotes, vascular remodeling associated with neck elongation gave rise to the coronary arteries as an evolutionary novelty. These findings suggest that the mammalian heart system evolved in close connection with the developmental rearrangement of the head-trunk interface. According to its position, the heart should serve as a morphological key to understanding vertebrate evolution and offer new insights into long-standing questions, including the origin of the neck.

Using Quantitative Genetics to Explore the Relationship Between Molar Size Variation and Jaw Length

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Two ratios are commonly used to reflect the genetics of mammalian relative molar size variation: Inhibitory Cascade (IC; the product of breadth and length for M3/by that for M1) and the Molar-Module-Components (MMC) that relies on the same ratio but includes only molar length, as breadth is genetically correlated with body size. We used quantitative genetic analyses to explore how these two ratios relate to jaw size. We collected linear length and breadth of maxillary M1-3 and two dimensions of jaw length (total dorsoventral length of the maxilla, tDV; and, length of the maxilla without the premax, maxDV) for 974 pedigreed baboons at the Southwest National Primate Research Center (USA). We used maximum likelihood variance decomposition to estimate the phenotypic, genetic and environmental correlations (ρ_P , ρ_G & ρ_E) between the molar ratios and the two measures of jaw size (tDV & maxDV). Quantitative variation in all traits is heritable ($h^2_r = 0.21$ to

0.57). Pairwise ρ_P and ρ_E between IC and both jaw length measures, and between MMC and tDV are statistically significant. However, no estimates of ρ_G were significant. Therefore, despite the significant ρ_P both the IC and MMC have with jaw length, neither is genetically correlated with it. But IC and MMC reflect somewhat different biologies, given the differing ρ_E results, likely the result of IC's interrelationship with body size.

Domestication Induced Dental Divergence In Atlantic Salmon

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Changes in trophic morphology are likely common when vertebrates undergo human domestication. Humans often provide animals with easily acquired, abundant and more readily processed foods that might strongly relax selection. In many domesticated terrestrial vertebrates, this has frequently led to changes in dental morphology. However, there have been few investigations into the consequences of domestication for aquatic vertebrates such as bony fishes. Therefore, we examined phenotypic divergence in the dentitions of Atlantic salmon (*Salmo salar*) populations from both aquaculture and the wild. We discuss the phenotypic divergence in their tooth morphology and will touch on changes in gene expression that could underlie this putative domestication-driven trophic divergence.

Heart Ventricle Regeneration in the Lizard *Eublepharis macularius*, the Leopard Gecko

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Injuries to the heart of adult mammals typically result in fibrosis and a permanent reduction of cardiovascular function. However, the same is not true for all species. It is well-understood that some teleost fish and salamanders can near perfectly rebuild damaged ventricular tissue and regain heart function. Whether this regenerative ability is conserved across other vertebrates remains unclear. Here, we investigate ventricular self-repair in the leopard gecko (*Eublepharis macularius*). Geckos share several features of cardiac muscle cells common to other heart regenerating species, including being relatively small in size and primarily diploid. To create a lesion, we used a cryoinjury: a liquid-nitrogen cooled metal probe placed directly onto the ventricle. Within days, we documented an increase in proliferation among local (lesion-adjacent) and global (lesion-distant) ventricular cell populations. By 100 days post-cryoinjury the once damaged ventricular myocardium was virtually restored. To investigate changes in cardiovascular function, we used 2D echocardiography to measure Fractional Area Change (FAC). As expected, there was a significant decrease in FAC following cryoinjury. However, by 100 days post-cryoinjury FAC of lesioned geckos had significantly

improved and was no longer different from shams and uninjured controls. Taken together, this study expands the comparative framework of heart regeneration to include squamate reptiles and indicates that the ability to replace missing or damaged cardiomyocytes is shared across more than 350 million years of evolution.

Temporal Variation in Mesozoic Bird Flight Style

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Studies on bird flight mostly focused on its origins. Wings cannot be optimised for fast flapping and efficient gliding flight; most birds have one that trades-off between the extremes, creating a continuum of wing shapes. Glide ratio, aspect ratio (AR), and wing loading (WL) are common metrics for assessing wing performance. We examined changes in flight style across the Mesozoic bird clades, avialians, enantiornithes and euronithes, using glide ratio, AR, WL and wingbeat frequency (f), as a proxy for manoeuvrable flight. We hypothesised that wing areas started small and then increased. Subsequently, with the increasing flapping and flight performance, a decrease in wing areas relative to body mass. We predicted an initially low glide ratio, high WL, low AR wing, evolving into a high glide ratio, low WL and high AR, followed by a high WL, lower glide ratio and AR. Glide ratio, AR and WL increased with time. Contrary to our hypothesis, glide ratio and AR decreased with clade age. Avialans, with high glide ratios, ARs and WLs imply optimisation for gliding flight, whereas enantiornithes with intermediate glide ratios, ARs and WLs, suggest a compromise for general flapping and gliding flight. Euronithes had low glide ratios and ARs but high WLs wings, adaptations suggesting fast flapping manoeuvrability. Flight capabilities potentially evolved rapidly in the earliest Mesozoic birds, with later changes likely masked by ecological factors.

3D Shell Asymmetry as a Monitoring Tool for Environmental Stress in India's Freshwater Turtles

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Turtles (Order Testudines) are a unique group of vertebrates enclosed in a bony shell covered in protective scutes. Over 220 million years, they have diversified from terrestrial ancestors into various habitats, now found on most continents and oceans. Despite their ecological importance, over half of the ~360 turtle and tortoise species face extinction due to human activities like habitat degradation and overexploitation. Using geometric morphometrics, I aim to detect developmental instability in turtle shells. My analysis of 92 museum specimens revealed significant directional and fluctuating asymmetry related to ecology, indicating environmental stress. Additionally, I studied ontogenic allometry and shell developmental variation in *Melanochelys trijuga* (Indian pond turtle) using 3D scans. Environmental and health factors in *M. trijuga* will be linked to developmental instabilities, which provide valuable

insights into the factors influencing shell asymmetry and their potential consequences for turtle health and fitness. Furthermore, I conducted a citizen science project in India to collect water eDNA, assessing the distribution of invasive and native freshwater turtles. This multifaceted approach combines morphological studies with eDNA surveys to understand factors influencing turtle populations and inform conservation strategies, contributing to global turtle biology knowledge and preservation efforts. My project overall aims to contribute significantly to the knowledge of turtle biology and provide critical information for the conservation of these ecologically important species.

Bending Bizarre Backbones: Investigating Intervertebral Range of Motion in the Hero Shrew Using Digital Modelling

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The remarkable capability of animals to adapt to mechanical challenges has been a source of inspiration for biologists and engineers alike. One such example is the Hero Shrew, a tiny mammal whose elaborate backbone is thought to impart remarkable strength. Their vertebral joints are covered with tiny interlocking processes called tubercles, whose exact function is unknown. Here, we use digital modelling (AutoBend) to test the impact of tubercles on estimated range of motion (oROM) in two species of Hero Shrew (*Scutisorex somereni*, *Scutisorex thori*), compared to a more typical shrew (*Crocidura goliath*). Surprisingly, the presence of tubercles had little effect on oROM, with only a small reduction in axial rotation in the Hero Shrews compared to *C. goliath*. Further, axial oROM was negatively correlated with the number of tubercles within species, but only in the thoracic region where they are fewer. However, the number of tubercles was correlated with the area of intersection between the two vertebrae, a measure of the degree of bone-on-bone contact for any pose. In *S. somereni*, the Hero Shrew with the most complex column, many tubercles came into contact simultaneously during axial rotation. We hypothesize that the primary evolutionary function of *Scutisorex* tubercles is not to restrict ROM, but to increase the load-bearing capabilities of the joint by increasing the contact area during bending.

From the Largest to Smallest Parrots: Do Endocasts Vary Between Niches

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Parrots are known for their problem-solving skills, behavioural flexibility, and complex social interactions. These cognitive abilities have been linked to their relatively large brains, particularly an enlarged telencephalon, when compared to other birds. However, as a taxonomically and ecologically diverse group, parrots exhibit considerable variation in behaviour and cognition, which may be reflected in their neuroanatomy. To

explore how behavioural and cognitive differences relate to neuroanatomical variation across parrots, we used computed tomography (CT) scans representing 90 species, ranging from large macaws and keas to the small pygmy parrots. From these scans, we reconstructed digital endocasts and measured neuroanatomical proxies for cognitive and sensory abilities, including measurements of the brain cavity, orbits, and inner ears. In our preliminary analysis, we investigate correlations between these neuroanatomical features and ecological variables such as diet, foraging behaviour, movement patterns, and habitat use. By using phylogenetic comparative methods, we aim to identify both divergent and convergent patterns of neuroanatomical evolution, offering insight into the adaptations of parrot brains and sensory abilities.

Morphological Variation Among Chimaera Pectoral Fins Impacts Swimming Force Production

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Chimaeras are cartilaginous fishes that are principally found in deep-sea environments. They use their pectoral fins in a unique mode of swimming called flapping flight, where the pectoral fin is oscillated dorsoventrally, inducing undulatory bending along the fin. We characterize the morphological variation among 17 extant chimaera species and show that the 3 chimaera families occupy distinct parts of the morphospace. The most important axis of shape variation relates to aspect ratio and trailing edge shape – factors which both influence force production in rigid hydrofoils. To demonstrate the functional significance of this shape variation for fish-like fins, we constructed simple physical model fins and “swam” these fins in a standing tank using a robotic controller that mimicked the motions observed from freely swimming chimaeras. Particle image velocimetry was used to visualize and quantify flow around each model. We find that fin shape influences the spacing of vortices in the fin's wake, leading to differences in swimming force production. Notably, the pattern of vortex shedding strongly resembles that of a bluegill sunfish (*Lepomis macrochirus*), a teleostean separated from chimaeras by more than 400 million years and which differs from our models in internal structure and actuation mode. Our findings allow us to point toward functional morphological relationships that support flapping flight and suggest that swimming demands may have contributed to chimaera diversification.

Patterns of Mosaic and Concerted Brain Evolution in the Neocortex of Caniform Carnivorans

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Mammals exhibit remarkable diversity in brain size and morphology, shaped by ecological, taxonomic, and body size

radiations throughout the Cenozoic. Certain lineages have evolved specialized brain structures associated with specific functions and behaviors. Yet, a long-standing debate in evolutionary neuroscience concerns whether brain regions evolve independently (mosaic evolution) or in a coordinated manner (concerted evolution). Here, we examine endocranial morphology in caniform carnivores using high-density 3D geometric morphometrics to capture variation across major neocortical regions (i.e., the frontal, parietal, temporal, and occipital lobes). To test for modularity and integration within the neocortex, we assess correlations among neocortical lobes and relative olfactory bulb volume. Caniforms display significant correlations between the parietal and occipital lobes, and between the occipital and temporal lobes, supporting coordinated evolution among these regions. In contrast, the frontal lobe is less integrated with other regions, suggesting it may evolve in a more mosaic fashion. Furthermore, relative olfactory bulb volume correlates with the morphology of the frontal and parietal lobes, particularly their size and orientation, indicating a functional trade-off between somatosensory and olfactory information in caniforms. These findings suggest that both mosaic and concerted evolution shape neocortical organization in carnivores. Functionally distinct regions exhibit varying degrees of evolutionary independence, supporting the view that these evolutionary modes are not mutually exclusive, but together contribute to the evolution of complex behaviors and sensory specializations in mammals.

Dental Age Estimation and Molar Progression in Eastern Grey Kangaroos

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The age distribution of a population is essential information for demographic studies and informing conservation management. In macropodid marsupials (kangaroos and kin), age can be estimated from aspects of tooth growth, wear and progression. Macropodid incisors are ever-growing, displaying predictable rates of growth and wear that are reflected in the lengths of the root and crown, respectively. Molars follow a distinct progression, with successive molars erupting and moving anteriorly with age, the extent of which can be quantified by a molar index. However, the mechanism underlying molar progression is poorly understood. We compare the accuracy of incisor crown length, incisor root length and molar index as predictors of age, using models derived from known-age Eastern Grey Kangaroos (*Macropus giganteus*). Regression models for 52 *Macropus giganteus* skulls identified molar index as the most accurate predictor of age; however, incisor crown and root lengths are still reliable age proxies. We also used 3D geometric morphometrics to analyse skull shape and molar movement over an age series of 1-12 years. Geometric morphometrics revealed the anterior progression of molars with age, whereby the teeth themselves shift position relative to all other elements of the cranium. This mechanism of molar progression suggests that tooth movement is facilitated by the active resorption and deposition of bone surrounding the teeth rather than differential cranium growth posterior to the tooth row.

Relating the Craniofacial Growth Rate in Mouse, Pig and Human During Postnatal Ontogeny

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Background: Mouse and pig have been widely used as animal models of choice for preclinical testing of various technologies in human craniofacial system. This study compares postnatal craniofacial growth rates to identify age-related analogies among mouse, pig, and human from birth to puberty. Methods: CT data from 277 normal humans (0–11.5 years), 32 pigs (Yucatan and domestic, 0–6 months), and 34 wild-type mice (E18.5–P42) were used for skull reconstruction. 35 cross-species landmarks were placed on each model for measurements, including six linear dimensions and intracranial volume (ICV). Cranial module (CM, the average of maximum cranial length, height, and breadth) and two cranial indices were calculated. ICV growth rates were also assessed. Principal component analyses (PCA) examined ontogenetic patterns in cranial size and shape. Results: The overall cranial size of pigs and humans appears to vary within a similar range. ICV increases nearly linearly with overall cranial size throughout postnatal ontogeny in all three species, though at different rates. For instance, ICVs reach 50% and 80% of adult size by P5 and P14 in mice, 1 and 3 months in standard pigs, and 0.5 and 2 years in humans. PCA shows pig cranial form trajectories are more similar to humans than mice. Conclusion: Pig cranial growth better approximates human patterns than mice, despite mice sharing similar suture morphology.

Standing Tall, Head Held High: Vertebral Morphology of Phytosaurs Shows Capacity for Strong Neck Extension and Trunk Support

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The vertebral column is integral to the support of the body and locomotion in tetrapods. By studying vertebral morphology in fossils, paleontologists can reconstruct the bracing mechanisms and types of movement allowed by the spine in extinct vertebrates. While the spines of extant and extinct crocodylomorphs have been studied and compared on morphofunctional grounds, few studies have compared them to other extinct semi-aquatic archosauriforms. In our study, we sought to understand the bracing mechanisms and movements allowed by the presacral vertebrae of phytosaurs, an extinct group of gharial-like reptiles from the Triassic, by comparing them with extant crocodylians. We found that phytosaurs have larger inter-central joint areas, taller centra, and taller neural spines. This suggests that the spine was stiffer overall, particularly in the sagittal plane, while also having epaxial muscles with larger lever arms

for the extension and stabilization of the spine. The zygapophyseal angles are narrower in the cervical region than in the dorsal region, suggesting that the neck predominately moved dorsally and the trunk predominately moved laterally. Lateral flexion was possible in the neck, but was likely more limited. The trunk could likely support most of the locomotor modes used by extant crocodylians, including the high walk, low walk (sprawling), and axial swimming. However, the large degree of sagittal stiffness in the trunk likely prevented the use of asymmetrical gaits like galloping.

Using Ai-Driven Digital Dissection Techniques to Study Ontogenetic Changes In Chameleon Cranial Anatomy

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Unlike other squamate reptiles, the veiled chameleon, *Chamaeleo calypttratus*, is unique in that their development is only at the early gastrula stage at the time of oviposition, meaning that females do not need to be killed to be able to study embryonic growth. This, combined with its simple husbandry requirements and large clutch sizes, has led to *C. calypttratus* being adopted as a model system for the study of reptile development, biomechanics, evolution, and ecological niche specialisation. Their cranial anatomy is of particular interest because they have an extremely enlarged cranial casque relative to other chameleon species. Despite this, there has been a distinct lack of research on the anatomy of this species, and soft tissue anatomy for chameleons in general. Here, we present the first 3D digital atlas of *C. calypttratus*. Using contrast-enhanced microCT scans and deep learning models in Dragonfly 3D World, we have digitally dissected the cranial musculoskeletal anatomy across four developmental stages in both males and females. We discuss how major anatomical differences, such as variation in bone contacts and muscle topology, could be linked to variation in function across ontogeny. Secondly, we report the potential drivers of morphological variation between sexes. Finally, we demonstrate how our digital reconstructions of this emerging model organism could be used for future research and education on vertebrate anatomy and function.

How to Take the Ankle Express When You Are a Sauropod? Morphological Innovations in the Astragalus of Sauropodomorph Dinosaurs Related to the Evolution of Columnarity and Gigantism

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Sauropods were the largest land-dwelling animals. Their evolution is associated to the acquisition of a suite of traits particularly efficient to support a gigantic body. The

sauropod bauplan is indeed notably characterised by obligate quadrupedality and a peculiar columnar limb architecture. However, this clade is nested within saurpodomorphs, whose earliest representatives were small bipeds. While the evolution of sauropodomorph limb long bones in relation to gigantism received increasing interest in the recent decades, the tarsus, mainly represented by the astragalus, received much less attention, despite its critical position in limb architecture. Relying on surface 3D geometric morphometrics, we conducted a quantified comparative analysis of a large sample of sauropodomorph astragali to assess how shape varies in relation to the acquisition of columnarity and size variation. The acquisition of sauropod-related features appeared to be rather stepwise, similarly as previously observed in the hindlimb zeugopod. Allometric analyses favour the hypothesis of a shared trend in columnar and non-columnar sauropodomorphs: largest astragali tended to have flatter distal articular surfaces and more tightly connected proximal ones. In sauropods, the orientation of the distal articular surface is remarkably subhorizontal, similarly to the condition seen in columnar proboscideans. This peculiar pes organisation evolved within both clades from very different evolutionary trajectories, but seemed to be a prerequisite to the evolution of an extensive foot pad as only observed in those groups.

Using the Axial Skeleton As Armor: The Structure-Function Relationship of Sea Turtle Shell Bone

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Turtle shells are formed of bone overlaid by keratinous scutes. Often considered a form of boney armor, the bones of the carapace are arranged as large plates connected by sutures. Though this composite structure acts as a first line of defense against attack or impact, it's only recent that the turtle shells mechanical behavior and microarchitecture have been investigated. Most of this study has focused on freshwater turtles and tortoises, while marine turtles receive relatively less attention. We investigated the shell's mechanical behavior and microstructure in green (*Chelonia mydas*), loggerhead (*Caretta caretta*), and Kemp's ridley (*Lepidochelys kempii*) turtles across a wide range of body sizes. Carapace samples were mechanically tested under compression to measure the shell's material properties and non-destructively imaged using micro-CT to investigate the effects of bone microarchitecture on mechanical behavior. Our study found that marine turtle shells are compliant and less resistant to deformation when compared to non-marine turtles. Material properties also differed across species and ontogenetically. The shell's greater flexibility may reflect tradeoffs for life that include experiencing pressures from diving in marine environments. In line with this, trabecular structure suggests that the shell experiences multiple loading regimes, requiring a balance between stiffness and compliancy. Inter-specific mechanical differences are also likely driven by variation in trabecular architecture. Turtles with highly stiff shells had thicker and more densely packed trabeculae while those with flexible shells had more loosely oriented trabeculae.

Predictive Simulations Reveal How Scaling Shapes Avian Sit-To-Stand Biomechanics

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Body size strongly influences vertebrate locomotor mechanics, yet the mechanical and morphological constraints underlying size-dependent transitions in limb posture remain poorly understood. Using birds spanning over two orders of body mass, we examined how musculoskeletal morphology influences the sit-to-stand (STS) transition. Experimental data on ground reaction forces (GRFs) and hindlimb joint kinematics show that larger birds (e.g., emus, *Dromaius novaehollandiae*) exhibit greater joint excursions and higher peak GRFs, producing increased forward momentum to facilitate rising, while smaller birds (e.g., pheasants, *Phasianus colchicus*) achieve smoother transitions with lower mechanical demands. To interpret these patterns, we developed 3D muscle-driven simulations validated against empirical data. Performance across species was best explained by minimising a cost function combining muscle activation and force rate, suggesting conserved neuromuscular strategies despite varied morphologies. We then scaled an emu model (1–80 kg) and assessed how muscle capacity, contraction speed, and body height affect STS performance. Results show large birds exhibit larger forward momentum and face mechanical limits—e.g., a simulated 100 kg emu cannot rise due to ankle extensor weakness. Analytical models revealed two constraints on STS speed: limited muscle work and height displacement—with all experimentally observed performances falling within these bounds. This study links morphology, mechanics, and control theory to reveal how scaling shapes avian limb function, with implications for constructing movement in extinct species and designing bioinspired robots.

Water Temperature Modulates Multilevel Plastic Responses to Water Flow During the Ontogeny in a Neotropical Fish

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Concomitant environmental signals during development may amplify or minimize plastic responses at different levels, and knowing how external information shapes complex plastic phenotypes is essential to predict potential evolutionary trajectories driven by developmental plasticity. Here, we manipulate water temperature to evaluate its effects on the well-described phenotypic accommodation of fish growth in the presence of water flow, using the neotropical species *Astyanax lacustris*. We include larval and juvenile ontogenetic stages to examine the interaction between these two environmental signals in plastic responses related to body size and shape, skeleton ossification, and gene expression. We use *bmp4* as a proxy for ossification pathways. Our results demonstrate that water temperature plays a crucial role in determining the expression

of plastic variation at all dimensions, and the effects of water flow were restricted to specific thermal regimes. A combination of high temperature and water flow unveils unique shape morphotypes. Multilevel plastic responses in running-water environments likely involve a functional relationship with swimming performance. Our findings highlight the importance of studying developmental plasticity in complex environments using a multidimensional approach, especially considering temperature increases expected due to climate change.

Evolution of the Avian Tongue Skeleton in Relation to Feeding Ecology

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Since Darwin, the connection between beak shape and feeding ecology in birds has become the canonical example of how natural selection shapes structure in response to function. While beaks in relation to feeding ecology have been extensively studied, birds also rely on their tongue to feed. The avian tongue is supported by bones of the hyobranchial apparatus (HBA). Comparative studies of avian tongues focus primarily on gross external morphology rather than HBA characteristics. The goal of this study is to quantify the three-dimensional shape diversity of the HBA across birds and to use phylogenetic comparative methods to evaluate if feeding ecology is associated with shape. To do this at a macroevolutionary scale, we leveraged online databases of micro-CT scans. We performed segmentation, landmarking, and 3D geometric morphometrics for 149 species (118 families). We find that convergent evolution of tongue protrusion has a strong impact on shape analysis. Hummingbirds, sunbirds, and woodpeckers were outliers on PC1 (49% of shape variation), reflecting their extremely long and curved epibranchial bones. Examining diet showed a significant difference between nectivores and most other diets, but the association between diet and shape was less clear after removing extreme protruders. Our work suggests that tongue function rather than diet may be more associated with HBA shape, with an extreme functional innovation (protrusion) associated with the greatest departure from the general Bauplan.

Advantages and Anatomical Relevance of Murine Models In Vocal Fold Research

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Murine models are now frequently used in vocal fold (VF) research despite differences in vocalization. In addition to their low maintenance cost, short gestation period, and large litter sizes, their primary advantage is their amenability to genetic manipulation. The murine larynx and VFs share many morphological and functional similarities with their human counterparts, as well as comparable development. Like humans, the murine laryngeal framework is composed of cartilages—including the epiglottis, thyroid, cricoid, and arytenoid—along with intrinsic laryngeal muscles that perform similar functions, such as VF abduction and adduction. A unique feature in rodents is the presence of the alar cartilage and a pair of muscles

called the superior cricoarytenoid muscles, which assist with VF approximation and contribute to ultrasonic vocalization. Histologically, murine VFs resemble human VFs: the supraglottis and VFs are lined with non-keratinizing stratified epithelium, and the subglottis has pseudostratified mucociliary epithelium. Though the murine lamina propria lacks distinct layering, its extracellular matrix contains similar components, such as collagen I and elastin. Lastly, during embryonic development, key stages such as the approximation of developing VFs, their midline fusion, and subsequent recanalization are also observed in mice. These features make murine models valuable for studying the cellular and molecular mechanisms of VF development and mucosal regeneration, as well as for conducting biomechanical studies.

Influence of Environmental and Behavioral Variation on the Intraspecific Variation of the Bony Labyrinth of North American River Otter

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Inner ear morphology has been studied extensively across mammals to characterize evolutionary relationships and behavioral variation. Yet despite our interspecific understanding of this system, little is known about how behavioral and environmental variation influence intraspecific bony labyrinth morphology. Using *Lontra canadensis*, a geographically, environmentally, and behaviorally diverse species, as a model, we tested this relationship. Using both linear measurements and 3D geometric morphometrics, we quantified the shape of the bony labyrinth in 56 specimens of *L. canadensis* (24 across geographic range; 32 isolated geographically to test sexual dimorphism). For these specimens we also collected environmental data, including climatic and water system data. We found that the shape and size of the semicircular canals differed across the geographic range of the species, correlating with water discharge levels. Specifically, we found that those populations living in regions with fast-moving bodies of water had more robust and differentially oriented lateral semicircular canals. We found no effect of sexual dimorphism on the bony labyrinth, despite the sexes exhibiting variation in hunting behaviors and cranial shape. The results of this study suggest that the water speed influences the vestibular system of otters, likely driven by a need to maintain balance and adjust during aquatic locomotion and prey capture. Further research into locomotor variation among these populations may reveal further information.

Suction-Feeding as an Ambush Strategy in a Giant Salamander (*Andrias*, Cryptobranchidae): A Computational Hydrodynamic Approach

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Suction feeding is a prey capture mechanism used in aquatic environments, where the predator rapidly draws water and prey into its mouth. This specialized strategy has been employed by various taxa, including the salamander family Cryptobranchidae, since the Jurassic. Modern *Andrias* salamanders have retained this feeding method with minimal morphological change since the Oligocene. Studying its biomechanics helps clarify the physical and morphological adaptations supporting it, as well as its evolutionary relevance among aquatic amphibians. We developed a two-dimensional Computational Fluid Dynamics (CFD) model of suction feeding based on micro-CT scans of a first-generation hybrid *Andrias davidianus* × *Andrias japonicus* from Okayama, Japan. Transient CFD simulations were conducted using unstructured dynamic meshes and an overset approach, enabling interaction between fluid and prey. The model incorporated translation and rotation of the skull and lower jaw, surface deformation, and hyoid depression. Mesh inertial properties were defined using prior data from *Andrias davidianus*. Prey characteristics including position, size, and weight were varied. Results indicate that cranial geometry, hyoid motion, and prey properties influence the generation of subambient pressures required for successful suction. This study enhances the understanding of hydrodynamic principles underlying suction feeding and lays the groundwork for future comparisons among both extant and extinct amphibian species.

New Perspectives on Head and Neck Allometry and Ecomorphology in Tetrapods

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The skull and neck are vital parts of the body, influencing feeding ecology, habitat exploitation and locomotion. Numerous studies have sought to understand how the size of these segments vary with ecology and scale with overall body size. However, across past literature many different metrics have been used to represent both head and neck size, alongside disparate methods for body size normalisation and varied statistical approaches. Therefore, a new analysis of head and neck proportions using a data set of 410 three-dimensional digital skeletons is presented, sampling a wide taxonomic breadth of extinct and extant tetrapods, with head and neck size quantified using multiple metrics across previous studies. We find that all metrics suggest negative allometry in skull size, whereas the pattern of allometry seen in the neck is influenced by the metric used (length vs volume). We also find that allometric patterns in linear metrics for head and neck size are better described by a linear model, whilst volumetric measurements are better fitted by a quadratic model. Distinct allometric trends in skull length and width are recovered across taxonomic and trophic groups, which may represent mechanical interactions between bite force and velocity in different feeding modes. Future work should therefore carefully consider the choice of parameter used to represent skull and neck size when comparing trophic and taxonomic groups and making ecological and macroevolutionary inferences.

How Lizards Bite: A State-Of-The-Art Computational Approach to Model Skull Kinesis

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The vertebrate skull faces a critical challenge in simultaneously protecting vital structures, such as the brain, while enabling efficient food processing. To address this, we developed a new workflow that improves upon previous computational models in the field in terms of complexity and reliability. This workflow combines a musculoskeletal model using Multibody Dynamic Analysis (MDA) with Finite Element Analysis (FEA) and utilizes genetic algorithms in forward dynamics to optimize biting under different configurations. This approach was applied to evaluate the cranial kinesis of the Gran Canaria giant lizard (*Gallotia stehlini*). The skull model was reconstructed using micro-CT, and the adductor muscles were modelled to build the musculoskeletal system, enabling bite force optimization for the FEA model. Both musculoskeletal and FEA models were tested under three kinetic configurations: akinesis, streptostyly, and amphikinesis. Cranial sutures were incorporated with contact elements, and material properties were derived from nano-indentation tests. This approach helped understand how different kinetic and suture configurations balance skull protection and efficient food processing. Our findings show that streptostyly reduces stress in critical regions of the skull and mandible, preventing damage. In contrast, akinetic and amphikinetik configurations exhibit higher stress, increasing failure risk. Additionally, biting force measurements from living specimens confirm that models with streptostyly best match the observed in vivo forces.

Energetics and Dietary Constraints on the Flight Ecology of Azhdarchid Pterosaurs

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Azhdarchid pterosaurs, a lineage of Mesozoic flying archosaurs, include the largest flying animals ever known. Larger representatives, such as *Quetzalcoatlus nortropi*, had a wingspan of over 10 m, a large head, massive wingspans, a shoulder height equivalent to an extant giraffe and a weight of more than 200 kg. Because of their large features, these pterosaurs have ecological interpretations as major predators. Here we examine the probability of that from an energetics perspective. 200 kg is very light for the size of these giants. On top of this, the body length (gleno-acetabular distance) of these pterosaurs is relatively small (a volume of ~1.5 times that of an average sized human male for *Q. nortropi*). When factoring in lung volume this restricts the gut capacity and thus prey size. This measurement allows us to explore the Basal Metabolic Rate (BMR), Field Metabolic Rate (FMR), and Daily Energy Expenditure

(DEE) of various azhdarchid species using extant mammalian and avian measurements. We explore the potential of flight and terrestrial stalking using soaring and walking, also from mammalian and avian measurements. This data gives great insight into the true ecology of these giants and refutes the interpretation of them being major predators.

The Mechanics of Jumping Down: Compliant-Limbed Lemurs Achieve Softer Landings

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The limbs of arboreal primates are morphologically and/or behaviourally more compliant than terrestrial primates, leading to hypotheses about the role of limb compliance in on-branch stability and moderating forces. Generally, models address the mechanical compromises required to avoid injurious falls from compliant branches, or achieve good locomotor economy, but rarely consider both together. Here we explore a transition between the two environments – the mechanics of 0.7m drop-landings in two similarly sized lemur species, the arboreal blue-eyed black lemur (*Eulemur flavifrons*) and the more terrestrial ring-tailed lemur (*Lemur catta*). *Lemur catta* descends rapidly, with greater spring stiffness and peak force (~4.5x BW), while *E. flavifrons* has a spring stiffness about half that, and a peak force of 3.7 times body weight applied over a longer descent period, through the greater range of motion in its flexible limb joints. This is exemplified by the time taken to land through the foot, with time from first touch to full contact in *L. catta* half that of *E. fulvus*. While falling at the same speed over a greater range of motion should slow the animal's descent, we might also expect greater contributions from eccentric contraction of extensor musculature to support and protect the looser joints. Landing mechanics show fundamental adaptations to habitual locomotor ecology, and the challenges of moving from trees to the ground.

A Framework for Scaling Muscle Forces to Obtain Meaningful Results in Comparative Finite Element Analysis of Skulls

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Comparative finite element analysis (FEA) involves standardisation of model parameters to enable meaningful comparisons of loading conditions across species. In the context of skull biomechanics, however, the definition of 'equivalent' loading depends heavily on the specific research question. By analysing 13 marsupial skulls from bettongs and potoroos with varied skull size and mechanical advantage—including the extinct *Caloprymnus campestris*—we show that the way muscle forces are scaled can lead to markedly different comparative patterns of stress and strain between species. These differences emphasise the importance of selecting an appropriate scaling method that aligns with the hypothesis being tested. We therefore present a framework identifying three main

categories of hypotheses related to biting mechanics, each requiring a distinct muscle-scaling approach to yield appropriate results: (1) evaluating how effectively skulls transmit muscle force to the bite point, which involves scaling muscle force relative to skull size; (2) assessing structural adaptations for biting by standardising mechanical advantage to simulate size-corrected bite scenarios; and (3) examining ecological relationships such as niche partitioning by scaling to equalise bite reaction forces. Applying these approaches reveals that *C. campestris* had a biomechanically efficient skull capable of generating strong bites, but this appears to be mostly a compensatory adaptation for its relatively small skull compared to other bettongs and potoroos.

Kinematic Evaluation of Descent Slowing Behavior During Falls in Lizards

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Animals living in arboreal habitats encounter numerous discontinuities in their environment, which expose them to a significant risk of falling. Such species may be expected to adjust their body and limb positions during falls to modulate their position of impact upon landing. However, species with different limb and body configurations may differ in their ability to make such adjustments and moderate impact forces. To test this hypothesis, we constructed an apparatus to simulate natural aerial drops by releasing animals onto a cushioned landing pad 1.5 m below. We compared trials for each of three arboreal lizard species that varied in body height and tail proportions: *Chamaeleo calyptrotus* (tall-bodied, intermediate tail), *Gastropholis prasina* (low-bodied, long tail), and *Anolis equestris* (low-bodied, shorter tail). Using high-speed video, we tested whether differences across taxa in body, limb, and tail movements during falls were correlated with differences in morphology. Despite body configuration differences, each species sprawled their limbs out similarly in a lateral and slightly dorsal orientation, with the anterior body pitched forward. These results suggest a conserved method of reducing falling velocity in arboreal lizards, indicating a decoupling between morphological and behavioral specializations. Despite their different body configurations, falling kinematics across these species were more similar than expected.

Relationship Between Body Posture and Force Generation in Slithering Snakes

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Snake locomotion is characterized by the organism's use of its long, curving body moving through complex terrain. Slithering, the most common mode of limbless locomotion, works by generating body bends which push on contact points to generate reaction forces. As a snake moves forward in its path, contact points are continuously generated and lost leading to a constantly changing system of forces which can vary in magnitude and direction. This movement is dominated by kinetic

frictional forces and for a snake to move forward, complex coordination of these dynamic contact points is required to ensure net forward reaction force. However, it remains unknown whether individual contact forces are determined by the total balance of forces at all contacts along the body or only by local body geometry and friction. We test for governing parameters of contact force generation in slithering by measuring the forces exerted on a single contact point among the many along the body. We captured the kinematics of snakes while slithering across a rigid, flat substrate with equally spaced pegs. A single peg in the center of the board was instrumented with a force sensor which recorded contact reaction forces during locomotion. Preliminary results suggest snakes have a consistent relationship between body posture and contact force orientation. This has implications for inferring forces based on body posture across limbless organisms.

How to Replace Teeth Like a Shark

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Could humans 1 day grow teeth like sharks? Possibly! The successional lamina, the tissue that produces more teeth, is maintained in sharks while it degrades in humans. In mice, only one set of teeth form with no replacement. The decision to form replacements, or, not is controlled through an interplay of activating and inhibiting molecules regulated partly through the Shh and Wnt pathways. Using the Shh inhibitor, Vismodegib, we aimed to revitalise tooth regeneration in mice. Vismodegib was administered to pregnant mice in vivo and ex vivo in mouse molar placode cultures. In both in vivo and ex vivo experiments, the successional lamina was revitalised, with replacement molars produced lingual to the primary molars. Using histological sectioning with trichrome staining, and 3D scanning and modelling, we confirmed tooth cell and tissue layer types in these new molars. Using immunofluorescence, we compared spatial and quantitative differences in the expression of key tooth development genes between the control and experimental conditions. Our results demonstrate the presence of an ancestral tooth regenerative capacity, that could be unlocked in mice. In the future this knowledge may help explain and treat hypodontia (lack of teeth) and hyperdontia (excess teeth) in humans.

Aquatic Bite Club: Canine Tooth Structure and Function in Aquatic Mammals

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Over the last 250 million years, many different animal groups have independently evolved adaptations to living in water. For predators, the functional demands of aquatic life necessitated changes in prey capture, leading to the evolution of new feeding styles and anatomy. Canine teeth are essential tools for feeding,

and in terrestrial carnivores, there are well-established links between their form and function. However, it is unclear whether these patterns hold in aquatic mammals, such as otters or seals. We conducted a combined analysis of canine tooth shape and biomechanics in a sample of 215 teeth representing a broad range of terrestrial, semi-aquatic, and aquatic mammals. First, we used geometric morphometrics to quantify tooth shape, then tested for associations between shape and feeding style. Next, we assessed the biomechanics underlying these associations by performing finite element analyses to model stress and physical puncture tests to quantify puncture force. Shape analysis indicates that suction feeders have robust, curved canines, while raptorial species have straighter, thinner canines. Biomechanical testing demonstrates that the canines of raptorial species penetrate more easily but are more fragile than those of suction feeders. These patterns can aid in understanding the feeding biology of difficult-to-observe and extinct marine species.

Geographic and Sexual Skull Variation in the Subgenus *Charronia* (*Martes flavigula* and *Martes gwankeinsii*) (Carnivora; Mustelidae)

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The subgenus *Charronia* (Mustelidae; *Martes*) includes two species, *M. flavigula*, found from southern Siberia to the Sunda region, and *M. gwankeinsii*, endemic to the Western Ghats in India. *Charronia* is usually associated with forested environments, hunting solitarily, in pairs, or congregating in packs to hunt larger prey, but also eating honey and fruits. However, any cranial or functional variation associated with different environments or local adaptations remains unknown, besides its taxonomy still being poorly understood. Here we present a reassessment of morphometric and functional skull variation in *M. flavigula* and *M. gwankeinsii* according to sex and geographical origin. Seventeen measurements on 73 *M. flavigula* and three *M. gwankeinsii* from its entire geographic distribution were analyzed using univariate and multivariate statistics. Significant differences were found between the sexes in all measurements. Individuals of *M. flavigula* from most of continental Asia show great superimposition in measurements, suggesting a cline with Indochinese specimens in the lower end and southern Chinese specimens in the upper. Individuals from southern Siberia show significantly larger measurements, while specimens from the Sunda islands are distinct and with little superimposition with other regions. Despite the low number of individuals analyzed, *M. gwankeinsii* measurements are similar to smaller *M. flavigula*, with the single male measured showing remarkably similar proportions to the females.

The Musculotendinous System of Selected Mesopelagic Fishes

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Every night, the greatest migration on Earth starts in the deep pelagic oceans. Organisms ascend to the meso- and epipelagic zones to feed and return to deeper waters during the day. Among the dominant vertically migrating fish taxa are the dragonfishes (Stomiiformes) and lanternfishes (Myctophidae). Together with the fins, the musculotendinous system (MTS) forms the functional unit for locomotion. This study explores the functional morphology and architecture of the MTS in stomiiforms, serving as a baseline for ongoing and future research on deep-sea fishes, e.g., myctophids. Stomiiforms lack anterior cones in the anteriormost myosepta, which develop at the level of the dorsal fin and elongate gradually in more posterior myosepta. In almost all investigated taxa, the horizontal septum is reduced. Red musculature overlies laterally the white musculature and exhibits strong tendons in each myomere running to the horizontal midline. The amount of red musculature increases immensely towards the caudal fin. The elongated lateral tendons of the posterior body segments attach in a highly complex pattern on the caudal fin rays, which indicates that the posterior-most myosepta are equipped for a multi-segmental force transmission towards the caudal fin. This unique anatomical condition might be essential for steady swimming during diel vertical migrations, when prey is rarely available. In future studies, this will also be investigated in other groups and families of deep-sea fishes.

Sharp Insight: Exploring Constraints on Pointed Tooth Form in Tetrapods

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Life on Earth exhibits a staggering array of forms. A central challenge in evolutionary biology is to understand the processes that shape this diversity. Seilacher's 'morphodynamics' offers a framework for exploring this, proposing that an animal's form is the product of interacting functional, developmental, phylogenetic, and ecological factors. Pointed teeth are the most common dental morphology in tooth-bearing tetrapods. Their well-studied development, function, and ecology, along with recent methodological advances, make them an analytically tractable system for investigating the drivers and constraints on form. Here, we applied a unique approach that integrates 3D morphometrics, a morphogenetic model (the Power Cascade), biomechanical testing, with phylogenetic and ecological analyses. First, we used the Power Cascade to generate 75 tooth models representing the range of developmentally possible forms. These were integrated into a combined morphospace with empirical teeth from 205 tetrapod species via 3D geometric morphometrics. Next, in a subset of teeth, we assessed functional performance and optimality via a Pareto approach. Finally, we included phylogenetic and dietary information to test for relationships with shape. Results show that empirical

forms are constrained within the morphogenetic model, occupying less of the morphospace; however, the areas they do occupy are associated with higher optimality. Surprisingly, phylogenetic and dietary analyses show weak or no relationship with shape. Thus, we identify functional optimality as the dominant force shaping pointed tooth morphological diversity.

Study of Cranial Growth Trajectory in Boreoeutherian Mammals with Special Reference to Bats

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The ability of laryngeal echolocation which characterizes bats (Order Chiroptera) have significantly constrained their skull. Our understanding of the evolution of cranial morphology in mammals is fundamentally informed by the analysis of cranial development, which could be crucial to reveal whether laryngeal echolocation evolved once in the common ancestor of all bats or twice convergently in rhinolophoids and yangochiropterans. Fetal development is currently understudied, although the majority of morphological differentiation among species occurs prenatally. Here, we studied the ontogenetic trajectories of cranial elements from fetal to adult stage series of the three major bat lineages (i.e., pteropodids, rhinolophoids, and yangochiropterans) and compared them to other boreoeutherian mammals to observe whether heterochronic changes occurred across bat lineages. Around 350 crania of fetuses and neonates from 17 bat and 11 non-bat boreoeutherian species were 3D scanned and all cranial elements were individually segmented. Volumetric data were extracted to quantify growth rate of each cranial element. Principal component analysis and ancestral state of growth rate were used to reconstruct developmental patterns and evolution of bone growth within bat phylogeny. Our results show yangochiropterans undergo slower bone growth compared to pteropodids and rhinolophoids. Yangochiropterans exhibit a different developmental pattern to shape their skull compared to other bats, which could explain alternative approaches to emit echolocation calls and convergent evolution of laryngeal echolocation with rhinolophoids.

Can Morphology and Molecular Approaches Reach a Consensus in Fish Taxonomy?

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Identification of species of clupeids with high phenotypic and ecological diversity, based on their morphology is often challenging. We studied their scales, otoliths, caudal skeletons, and gene sequences for reconstruction of the phylogenetic relationship between 22 species habiting in the Iranian water resources. Collecting sequence data from 2644 of the 3913 total target loci applying gene capture method showed that our target gene tools yield data sets providing robust inferences at a range of taxonomic scales in the clupeids. The morphology of clupeoid scales, classified as “clupeoid”, that is different from the other usual types of scale in the teleosts, were morphologically categorized into four types in studied species. For each species, 14 otolith features were described and 14 otolith variables were calculated and used as input for the statistical analysis. Our work revealed seven morphotypes between studied otoliths. The univariate analysis showed that 12 variables were significantly different among the clupeid species. In addition, a comparative analysis of the vertebral column and caudal skeleton of collected species, conducted based on X-ray imaging and staining method of bones and cartilage, showed that some osteological characteristics could be used as suitable features for the identification of the studied clupeids at the species and genus levels. The results of the analysis of genes, scale and skeleton characteristics were largely consistent with the phylogenetic relationships of the studied group.

The Ultrastructure of the Cretaceous Feathers Highlights the Evolution of the Feather

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The well-preserved Mesozoic feather fossils highlight the evolution of the macroscopic morphology of the feather. However, there are few studies on the changes in the ultrastructure of the feather during its evolution because of the lack of the distinct detailed structures in most Mesozoic feather fossils. In this study, we employed a peeling dissolution experiment to process the mid-Cretaceous (99 Ma) feathers, allowing their ultrastructures to be observed under the scanning electron microscope and confocal laser scanning microscopy. The morphology of these Cretaceous feathers provides significant evidence for the hypothesis that the barbs of the pennaceous feathers originated from the knotted barbs of the downy feathers, the presence of the hook-and-groove mechanism and the slide-lock system during the mid-Cretaceous, and a relatively weak aerodynamic performance in the mid-Cretaceous asymmetric pennaceous feathers. Based on the shape and the orientation of the melanosomes, the colors of these feather fossils were reconstructed.

Codifying the Taxonomic Confidence Into Large-Datasets

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Taxonomy remains foundational to biology, yet it is often marginalised in practice and publishing purely taxonomic work is increasingly constrained. Paradoxically, large-scale biological and

palaeobiological research increasingly depends on taxonomic data from aggregators like GBIF and PBDB. These repositories do not encode the nuanced certainty in taxonomic identification captured in original monographs (e.g., synonymy, remarks), where every name has the same weight. This homogenisation of certainty challenges physiology, ecology, and evolutionary biology analyses. Here, a formalisation of taxonomic identifications using named-set theory, a framework from database architecture, is proposed to visualise and evaluate uncertainty in taxonomic identifications. This approach enables sensitivity analyses of macroevolutionary models by capturing variance in taxonomic consensus and identification precision. The retrospective reproductive community concept of species (RRCC) considers that delineation of species can be viewed as a form of measurement, where identifications range in precision and accuracy, much like statistical estimates. However, precision and accuracy cannot be succinctly coded in a relational database compiling a list of taxa collated elsewhere. For example, an indeterminate vertebrate fossil is less informative for lineage-specific questions than a species-level identification. Although prior studies suggest that taxonomy has minimal impact on macroevolutionary trends, this may underestimate biases relevant to ecological or biogeographic interpretations where alpha-diversity is important. This framework allows for integrating taxonomic uncertainty into large datasets, promoting more transparent and reproducible analyses.

Biomechanics of an Arthritic Mosasaurid Elbow Joint

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Returning to marine environments involved significant modification in limb morphology in mosasaurids as terrestrial legs turned to flippers. The Tylosaurinae possessed perhaps the most basal limb morphology of the four mosasaurid subfamilies with limbs characterized by: stylo- and zeugopodia that lack both the complex muscle attachment sites and the proximodistal shortening observed in other mosasaurs, reduction in the number of ossified carpals/tarsals to two (ulnare + distal carpal IV; astragalus + distal tarsal IV), and elongated autopodia due to hyperphalangy. Whereas previous studies on mosasaurid pathology have been largely restricted to avascular necrosis and bite marks, here we analyze an advanced case of osteoarthritis in the right fore-paddle of an especially large specimen (14 m) of *Tylosaurus proriger*. Investigation found considerable evidence of cartilage breakdown and bone-on-bone friction based on the presence of large osteophytes and subchondral sclerosis along the articular ends of the humerus, radius, and ulna. Observed abnormal remodeling of joint tissues resulted in joint space narrowing and would have manifested as altered loading and utilization in life. We predict that synovium inflammation and subsequent ligament degeneration likely resulted in a slow progression to joint failure. This new data offers insight into the origin, progression, and locomotive implications of arthritides in the largest mosasaurids.

New Material of the Miocene Ziphodont Crocodylian *Quinkana timara* and the Phylogeny of Mekosuchinae

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The extinct crocodylian clade Mekosuchinae is represented by taxa of diverse body sizes and craniomandibular morphologies, with species of the genus *Quinkana* being one of the most distinctive mekosuchines. *Quinkana* is characterized by a combination of morphological features absent in extant crocodylians, such as an altirostral snout, anterodorsally opening external naris and ziphodont dentition. With four recognized species spanning from the Oligocene to the Pleistocene, *Quinkana* was an integral component of Australia's carnivorous fauna during the Cenozoic Era. Unfortunately, despite its taxonomic and paleoecological significance, *Quinkana* is arguably the least understood mekosuchine genus due to the highly fragmented nature of the currently described material for its species. Newly discovered remains from the Middle Miocene site of Bullock Creek in the Northern Territory, Australia are referable to *Quinkana timara* and substantially expand our knowledge of the morphology of this taxon. The new material derives from multiple individuals and is representative of most craniomandibular elements of *Q. timara*. Information obtained from the undescribed *Q. timara* fossils was incorporated into an updated phylogenetic matrix to evaluate the evolutionary relationships of Mekosuchinae. Preliminary results recovered a monophyletic Mekosuchinae as a sister clade to Longirostres, with the species of the enigmatic Asian clade Orientalosuchina also found as a part of Mekosuchinae.

Quantifying Morphological Disparity in the Petrosal Bone and the Bony Labyrinth: A Case Study Using Extant Camelids

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The otic region of mammals includes the petrosal bone and the bony labyrinth (BL). The petrosal surrounds the BL, which contains the organs of hearing and balance in life. Advances in μ CT scanning have allowed the petrosal and BL to be used more widely in comparative morphology, but variation within species and among closely related species remains understudied, and many inferences are made from limited material assumed to represent an average morphology. To quantify petrosal and BL variation in camelids, we developed 3D geometric morphometric landmark schemes, with a total of 136 and 93 landmarks, respectively. A sample of 14 adult camelids shows that the petrosal is more morphologically variable than previously thought, which we visualized with a principal component analysis. Camelinins and aucheniinins occupied distinct areas of the morphospace, with camelinins more dispersed than aucheniinins. Bactrian and

dromedary camels were separated, suggesting undescribed differences between their petrosals. Conversely, the aucheniinins exhibit a great deal of intraspecific variation that may be equivalent to their interspecific variation. A similar pattern was present in the BL, although camelinins and aucheniinins had less separation. Comparing the Procrustes distances of the petrosals and BLs, we found that the petrosals had significantly more variation ($p < 0.001$) than the BLs. This suggests that the morphological variability of these structures is quite different and more intensive sampling of petrosals is needed.

Development of Bone Ridges and Trabecular Structures on the Lateral Side of the Vertebral Centrum in Teleost Fish

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The lateral sides of teleost vertebral centra develop into diverse structures during the late growth stages, although these lateral structures are not apparent in the early stages. The lateral structures contribute significantly to the diversity of teleost vertebrae, but their formation mechanisms remain unclear due to limited research on teleost vertebral centrum growth. To clarify this, we analyzed the morphological and histological changes in the vertebral centra of Pacific bluefin tuna during growth and compared them with those of zebrafish. Micro-CT scans showed that the tuna vertebral centrum formed a plate-like lateral ridge extending cranio-caudally, which thickened and expanded laterally. Simultaneously, the proximal region of these ridges became porous, forming bone marrow cavities. Histological observations showed osteoblasts accumulating on the distal edges of the lateral ridges, whereas osteoclasts were distributed within the marrow cavities. This suggests bone synthesis at the ridge edges and bone resorption proximally to form marrow cavities. Conversely, the zebrafish vertebral centrum developed a thin lateral ridge that lacked marrow cavities. Osteoblast accumulation sites shifted from covering the entire lateral ridge surface to its dorsal and ventral surfaces, and osteoclasts were present within the bone. This suggests that the osteoblast activities involved in extending the ridges laterally are similar between these species. However, variations in osteoblast and osteoclast activities can regulate ridge thickness and the presence of marrow cavities.

Shifts in Developmental Trajectory and Body Proportions in Rook (*Corvus frugilegus*) Ontogeny

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Despite the considerable interest of researchers in the issue of bird growth, detailed studies of changes in body proportions along the embryonic and postnatal periods of ontogenesis in wild-living birds are few. We studied changes in body proportions (relative sizes of head, skeletal elements of wing and leg) along the embryonic and

postnatal development of the Rook (*Corvus frugilegus*). We distinguished four periods in the dynamics of relative sizes when the growth trajectories of traits change significantly, often reversing direction. The studied traits were mainly positively allometric on body mass in the first period (from the 10th to 13th days of embryogenesis) and third period (from the 5th to 23rd days of the postnatal period), negatively allometric in the second period (from the 14th day of embryogenesis to the 3rd day of postnatal development) and isometrically in the fourth period (from 25th to 30th days of the postnatal period). Despite the roughly consistent change in the organism within the designated periods, the hindlimb had the highest growth rate in embryogenesis and the forelimb during most of the postnatal period. We assume that changes in the dynamics of body parts growth and, as a consequence, changes in body proportions are associated with the preparation of different organs for functioning and with the influence of factors limiting the growth of the entire body.

Muscle Shortening and Vertebral Column Curvature During Propulsive Vertical Bending in Snakes

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Snakes' multiarticular muscles let them move through cluttered environments by generating complex bending patterns. While muscle strain directly corresponds to curvature in purely lateral bends, recent studies have shown that they can also generate propulsive forces through vertical bending, either in combination with lateral bending or via a single vertical bend. Given the likely importance of three-dimensional movements during snake locomotion in natural environments, the muscular basis for propulsive vertical undulation can provide a broader understanding of the mechanics of limbless locomotion. To quantify muscular strain during three-dimensional slithering, we implanted radio-opaque metal beads into three muscles in four corn snakes (*Pantherophis guttatus*), and then we recorded X-ray videos to measure muscle length and vertebral column curvature during vertical bending. A preliminary analysis suggests that muscle length change and vertebral column curvature are closely related. Observed muscle shortening patterns during vertical and lateral bending confirm functional predictions from muscle anatomical positions. Additionally, particular combinations of vertical and lateral bending allow certain muscles to remain isometric or near-isometric despite continuous motion. Because overcoming frictional forces is a major requirement for effective limbless locomotion, snakes may benefit from these lower shortening speeds due to increased muscle force output.

Integrating Morphology and Hydrodynamics in Freshwater Stingrays: A Comparative Study of *Potamotrygon motoro* (Müller & Henle, 1841) and *Paratrygon aiareba* (Müller & Henle, 1841) (Batomorphi: Myliobatiformes: Potamotrygonidae)

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The subfamily Potamotrygoninae includes diverse Neotropical freshwater stingrays with varied morphological adaptations to riverine environments. Body shape strongly influences locomotion and hydrodynamics, affecting habitat use and ecological specialisation. This study examined morphology-hydrodynamics relationships in *Potamotrygon motoro* (Müller & Henle, 1841) and *Paratrygon aiareba* (Müller & Henle, 1841). Using high-resolution 3D scans and Computational Fluid Dynamics (CFD), we quantified drag forces (Fd) and drag coefficients (Cd) across flow velocities (0.25–3.0 m·s⁻¹). *P. motoro* showed lower mean Cd (0.0258 ± 0.0029), suggesting a streamlined form adapted to active swimming in shallow, complex habitats. In contrast, *P. aiareba* had higher Cd (0.0347 ± 0.0015), consistent with a more stable morphology suited for deeper, less structured environments and a sedentary lifestyle. Statistical tests confirmed significant interspecific differences (Mann-Whitney U, $p = 0.0002$; Student's t, $p = 1.0 \times 10^{-10}$). Boundary layer analysis indicated minimal impact of dermal denticles on macroscopic hydrodynamics under the studied conditions. These findings support the view that morphological variation in Potamotrygoninae is closely tied to ecological and habitat differentiation. This integrative ecomorphological and CFD approach sheds light on the adaptive radiation of Neotropical stingrays and highlights the functional implications of morphological diversification in dynamic freshwater ecosystems.

Osteological and Histological Evidence for the Vomeranasal Organ in Roundleaf Bats

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In yinpterochiropteran bats, current evidence indicates all pteropodids lack any vestige of a vomeronasal organ (VNO), a chemosensory structure of the nose. In contrast, some of the rhinolophoid bats lack a functioning VNO but retain a vestigial epithelial tube where the VNO typically sits in mammals. Using microCT, we examined a sample of 13 species of roundleaf bats (*Hipposideros* spp.) to assess osteological evidence for site of articulation of the vomeronasal cartilage with the palate. In addition, three of the specimens were histologically sectioned. Histology reveals one species (*Hipposideros bicolor*) possesses a neurally intact VNO (i.e., with a neuroepithelium and vomeronasal nerves), suggesting the VNO is fully functional in this species. Three-dimensional reconstructions of the hard palates reveal that all specimens have the crescent shaped impression on the premaxilla, which histology verifies as the site of vomeronasal cartilage articulation. Sites of articulation are also observed on the maxilla, but these vary, being sometimes deep, sometimes shallow, and sometimes absent. The variability at the maxillary articulation site suggests a trend toward caudal regression of the VNO and its capsule. If so, there may be evidence of reduction of vomeronasal structures over time in fossil hipposiderids. Although the VNO is lost or vestigial in most

known extant yinpterochiropteran bats, our results demonstrate the need for further inquiry.

Multifaceted Relationships Between Fossorial Behaviors and Extinction Susceptibility Across Extant Mammalia

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Mammalian fossoriality is often considered a “key innovation” because digging facilitates access to novel food sources, shelter from climatic extremes and predation, and protection for offspring. This lifestyle can strongly constrain morphology, and specialized fossorial mammals in particular display convergent body plans, bone and soft tissue morphology, and sensory adaptations. Because fossorial mammals are crucial for ecosystem functioning, we need to better understand how ecology affects their extinction susceptibility, particularly in light of varying degrees of specialization, as generalist organisms often outsurvive specialists during mass extinctions and ecological upheavals. Here, we survey degree of fossorial specialization (non-fossorial, semifossorial, fossorial, and subterranean categories as a proxy for morphological and behavioral specialization), “exploitative fossoriality” (i.e., utilizing existing burrows, crevices, etc.), IUCN Red List status, body size, geographic range size, and sociality across 3,390 extant terrestrial mammal species. Bayesian phylogenetic regressions suggest that subterranean species are more likely to be data deficient (DD) than less specialized species, whereas exploitative fossoriality is “protective” against data deficiency, although rodents drive the former result and non-rodents drive the latter. Among non-DD species, semifossorial and subterranean specialization and exploitative fossoriality correlate with lower extinction susceptibility. Next steps include investigating how degree of fossorial specialization and exploitative fossoriality affect evolutionary rates by generating tip-level diversification rate estimates from ClaDS2 and modeling them as a function of the variables of interest and covariates.

Saga of the Strongest Spine: Decoding the Mechanics Behind the Hero Shrew's Unique Vertebral Adaptation

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Hero shrews (genus *Scutisorex*) possess uniquely structured backbones featuring numerous (50–80) finger-like lateral processes called tubercles that interlock with adjacent vertebrae. Despite previous research, the functional significance of this remarkable spine morphology remains unclear, largely due to limited access to live specimens and scarcity of cadavers for detailed study. Here, we apply in-silico methods to investigate the mechanics underlying this distinctive vertebral architecture and explore the functionality of tubercles under various loading conditions. Employing high-fidelity finite-element modelling, we simulated mechanical responses of

mid-lumbar spinal segments (two vertebrae with an intervertebral joint) from two hero shrew species (*Scutisorex somereni* and *Scutisorex thori*) and compared them with the Goliath shrew (*Crocidura goliath*), a typical shrew found in similar habitats. The segments were subjected to physiologically relevant loading conditions in axial compression, torsion, sagittal, and lateral bending. Our results reveal that tubercles enhance compressive strength and torsional stability in hero shrews without limiting sagittal or axial flexibility. Furthermore, higher tubercle count in *Scutisorex somereni* leads to more uniform stress distribution in the interlocking lateral processes during axial rotation compared to *Scutisorex thori*. This suggests that Hero Shrews evolved increased tubercle numbers to mitigate stress-induced fracturing, and that *Scutisorex thori* is functionally intermediate between *Scutisorex somereni* and other shrews. Ultimately, this study underscores the versatility of computational approaches for exploring the biomechanics and adaptations in rare and difficult-to-study species.

The Development of the Acrocoracoid Process and its Implications for the Evolution of Avian Flight

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Modern birds possess a specialized musculoskeletal system in the shoulder region that enables powered flight. All volant birds rely on two pectoral muscles —*musculus (m.) pectoralis* and *m. supracoracoideus*— to produce the force necessary for wing flapping. *M. supracoracoideus*, though ventrally located, drives the upstroke that lifts the wings dorsally. This is achieved through a bony structure called the acrocoracoid process, which develops at the dorsal coracoid and plays an important role as a pulley when *m. supracoracoideus* contracts. The aim of this study is to elucidate the developmental mechanisms underlying the unique function of *m. supracoracoideus* in birds. To this end, we focused on the formation of the acrocoracoid process during embryogenesis. We reconstructed the three-dimensional morphology of the developing coracoid and the attachment sites of surrounding muscles on the surface of the acrocoracoid process in chick embryos. We also examined the distribution of Sox9+/Scx+ cell populations, which have been shown to give rise to bony processes. Our results suggest that the attachment of several muscles to the dorsal coracoid contributes to the development of the acrocoracoid process. We discuss putative mechanisms that drive the development of the acrocoracoid process and implications for the developmental change underlying the evolution of the avian flapping flight.

Strain Measurement in the Periodontal Space of Macaque Incisors

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Mechanical stresses on incisors are transmitted to the periodontal ligament (PDL), which supports the teeth during mastication. Previously, fiber optic strain measurements in pig

incisors have shown similarities between in vitro and in vivo biomechanical models and similar strain response to multiple orientations of applied load. The goal of this study is to extend our understanding of the relationship between direction and magnitude of force applied and strain response to primates in vivo. Fiber Bragg Grating (FBG) sensors were inserted into the labial and lingual PDL spaces of an anesthetized rhesus macaque's incisor. Using an anesthesiometer, force was applied continuously and intermittently in two directions: vertical intrusion on the incisal edge and horizontal tipping on the labial face. Vertical intrusion showed compressive microstrain in the labial and lingual PDL spaces. Horizontal tipping showed tensile microstrain on both sides of the tooth during continuous force application, but compression in the lingual and tension in the labial PDL spaces during intermittent force application. Stress-strain curves showed peaks of up to 20 $\mu\epsilon$ at 100 grams of loading. Compressive strain in both PDL spaces suggests that mechanoreceptors transmit the same strain. Tensile strain in the PDL during continuous horizontal tipping and mixed compressive and tensile strain in the PDL space during horizontal tapping shows the lower right incisor responds differently to the tempo and direction of force application.

Dice MicroCT Imaging of Renal Morphology Following Pkd Infection in Irish and Norwegian Atlantic Salmon

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Atlantic salmon is a globally significant aquaculture species. However, these fish are vulnerable to *Tetracapsuloides bryosalmonae*, the causative agent of proliferative kidney disease (PKD). This parasitic infection induces renal inflammation, being a source of economic loss and damaging wild populations. Understanding the variation in inflammation across strains is critical because the kidneys are the primary site of *T. bryosalmonae* infection in salmonids. This study investigates renal morphological differences between native Irish salmon and commercially bred Norwegian strains using noninvasive DICE-microCT soft tissue imaging. Norwegian salmon exhibit significantly larger kidneys than their Irish counterparts. These results indicate potential strain-specific morphological plasticity associated with infection that is possibly linked to genetic background or environmental adaptation. High-resolution 3D models of salmon kidneys will form the foundation for subsequent analyses to determine infection status and strain-based differences in PKD-induced inflammation.

A Comparison of Hydrofoil Structure and Thrust Production Patterns During Loggerhead and Leatherback Sea Turtle Swimming

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As hatchling sea turtles emerge from nests, they exhibit an innate hyperactive state: rapidly crawling to the water, followed

by almost continuous swimming for 24-48 h. This “frenzy” is dominated by powerstroking – characterized by bilateral “flapping” of hydrofoil-shaped flippers. Sea turtles continue using the powerstroke less vigorously in the open ocean. However, loggerheads (*Caretta caretta*) find refuge in floating mats of seaweed opportunistically feeding and hiding from predators, while leatherbacks (*Dermochelys coriacea*) prefer the open in search of gelatinous prey. We hypothesize this different life corresponds with species-specific morphometrics and kinematics of the flippers. To test these hypotheses, 31 loggerhead and 28 leatherback hatchlings were collected on the day of emergence, measured, and tethered in a seawater-filled tank to swim. Swimming video and force data were collected synchronously to measure thrust patterns in concert with flipper motions as hatchlings and after 4-16 weeks of growth. Corresponding morphometrics of mass, straight carapace length, flipper length, flipper surface area, and hydrofoil thickness were taken at both time points. Our results demonstrate that both species exhibit allometric growth between flipper and body length. Loggerheads have significantly smaller, stouter flippers and steeper peaks of thrust mainly in the downstroke. Leatherbacks have longer, thinner flippers and have wider peaks of thrust produced during the upstroke and downstroke. We propose how the flipper hydrofoil dynamics could explain these differences.

Macroevolutionary Role Reversals In the Earliest Radiation of Bony Fishes

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The origin of jaws is hypothesized to have fueled evolutionary radiation among vertebrates, contributing to their overwhelming success in the present day. Past work shows rapid early expansion of diversity in jaw structure, however, the evolutionary dynamics underlying this pattern are unclear and hindered by the lack of a comparative phylogenetic framework. Here, using a macroevolutionary approach, we explore the initial diversification of lower jaws using early bony fishes as a model, owing to their exceptionally well-preserved fossils which enable insights into functional and ecomorphological diversification. Using newly generated three-dimensional mandibular shape data from 86 species, we find evidence of adaptive radiation in jaws during the earliest interval of bony fish evolutionary history. These patterns are principally driven by early lungfishes and coelacanths, which display high rates of jaw diversification, rapid shifts into novel functional regions of trait space, as well as substantial innovation in jaw morphology and feeding ecology, standing in contrast to their “living fossil” descendants of today. Conversely, ray-finned fishes and tetrapodomorphs, morphologically diverse groups in the present day, show little indication of their future success, possessing slow rates of jaw evolution and low functional diversity. Overall, our findings provide insight into the evolutionary

dynamics associated with the origin of jaws and provides context for the role of jaws in vertebrate success.

Insights into the Effect of Industrialization on the Mandible from a Mouse Model and Archaeological Human Population

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In recent centuries, the human mandible has become narrower and smaller. This trend has been accompanied by misfits with the dentition. Cultural changes in diet texture and vitamin D level that influence jawbone growth likely affected these misfits. Here we quantify the effects of diet texture and vitamin D level on mandible growth using lab mouse and archaeological humans. In England, preindustrial (ca.1500-1700) people typically had sufficient vitamin D and ate harder diets, versus post-industrial people (ca.1850+) who often lacked sufficient vitamin D and ate softer diets. We measured mandibles from preindustrial (n=52) and postindustrial (n=54) non-adults from English skeletal collections. For the mouse experiment, C57BL/6 mice were raised on hard diets with normal vitamin D, or soft diets with either normal or no vitamin D. Adult mouse mandibles were μ CT-scanned, 3D-landmarked, and measured. Mice fed a hard/VitD diet had longer mandibles ($x=10.57 \pm 0.25$ mm, $p < 0.001$) than mice fed a soft/noVitD diet ($x=10.29 \pm 0.20$ mm). Human preindustrial ($x=7.6 \pm 0.33$ cm) non-adults had longer mandibles than postindustrial non-adults ($x=7.06 \pm 0.45$ cm, $p > 0.05$). Bicondylar breadth was wider in preindustrial non-adults ($x=11.77 \pm 0.56$ cm) versus postindustrial ($x=10.82 \pm 0.38$ cm, $p < 0.05$). Our results support that a hard diet and sufficient vitamin D facilitate greater mandibular growth in mice and humans. The cultural shift during industrialization likely influenced contemporary human mandible size, and misfits between jaws and teeth.

Elucidating the Consequences of Perturbations During Snake Slithering

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A key challenge during locomotion for most terrestrial animals is supporting body weight and controlling their inertia via contact with the substrate at several discrete points (e.g., feet). Snakes, however, have an elongate, limbless body plan that can maintain continuous contact with the substrate, and their locomotion is typically dominated by frictional rather than inertial forces. Coordinating body posture across hundreds of vertebrae to control the reaction forces across many push points is a significant challenge, yet the potential responses to perturbations during snake slithering remain untested. We examined the response to the sudden loss of contact, mirroring “tripping” tests in limbed animals. We recorded kinematics as snakes slithered through a rigid, flat substrate with equally spaced vertical pegs, a subset of which will break free when triggered. When contact is lost, a local area of the snake’s body

no longer has a peg to push against and continues to slide past the peg hole. We characterized the responses of snakes using slip angle (angle between velocity and body tangent vectors) and body slide distance. Preliminary analysis suggests that disturbance effects propagate posteriorly. Insights into these perturbation responses have implications for the potential differences in selective pressures on locomotor control in limbed versus limbless taxa.

A Tale of Two Patellae: Lineage-Specific Mechanisms for the Development of the Patellar Sesamoid

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The patella is a large sesamoid bone in the knee of several different lineages of vertebrates. Sesamoids are skeletal elements located in close association with the connective tissue of joints that influence (and are influenced by) the forces transmitted through them. A recent characterization of the mammalian patella reveals that it develops from a projection of the cartilaginous anlage of the femur consisting of progenitors expressing the Sox9 and Scx transcription factors. Eventually, the patella individualizes through the formation of a joint in a process dependent on embryonic muscle activity. However, the development of the analogous patella in other tetrapods is yet to be described. Here, we describe the development of the patella of the domestic chicken, as a proxy for Aves, as it compares to its mammalian counterpart, noting key differences in tissular origins, gene expression patterns, and influence of mechanical signals. Also, we place this developmental mechanism in context with the morphological disparity of the patella in some extant and extinct birds. This analysis highlights the relevance of similar anatomical environments on the convergent evolution of novel skeletal structures, while developmental mechanisms unique to each lineage constrain the resulting morphological diversity. Furthermore, this study reveals new questions and challenges ahead to fully reconstruct the evolutionary history of the patellar sesamoid.

Life Upstream: Uncovering the Palaeoecology of the Australian Lake Dolphin

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Australia's arid interior was once home to a much more diverse range of environments, including several large lakes from which fossils have been discovered. Here, we examine the palaeoecology of a fossil dolphin from the Upper Oligocene (27-23 MYA) Namba Formation of South Australia. This new species is potentially the first known dolphin to inhabit a lake and the earliest known appearance of an obligate freshwater species. To unravel its palaeoecology, we conducted shape, convergence and trace element analyses. 56 cetacean earbones from 53

species were examined for comparative morphological analysis. The results showed similarities in echolocation abilities to smaller extant dolphins and two closely related species, suggesting that it used echolocation to navigate turbid waters. 3D geometric morphometrics of the cochlea revealed that it has evolved convergently with some species of 'river' dolphins, leading us to hypothesise this morphology was a trait that facilitated transitioning from marine to freshwater environments. Analysis of trace elements within the fossil, including Barium and Strontium, confirms a freshwater environment, and places the dolphin in the lake's highest trophic level. Overall, our results display this dolphin species invaded freshwater environments earlier than previously discovered and is the first known in a lacustrine setting.

Unraveling Eutherian and Metatherian Divergence Through Dental Evolution

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The emergence of therian mammals stands as one of the most significant transitions in vertebrate evolution, marked by profound evolutionary innovations, notably the conserved dental formulae of postcanines in eutherians (placentals and kin) and metatherians (marsupials and kin). However, elucidating evolutionary paths of these dental transformations has posed enduring challenges. We reconstruct ancestral dental formulae at key nodes of Theria, Eutheria, and Metatheria under an updated phylogenetic framework. Our results reveal distinction among three dental formulae at key nodes of Eutheria, Metatheria, and Theria. We propose an innovative Premolar-Molar Independence model, emphasizing independent homology in premolar and molar classes, to interpret dental transformations in early therians based on a synthesis of paleontological and developmental criteria. It reveals that eutherians lost the distal molar, while metatherians underwent premolar loss, when diverging from the therian common ancestor characterized by five premolars and four molars. Furthermore, the subsequent evolutionary loss of the middle premolar exhibits convergence in eutherians and metatherians. The pattern of dental transformations suggests distinct evolutionary experiments over deep time and conserved developmental controlling mechanisms, ultimately shaping phenotypic diversity.

Effects of Vertebral Patterning on Visceral Topography

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Highly elongate animals are often studied to understand the dramatic changes to their musculoskeletal systems including increasing the number of vertebrae, lengthening the vertebral centra, and/or increasing the length of the head. In this study, we comparatively document the effect of body elongation on patterning of the gastrointestinal tract in different fish lineages

as well as a member of Dipnoi. We compare the patterning of the abdominal cavity in *Lepidosiren paradoxa* (South American lungfish), *Anguilla rostrata* (American eel), *Monopterus albus* (Asian swamp eel), with previous studies that described the patterning of members within the Polypteriformes and Muraenidae. This grouping of species allowed us to examine the effect of differential changes to the vertebral column on visceral topography to see whether lineages that are known to elongate via a region-specific increase in vertebrae have similar changes in gastrointestinal patterning. We measured the anterior and posterior position of the abdominal organs. We then cleared and stained each specimen so that we could determine the specific vertebral positioning of each organ. We found that while the overall anteroposterior patterning of the organs stayed consistent, the specific vertebral position and vertebral span of the organs differed across lineages. This study expands our understanding of the anteroposterior patterning of organ systems that accompany body shape changes in vertebrates.

Large Scale Mouse Mutagenesis Reveals High Developmental Plasticity and Modularity in the Mammal Sternum

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The mammalian ribcage is vital in supporting ventilation, locomotion and stability. Despite this little is known about genetic underpinnings of variation in the ribcage, nor its integration with other body systems. This study asks what genes are driving morphological variation and how they correlate with other anatomical systems using the International Mouse Phenotyping Consortium (IMPC). Of 3633 mutant knock-out mice phenotyped by the IMPC, 3.3% produced an abnormal thoracic cage morphology. The majority of these are associated with abnormal sternum morphology (68%) while the remaining genes are associated with abnormal rib (13%) and vertebrae (3%) morphology. Changes to the ribs are strongly pleiotropic, usually accompanied by changes to the whole skeletal system, whereas sternal changes tend to appear in isolation. Sternal and rib phenotypes were never associated with one another, suggesting that morphological variation is independently patterned. While the IMPC provides enormous opportunities for understanding the developmental basis of phenotypes, it also has challenges. 28% of the thoracic phenotypes did not have x-ray data of high enough quality to classify the morphology as so were excluded. Despite this, it has proved a valuable resource for identifying candidate genes that may be relevant for understanding evolutionary variation in ribcages across mammals.

Quantitative Analysis of Flight Capacity in a Paleocene Stem Palaeognath

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Lithornithids are an assemblage of Paleogene fossil birds thought to represent stem-group members of Palaeognathae. Among extant palaeognaths, which include flightless ratites such as ostriches, only tinamous (Tinamidae) are capable of flight, though they are reluctant fliers, employing anaerobic burst flight over relatively short distances to escape predators. Despite their limited dispersal capabilities, the phylogenetic interrelationships and geographic distributions of palaeognaths imply that their early relatives may have been capable dispersers, with extant and fossil flightless palaeognaths distributed on landmasses separated by ocean basins. Here, we quantitatively investigate the flight capabilities and ecology of the lithornithid *Lithornis promiscuus* using geometric morphometrics, and reject the hypothesis that lithornithids would have been reliant on tinamou-like burst flight. Instead, our results are consistent with aerobic flight styles such as continuous flapping. We show that the lithornithid sternum is geometrically dissimilar to that of tinamous and instead resembles those of several distantly related taxa with notable dispersal capabilities, including parrots (Psittaciformes) and pelecaniform waterbirds. Our results support the hypothesis that at least some stem palaeognaths were capable of long-distance flight, helping to clarify the origins of the geographic distribution of extant Palaeognathae.

Evolution Across Space and Time: Late Quaternary Microevolution of Endemic Mediterranean Island Reptiles In Response to Environmental and Anthropogenic Change

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What drives shape variation across time and geography remains an important question for evolutionary morphologists. Here, we use the Ibiza wall lizard, *Podarcis pityusensis*, which is found on the Balearic islands of Eivissa and Formentera and surrounding islets, as a system to link micro- and macroevolutionary trajectories due to the high-resolution fossil record provided by the Eivissa cave site Es Pouàs. The 30,000 year time period spanned by the cave fossils includes major environmental changes, including the end of the glacial period and human arrival to the island. We quantified shape using 3D geometric morphometrics of modern and fossil mandibles and Orientation Patch Count (OPC) of teeth. Form was linked to function via in-vivo bite force measurements of modern populations and Finite Element Analysis of fossil shapes. To analyze form-function-environment relationships, we included modern diet and life history data which was linked to isotopic data from fossil levels. For the fossil lizards, our results suggest that shifting climate has a more significant effect on shape and biomechanics than the arrival of humans, whereas in the modern individuals, we find diet and population dynamics both have a strong impact on the phenotype. Overall, the precise drivers of phenotype vary according to the level of evolutionary isolation investigated,

suggesting an incongruence between micro- and macroevolutionary levels.

Fossilised Skin of Dinosaurs Reveals the Evolutionary Steps to Avian Skin

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The evolutionary transition from scales to feathers is one of the most profound events in vertebrate evolution. Fossilised feathers have provided insights into the evolution of feather structures, but little is known about the underlying skin. Here we present fossil evidence, from five dinosaurs, for the evolution of skin structures in the scale-feather transition. Patches of mineralised skin, preserving epidermal layers, corneocytes and melanosomes, were identified in non-feathered regions of the ornithischian *Psittacosaurus* and feathered regions of the tyrannosauroid *Dilong*, non-avian maniraptoran *Beipiaosaurus*, paravian *Anchiornis* and basal bird *Confuciusornis*. The fossil skin of *Psittacosaurus* showed evidence for scales, corneocytes with fused cell boundaries and rich in corneous beta proteins, and melanin pigmentation in the epidermis; these features are consistent with retention of plesiomorphic reptile-type skin in non-feathered regions. The fossil skin of *Dilong* and *Beipiaosaurus*, however, showed a mixture of reptilian and avian features. Their skin lacked scales and had corneocytes with distinct cell boundaries, as in the feathered skin of birds; abundant melanosomes were present in the epidermis, a condition known in reptiles but not in *Anchiornis*, *Confuciusornis* or extant birds. Epidermal melanin pigmentation likely represents an ancestral condition retained in *Dilong* and *Beipiaosaurus* and may have provided critical UV protection complementary to that of early feathers. Collectively, our findings indicate that the avian skin evolved from step-wise modifications to the ancestral, reptile-type skin.

The Archosaur Mandible as a Potential Pressure Detector

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The lower jaw of Archosaurs typically includes a mandibular fossa. The lateral border of the mandibular fossa often includes the external mandibular fenestra, while the medial border includes the larger, and less defined, internal mandibular fenestra. Using a combination of anatomical and experimental techniques, we explored the mandibular fossa of one Archosaur, the American alligator (*Alligator mississippiensis*). The caudal portion of the mandibular fossa includes a discrete anatomical compartment, formed, in part, by the intramandibularis muscle. This mandibular compartment is coupled to the articular diverticulum, and, through the siphonum, the complex of paratympanic diverticula. Air injected into the mandibular compartment results in inflation

of the paratympanic diverticula. Using a vibrating probe as a stimulus and a laser vibrometer to measure displacement, we demonstrated functional coupling between the scalation over the external mandibular fenestra and the tympanum. The coupling between the mandibular fossa and the tympanum was consistently observed in hatchling and yearling alligators, but was not found in sub-adult specimens; presumably this reflects allometric changes in the paratympanic diverticula. This study demonstrated a mechanical coupling between the scalation over the external mandibular fenestra and the tympanum; but did not examine corresponding neural activation of the paratympanic organ or cochlea. Given the marked morphological variation in this system among Archosaurs, it seems likely that this mechanical coupling serves a sensory function in some taxa.

The Systematics of Marine Crocodylomorphs (Thalattosuchia)

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Thalattosuchian crocodylomorphs were a group of extinct crocodile-relatives known from the Jurassic and Cretaceous Periods. Within Thalattosuchia, the subclade Metriorhynchidae made the transition from land-to-sea, evolving flipper-like forelimbs and a hypocercal tail. Thalattosuchians are one of the most intensively studied crocodylomorph clades, with their fossils first described during the 18th Century, multiple species named before the term dinosaur was coined, and their anatomy and relationships were discussed by noted 19th and 20th Century workers, including Huxley, Owen, Cuvier, Haeckel, and Nopsca. Alas, our understanding of where in Crocodylomorpha thalattosuchians belong has proven to be elusive. There are four positional hypotheses, ranging from outside of Crocodyliformes, to being a member of the neosuchian 'longirostrine' clade. Different phylogenetic datasets recover Thalattosuchia in one of these four positions. We analysed our revised data set under equal weights and extended implied weights, and ran topological constraint analyses to enforce the differing hypotheses. When unconstrained, we recovered Thalattosuchia outside of Metasuchia, but within Crocodyliformes. However, we are unable to statistically differentiate between the four positional hypotheses, although the two hypotheses that posit a non-neosuchian origin have the best stratigraphic congruence. It is our contention that the issues plaguing crocodylomorph datasets are due to missing data (from the Late Triassic-Early Jurassic), which leads to too much noise in our analyses. Only new discoveries will be able to overcome these issues.

A Universal Power Law for Modeling Pterosaur Rostra

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Pterosaurs were a diverse clade of winged reptiles that lived during the Mesozoic Era, occupying various ecological niches

and exhibiting a wide range of cranial morphologies—from toothed rostra (snouts) to edentulous rostra (beaks). While some studies have examined the taxonomic and sexual significance of rostrum shape, the developmental mechanisms underlying these cranial structures remain poorly understood. The power cascade is a universal growth law that describes the log-log linear relationship between the radius of the rostrum with its length. We measured 26 specimens across 8 clades, specifically focusing on the premaxilla and maxilla, and found that 62% followed the power cascade model, including all edentulous taxa. The morphospace defined by the power cascade demonstrates that, although pterosaurs possess a range of cranial morphologies, the majority of species examined follow the power cascade growth model. Taxa which do not conform to the power cascade typically possess premaxillary crests, secondary structures that usually develop later in ontogeny. While the power cascade is not unbreakable, these findings suggest that underlying developmental mechanisms shape pterosaur rostra across their evolutionary history.

3D Architecture and Biomechanics of Snake Palatal and Pterygoideus Musculature

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Cranial kinesis plays an important role in tetrapod feeding mechanics and is especially extensive in snakes. Snakes use a complex “walk” of the palate and mandible to move over their prey during swallowing, and it is hypothesized that this behavior played an integral role in snake diversification. Rostrocaudal movement of the palate is a key element of this “walk” that is powered by a series of small muscles that are difficult to quantify via traditional dissection. To study the evolution and mechanics of the muscles responsible for kinesis of the palate across snakes, we used DiceCT and 3D fascicle tracking to model the architecture of the palatal muscles across six species. Our current sample consists of 5 muscles known to be responsible for palatal movement (mPPT, mLPT, mRPT, mPT, mPTa) in 5 snake species and a lizard outgroup. Fiber models produced via 3D fiber tracking algorithms were used to calculate quantitative data on muscle fascicle orientations. Muscle maps of attachment sites in DiceCT data were used to calculate individual force orientations for each muscle. We found that both the fascicle and force orientations of the dorsal constrictor muscles shift rostrocaudally as the palate becomes more specialized for swallowing, while the pterygoideus musculature is more conserved across snakes. Future work will expand the sample to include a synoptic breadth of snake diversity.

Identity and Homology of the Foramina and Apertures of the Erethizontidae Alisphenoid Bone (Mammalia: Rodentia)

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Cranial foramina and apertures are correlated with the presence or absence of vessels, nerves and muscles and the course of vascularization systems. However, few studies in Caviomorpha (Rodentia), particularly Erethizontidae, establish homologies between cranial foramina or their topographical correspondences. We compared the foramina in the alisphenoid bone of species representing all living genera of Erethizontidae. Forty-six skulls of seven taxa were qualitatively analyzed. The alisphenoid bone of Erethizontidae usually presents three large apertures: the buccinator-masticatory foramen (bmf), foramen ovale (fo), and alisphenoid canal (asc). An accessory foramen ovale (foa) may also be present, depending on the degree of ossification of the alisphenoid. The bmf may be divided into independent masticator and buccinator foramina, a state most commonly observed in *Chaetomys*. Despite their poorly ossified alisphenoid bones, members of *Coendou* (*Sphiggurus*) often show a better delimited asc. The foramina appear to follow the same topography in all specimens, with the bmf anterodorsal, the asc anteroventral, and the fo and foa posteroventral. In addition, many specimens present small apertures that may function as accessory passages or be related to the vascularization of the alisphenoid bone itself. Some of the variation found may be related to different functionalities, especially when associated with other orbitotemporal elements. Increasing the sample size of the species and describing the other orbitotemporal elements may contribute to shedding light on cranial evolution in Erethizontidae.

Scapula Shape in Neotropical Porcupines (Mammalia: Rodentia: Erethizontidae)

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New World porcupines (Erethizontidae) are arboreal or semi-arboreal slow-moving rodents inhabiting South, Central and North America. Although all species show arboreal and semi-arboreal behavior, there is considerable variation in size and locomotory habits among erethizontid species, which may be reflected in the shape and size variation of musculoskeletal elements of the fore- and hindlimb. We evaluated shape variation in scapulae of erethizontids using geometric morphometrics. Thirteen landmarks were selected in scapulae of representatives of four neotropical erethizontid species. A principal components analysis (PCA) of Procrustes-aligned coordinates resulted in three components representing ~60% of the total variance in the sample. There is significant overlap between the species in our sample along PC1, but *Coendou insidiosus* tend to have higher values along this axis, which is likely due to its flatter acromion, contrasting to *Co. longicaudatus*'s laterally projecting coracoid process in relation to its metacromion; species in the subgenus *Co. (Sphiggurus)* have on average greater values for PC1 than those within the subgenus *Co. (Coendou)*. Along PC2 and PC3, all species of *Coendou* overlap, but *Chaetomys subspinosus* has a higher value on average than any other taxon, likely due to its narrower scapulae with more curved posterior margins, which may be related to its more lethargic behavior. Next steps include integrating phylogenetic information

into analysis, performing morphofunctional analyses, and increasing taxonomic sampling to include all erethizontid species.

Insights into the Ontogeny of Peirosauridae (Notosuchia, Crocodylomorpha) Through Neuroanatomical and Paleohistological Study of a New Juvenile Specimen

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Disentangling morphological variation along an ontogenetic series from interspecific differences is particularly challenging in vertebrate paleontology. Few depositional settings allow for the preservation of such different semaphoronts. One such example is the Adamantina Formation (Bauru Group, Upper Cretaceous), Brazil, known worldwide for yielding semi-complete skeletons of notosuchian crocodylomorphs, including juveniles. Here, we use a multi-pronged approach to study a new juvenile peirosaurid from Adamantina Formation deposits, which consists of a complete skull, cervical and dorsal vertebrae, pectoral girdles and articulated forelimbs with humeri, ulnae and radii, as well as dorsal osteoderms. Our investigation includes both paleoneurological and paleohistological techniques to evaluate sensorial acuity, chronological age and growth strategies through cortex microtexture. Computed tomography data revealed a sigmoidal endocast with an anteroposteriorly short olfactory tract and a marked lateromedially expansion of the bulbs, representing 36% of total endocast length, and 71% of cerebrum width, respectively. Likewise, the cerebral hemispheres are distinctly rounded and transversely developed, similar to the closely related species *Uberabasuchus*, but departing from itasuchids like *Rukwasuchus*. Finally, preliminary histological work supports the specimen as a young semaphoront, far from skeletal or sexual maturity, with its right ulnar diaphysis, for instance, being mostly composed of rapidly accreting woven-fibered bone with reticular vascularization, lacking both endosteal lamellae and an external fundamental system (EFS).

Lightning Talks

Serpentine Segmentation: Regionalization within the Elapid Vertebral Column

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Snakes are a striking example of morphological evolution, evolving limb loss and extremely elongated bodies. While this body plan was once thought to be structurally uniform, recent

morphometric and developmental studies suggest that snakes may retain internal vertebral regionalization similar to other vertebrates. This presentation will discuss my study on whether regionalization exists within the vertebral columns of elapid snakes. By utilizing 3D geometric morphometrics, I aim to find consistent, discrete regions within elapid vertebral columns.

Unveiling the Structure of a Key Autapomorphy: Histology of the Hypertrophied Antebrachial Tubercle in *Pseudopaludicola* (Anura)

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The hypertrophied antebrachial tubercle is the most easily recognizable autapomorphy of the anuran genus *Pseudopaludicola*, setting it apart from all other Leptodactylidae. Here, we investigated the structural morphology of this tubercle in *Pseudopaludicola mystacalis* through histological and stereomicroscopic analyses of tubercle skin from 12 males and 8 females. Dissected skin was dehydrated, embedded in *Leica historesin*, serially sectioned at 3 µm, stained with toluidine blue and fuchsin, and analyzed via photomicroscopy. We provide the first histological description of this structure, identifying a high concentration of large glands within the dermis, with variable size and density in both sexes. Histological sections revealed a stratum corneum, a 3–4-layered epidermis, large multicellular glands occupying most of the spongy dermis, dense vascularization, and a calcified dermal layer separating spongy and compact strata. Two main gland types have been described: mucous glands are acinar, with basal nuclei and distinct cell regions; granular (poison) glands are syncytial, lack a lumen, and are characterized by peripheral nuclei and cytoplasm rich in secretory granules. The tubercle skin was thicker (up to 118 µm) and more vascularized than non-tubercle forearm skin (approx. 52 µm). These findings challenge the use of the term “tubercle” for this structure, as it closely resembles a macrogland. Further histochemical analyses will determine the nature of the secretions, seeking the possible differentiation of the tubercular glands as mixed and/or sexually dimorphic glands.

Deep Dives into Dental Crypts: Molecular and Morphological Conservation of the Primate Tooth-Bone Interface

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To understand the evolutionary and developmental (evo-devo) processes that shape the human dentition, we are studying how the teeth and jawbone (tooth-bone interface, TBI) develop in non-human primates and fossil hominins. Our comparative study explored primate TBI development using two methods. First, we analyzed CT scans (22–59 µm resolution) of fossil jaw fragments from *Homo spp.* (n=3; 1.9–0.2 mya) and *Paranthropus robustus* (n=6; 2.27–0.87 mya) to create 3D models of bony crypts and their

encased teeth, assess developmental stages, and describe crypt form and position. Second, we used immunohistochemistry on perinatal jaw sections from five primate species ($n=1$ each) to examine RANK/RANKL/OPG protein expression in developing tooth organs, follicles, and surrounding TBI tissues. We found that crypts were more spacious and spherical before crown completion, then became tighter and more tooth-shaped as roots developed. Crypts were interconnected regardless of tooth type, and gubernacular canals persisted throughout development. RANK, RANKL, and OPG were expressed in odontoblasts, ameloblasts, follicle cells, osteoblasts, and osteoclasts across all species. These findings suggest that tooth crypt formation, migration, and TBI protein expression are conserved across primates and not specific to tooth class, jaw type, or species. This interdisciplinary evo-devo anthropology approach reveals key insights into shared craniodental development processes in living and extinct primates.

Lattice-Like Trabecular Microanatomy of the Basihyal Facilitates Extreme Vocalizations In *Alouatta seniculus* (Venezuelan Red Howler Monkey)

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Loud vocalizations are widespread amongst Old and New World primates. The genus *Alouatta* produces the deepest vocalizations, reaching 140 decibels, due to the unique morphology of its hyoid. The basihyal, a U-shaped bone of the hyoid apparatus that supports tongue musculature, is hypertrophied and pneumatized by the laryngeal air sac, forming a bulla chamber. The well-developed laryngeal air sac of *Alouatta* reverberates within this space, using the bulla as a resonance chamber for sound production. Although the function of these specialized hyoids are known, the microanatomical adaptations enabling such extreme vocalizations are unclear. This study uses computed tomography to investigate the microstructure of the basihyal of *Alouatta seniculus*, which exhibits one of the most derived hyoid shapes in the genus. We find that the bulla is rimmed by a lattice of hexagonal trabeculae, 2.64 times thicker than the surrounding bone. We hypothesize that these trabeculae provide stability by evenly distributing weight across tessellating sides, supporting the bulla's integrity. This interlocking pattern efficiently fills large areas with the fewest number of shapes, allowing the bulla to grow in size without compromising the paper-thin surrounding bone during vocalization. This unique hexagonal structure in postcranial bone, only shared with birds and non-avian dinosaurs, enhances our understanding of the mechanical limitations of vertebrate bone architecture.

Locomotor Diversity in Early Mammals: Evaluating Postcranial Evidence for Arboreality In the Mesozoic Era

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Mammals and their extinct relatives exhibit a wide range of locomotor modes, including arboreality, which independently evolved many times throughout mammalian history. However, there remains uncertainty about the prevalence and timing of these evolutionary shifts to climbing behavior. This uncertainty is due in part to limited fossil postcranial data for early mammals, making it challenging to infer locomotor modes. Interpretations of recent fossil discoveries suggest that arboreality may have been the ancestral trait of major clades such as therians (placentals and marsupials). We test this hypothesis using anatomical features that are closely tied to locomotor mode in modern mammals. To this end, we collected linear measurements of appendicular skeletal elements for ~40 species of Mesozoic mammals. To infer locomotor modes of fossil taxa, we employ regression models derived from a large comparative data set of linear measurements taken from the postcranial skeletons of 236 extant mammal species. The models incorporate measurements that are strong predictors of tree-dwelling versus ground-dwelling behavior in extant mammals. We found less evidence than anticipated for arboreality across many early mammalian groups, with a notable exception being Jurassic gliding haramiyidans. These findings challenge recent conclusions that arboreality was the ancestral trait among many early mammal groups. By testing locomotor patterns across a broad range of taxa, our findings provide an alternate perspective on the evolutionary pathways that shaped early mammalian diversity.

Meristic Co-Evolution and Genomic Co-Localization of Lateral Line Scales and Vertebrae in Central American Cichlid Fishes

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Meristic traits, such as vertebral and lateral line scale counts, are fundamental to fish morphology and taxonomy, often exhibiting evolutionary plasticity. While their developmental origins are linked, the extent of their co-evolution and underlying genetic architecture remain largely uncharacterized across diverse lineages. Here, we investigate the co-evolutionary patterns and genomic basis of vertebral number and lateral line scale count in Central American cichlid fishes, a group renowned for rapid phenotypic diversification. We utilized a comprehensive phylogenetic comparative approach to assess trait covariance across multiple species, revealing significant and consistent positive correlations between these two meristic characters, suggesting a strong co-evolutionary relationship. Furthermore, through quantitative trait loci (QTL) mapping in interspecific crosses, we identified genomic regions where loci influencing vertebral number and lateral line scale count co-localize. These regions likely contain genes or regulatory elements that pleiotropically affect the development of both structures, or tightly linked genes under shared selective pressures. Our findings suggest that the integration of vertebral and

lateral line scale development contributes to their coordinated evolution, potentially facilitating adaptive diversification in response to ecological pressures. This study provides novel insights into the genetic architecture of meristic variation and highlights the importance of genomic integration in shaping phenotypic evolution in vertebrates, offering a deeper understanding of the processes driving cichlid diversification.

Which Came First: A Lagomorph or its Foot?

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Foot structure in lagomorphs, characterized by the presence of the fibular facet at the calcaneal eminence that allows for a direct connection with the fibula, has been regarded as one of the lagomorph characteristics, shared by all known members of 'true' Lagomorpha, although not by all Duplicidentata. This feature is also present in one of the archaic groups of Euarchontoglires, Pseudictopidae, and in the so-called 'gliriform mammals', an enigmatic Paleogene grouping. The calcaneal structure in lagomorphs is convergent on the calcaneus of ungulates. The latter also have the calcaneo-fibular facet, although its exact shape and size differ. The fibular facet of the calcaneus is absent in rodents, with the exception of *Trogotherium*, an extinct Eurasian beaver. However, it is known in the Eocene simplicitate *Rhombomylus*. The earliest known calcaneus from the middle Paleocene of Qianshan (China) attributed to *Heomys* or *Mimotona* (Glires) also has the calcaneo-fibular facet. Here we review the known fossil material of early lagomorph ankle bones and the calcanei of pseudictopids, including new material from the Eocene of China. The similarity of the ankle bone structure between lagomorphs (especially the earlier forms) and pseudictopids indicates the existence of a lagomorph-like grade of basal Euarchontoglires adapted to quick and agile locomotion and thus, favoring a strengthened ankle joint structure. Phylogenetically, the lagomorph foot appears to precede lagomorphs themselves, being a useful structural adaptation.

Hanging in There: An Updated Description of the Two-Toed Sloth Hind Limb

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Anatomical description of tree sloths has largely centered on the three-toed sloths, *Bradypus* spp., leaving a gap in the literature regarding the morphology of their relatives, the two-toed sloths in the genus *Choloepus*. Modern comparative descriptions have focused on the forelimb, with comparisons of the hind limb using data from the 19th century. Our study provides an update to the literature with respect to the hind limb, confirming and updating historical descriptions and providing new photographs and drawings. The specimen of *Choloepus* sp. was fixed in formalin and had been frozen before dissection. The thigh and hip region have large, thick muscles with disproportionate mass in the flexors compared to the extensors. This reflects a suspensory lifestyle; the flexors, keeping the limb bent, must exert enough isometric force to support the

weight of the hanging body. The muscle fibers are long and parallel. As in *Bradypus*, the gluteofemoralis appears to also be absent in *Choloepus*. The pectineus is present in this specimen, although it has been reported to be variably present. The flexor digitorum superficialis (*m. plantaris*) and the lateral head of the gastrocnemius are difficult to differentiate. Further dissection is required to determine whether they are fused in this specimen. This discovery further demonstrates variability in musculoskeletal anatomy within, and among, tree sloth species.

Distribution of Collagen I and III In the Tongue of the Captive South African Painted Dog (*Lycaon pictus pictus*)

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The African painted dog (*Lycaon pictus pictus*) belongs to a relic canid lineage, which inhabits the southern Sahara desert. The aim of this study was the analysis of the distribution of collagen I and III in the tongue of five adult *Lycaon pictus* females (each with a mean weight of around 20-25 kg). All animals were obtained from the Wrocław Zoological Garden. Samples of mechanical and gustatory lingual papillae, lingual glands and lyssa of the tongue were collected. The sections were fixed in 4% paraformaldehyde in phosphate-buffered saline (PBS) pH7.4 (Chempur, Poland). The staining protocol comprised picrosirius red stain for the differentiation of collagen type I and collagen type III fibers. The samples were observed with a Delta Optical microscope (Nowe Osiny, Poland) under polarized light. Polarized light microscopy found collagen I fibers (yellow/orange) to predominate over collagen III fibers (green color) in the connective tissue core and lamina propria of the mechanical lingual papillae as well as in all gustatory lingual papillae (fungiform, vallate and foliate papillae). The dominance of the collagen I in comparison to the collagen III were found also within lingual gland tissue, as well as in the lyssa of the tongue.

Morphology of the Zygomatic Gland of the Eurasian Wolf, *Canis lupus lupus* (Carnivora: Canidae)

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The goal of this study was the macroscopic and microscopic description of the zygomatic gland in 12 adult Eurasian wolves (*Canis lupus lupus*) (captive and wild animals). Samples of the zygomatic gland were collected for histological and histochemical analyses. Azan trichrome, mucicarmine, PAS, AB pH 1.0, AB pH 2.5; AB pH 2.5/PAS, and HDI stainings were used in the study. The oval zygomatic gland is located in the anterior part of the pterygopalatine fossa and is surrounded by the extraperiorbital fat body. The structure of the gland is irregular consisting of a slightly rounded cluster of small packets surrounded by a thick fibrous capsule. The zygomatic gland has 1 large major duct and 3 to 4 minor ducts that open into the oral

vestibule at the level of the last upper molar (M3). In the investigated captive wolves, thin and thick septa divide the gland into numerous large lobes and several small lobes, while in the free-ranging animals, the intralobar septa are thin, thus the larger lobes were detected. Mucicarmine stain revealed a strong reaction in mucous cells in captive wolves, but only a medium reaction in wild animals. The results of our histochemical study confirmed that the zygomatic gland has a complex branched tubular structure and produces mucous secretion, both in captive and free-ranging wolves.

Morphological Insights into Feeding Kinematics across Grazing Species of Waterfall-Climbing Gobiid Fishes

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Sicydiine gobies exhibit an amphidromous lifestyle, characterized by an oceanic larval phase that precedes migration to in-stream adult habitats. Many of these species graze on diatomaceous algae in freshwater streams. Grazing involves the extension and retraction of the upper jaw to scrape along rock surfaces, dislodging diatoms. However, grazing sicydiine species show divergent levels of upper jaw kinesis. The West African taxa *Sicydium brevifile* and *Sicydium bustimante*, respectively, show the greatest and least premaxillary protrusion during feeding cycles, with Hawaiian *Sicyopterus stimpsoni* and Caribbean *Sicydium punctatum* as intermediates. To understand the morphological underpinnings of these kinematic differences, we micro-CT scanned one specimen from each of the four taxa, then digitally segmented and isolated the functionally relevant bones of the upper jaw. We identified numerous morphological differences between taxa with potential implications for grazing performance. Notably, a posteriorly directed hook-like feature on the ascending process of the premaxilla is absent from *S. brevifile*, the species with the greatest premaxillary protrusion. The presence of this feature may limit the functional area of the ascending process, thus reducing the protrusible distance of the premaxilla during feeding. These morphological differences suggest a trade-off between the stability and mobility of the upper jaw in grazing gobiid fishes. Further studies will examine the implications of upper jaw mobility on waterfall climbing ability in these species.

Skeletal Elements of the Largest Multituberculate Mammal *Taeniolabis* from the Paleocene of North America

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The taxonomically rich and near globally distributed multituberculates are one of the most successful clades of early mammals, originating in the Middle Jurassic and surviving the Cretaceous-Paleogene extinction. Some of the late multituberculates reached large body sizes. Foremost, *Taeniolabis taoensis*, with an estimated body size of up to 40 kg, is the largest

multituberculate and in fact the largest non-therian fossil mammal. *Taeniolabis* is well known from craniodental material from the early Paleocene of North America, but the few postcranial elements referred to the genus have been questioned. We reviewed the scarce record of *Taeniolabis* and added new specimens from the San Juan Basin recently discovered in museum collections. The new elements, representing the ulna, radius, femur, and calcaneus, were found in the same strata as craniodental remains of *Taeniolabis* and share morphological features identified as unique or common to multituberculates (i.e., distinct femoral neck, greater trochanter extending proximally to femoral head, posteriorly protruding lesser trochanter, offset calcaneal peroneal tubercle separated by deep peroneal groove). The elements are larger and more robust than those of other multituberculates, not unexpectedly considering the heavily constructed skull of *T. taoensis*. *Taeniolabis* may have occupied a unique ecological niche in the early Paleocene, as a relatively large-bodied, ground-dwelling mammal, which could have implications for understanding the evolutionary pathways of multituberculates that survived and evolved after the end-Cretaceous mass extinction.

Variation in Teeth and Dental Formula in Felids (Mammalia: Felidae), with Developmental and Evolutionary Implications

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Felids, at least some species within Felidae, are known to take reduction in number of teeth to an extreme among mammalian carnivores. Little to no work has been done understanding inter- and intraspecific variation of the upper second premolars among non-Lynx felids. Here, 33 of the approximately 40 species of modern cats were studied to determine inter- and intraspecific variation. In addition to P2, variation was also found in the presence/absence of M1 and the number of incisors. Within subfamilies (Felinae and Pantherinae), felines show more variation in the presence/absence of P2, but pantherines show more variation in M1. Loss of some incisors (usually loss of 1 or 2) was present among felines, but not among pantherines. Among felid lineages, P2 variation varied; commonest in the *Lynx* lineage, followed by the *Caracal* lineage. M1 variation was highest in the *Panthera* lineage. Some of this variation may be due to lack of a tooth germ in the lamina, damage/resorption of a tooth germ, fusion to a neighboring germ, and/or from retention of the eruption process of a completely formed tooth, or even ancestry, as there is also the possibility of linkages between phenotypically active and inactive traits. Inactive traits may become phenotypically active on occasion, affecting their frequencies among taxa. Higher frequencies may provide clues to the possible evolutionary loss of these teeth among non-Lynx felids.

Burrowing Lifestyle in Snakes: Implications on Braincase Morphology

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Snakes are found in a wide variety of environments to which they have adapted and exhibit a range of morphological adaptations. The emergence of a burrowing lifestyle represents a major shift in the evolution of squamates, resulting in morphological convergence due to the physical constraints of the medium. As snakes use their heads to dig, a burrowing life-style is expected to impact the skull. The braincase is involved in the transmission of the force to penetrate the substrate but on the other hand, it houses the brain which needs to be protected from the compressive forces experienced during burrowing. Thus, it can be hypothesized that its shape varies depending on the force exerted during digging and the type of substrate. Here we explore the relationship between the maximal burrowing force measured using force plates and the shape of the braincase in snakes. The sample consists of 31 species, including both scolecophidians and alethinophidians. We used 3D geometric morphometrics to quantify variation in braincase shape and to test whether species using different substrates differ in shape. Next, we test for covariation between the shape of the braincase and the maximal forces exerted during burrowing. Our results show that the shape differs between substrates; the braincase of aquatic species is different from that of others, but we found no covariation between peak burrowing.

What is the Best Staining Strategy to Highlight the Cartilaginous Epiphyses in Modern Archosaurs?

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Limb bones consist of an ossified shaft (including the diaphysis and metaphyses) and of two extremities, the epiphyses. Since morphology of limb elements is tightly related to their function, one can infer some aspects of joint and limb function in extinct taxa with the shape of their fossilised bone remains. However, while epiphyses are ossified in mammals and lepidosaurs, they remain cartilaginous in other tetrapods, including archosaurs, and are almost always lost during fossilisation, impacting estimations of their locomotor capabilities. A possible workaround would be to reconstruct the lost cartilaginous part of limb bone epiphyses to better constrain estimates of joint morphology, relying on extant phylogenetic bracketing. However, shape diversity of epiphyses in extant archosaurs remains understudied, probably because of the poor preservation of cartilage on dry skeletons, and because this cartilage contrasts poorly in microtomographic scans. We explored which contrast-enhancing protocol could be optimal to highlight cartilaginous epiphyses in modern archosaur limb bones. We tested the performance of iodine, phosphotungstic acid and ruthenium red as potential contrast-enhancing candidates by scanning a set of dissected chicken femora before and after staining, by making pairwise comparisons of corresponding segmented meshes. Iodine provided the most promising results, contrastingly to conclusions of some previous studies. Outcomes of our comparative analysis will allow us to establish the best protocol to provide a clear delimitation of cartilaginous shape in minimal staining time.

Identification of Isolated Pubic Bones of Marine Reptiles from the Muschelkalk of the Germanic Basin: A Geometric Morphometric Approach

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The Middle Triassic Muschelkalk deposits of the Central European Basin have yielded numerous marine reptile fossils, predominantly sauropterygians. However, the majority of these remains consist of isolated skeletal elements, which poses challenges for reliable taxonomic identification. Girdle bones, in particular, can be problematic due to their considerable morphological variability and the frequent occurrence of convergent evolution resulting in similar shapes across unrelated taxa. In this study, we assess the potential of geometric morphometrics for the taxonomic classification of isolated pubic bones. Principal Component Analysis reveals that plate-like, rounded pubes—present in various sauropterygiomorph taxa such as cf. *Blezingeria*, *Hanosaurus*, *Largocephalosaurus*, *Pararcus*, and, to a lesser extent, *Pistosaurus*—form a distinct cluster occupying a separate region of morphospace relative to other reptiles. Nonetheless, given the substantial intraspecific variation observed within closely related species (e.g., *Nothosaurus* spp.) and instances of morphological convergence among distantly related taxa, taxonomic assignments based solely on morphometric data should be approached with caution.

Comparing the Power of 2D and 3D Molar Metrics to Predict Diet in Mammals: A Case Study on Noctilionoid Bats

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In mammals, 3D shape analyses of teeth are powerful tools for predicting diet. However, an issue with these methods is that they require 3D data which can be challenging to obtain, especially for fossil taxa. In contrast, 2D dental measurements are easier to collect via photographs and published images. Thus, our aim is to test whether 3D analyses provide greater predictive power than simpler 2D metrics that capture similar molar traits. We examine the relationship of 2D dental measurements and diet in mammals and compare the results to those of similar analyses using 3D metrics. We use extant noctilionoid bats as our base study system because they include considerable dental and dietary diversity. We collected 3D geometric shape data and 15 linear measurements for 120 species of noctilionoids (350 specimens), and we used phylogenetic comparative methods to examine relationships between molar morphology and diet. Although our results suggest that the 3D data are stronger predictors of diet than 2D linear metrics, the difference is minimal – 2D metrics differentiate diet categories to nearly the same degree as 3D metrics. These results suggest that 2D metrics are reliable tools for inferring diet in mammals of unknown diets, including fossils, especially when application of 3D metrics is not feasible. Future avenues for this project include exploring applying 2D metrics to fossil samples to study mammalian paleoecological diversity.

Evolution and Development of the Autopodium In Microteiid Lizards (Squamata: Gymnophthalmidae)

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The Gymnophthalmidae lizard family exhibits remarkable skeletal variation across the Neotropics, including two snake-like lineages: Gymnophthalmini (forelimb reduction) and Bachiini (hindlimb reduction). These lineages display gradients of limb modifications from partial autopodial loss (manus and pes) to complete reduction, coupled with body elongation and girdle restructuring. This study characterizes limb reduction patterns in Gymnophthalmidae, emphasizing autopodium and girdle structures. While previous studies examined limb reduction directly, recent work demonstrates that girdles provide crucial information about morphological transitions and substrate use associations. We employed two complementary approaches: 1) comparative skeletal anatomy characterizing limb elements (autopodium, zeugopodium, stylopodium) and girdle structures across species with varying reduction degrees; 2) 3D geometric morphometrics analyzing CT scan data to quantify pectoral and pelvic girdle shape variation across representative lineages. We investigated developmental genetics to examine molecular signatures related to identified morphological patterns, focusing on HOX genes involved in limb and axial skeleton development. Genomes of two Gymnophthalmidae species (*Calypotommatius sinebrachiatus*, *Tretioscincus oriximinensis*) and one Teiidae (*Salvator merianae*) were annotated to examine genetic mechanisms underlying differential limb reduction. Analyses revealed positive selection in several HOX genes in the limbless lineage (*Calypotommatius*), suggesting genetic modifications associated with limb loss. This combination of skeletal morphology with developmental genetics provides insights into evolutionary changes at structural and genetic levels, contributing to understanding morphological and molecular evolution in squamates and vertebrate adaptive radiation.

A Kinetic, Physical Model of a Dogfish Shark Skull As a Tool for Motion Simulation and Active Learning

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Understanding how the bones, muscles, and other internal structures of animals move during behaviors is challenging. X-ray Reconstruction of Moving Morphology provides an approach to precisely quantify in vivo internal motions, but is time-consuming and requires specialized equipment. Digital motion simulations can estimate motion but such simulations often require computational expertise. To test the potential of physical models to provide a more accessible motion simulation tool, I created a physical model of the dogfish shark skull (*Squalus acanthias*). I combined dissections, photogrammetry, and microCT scanning of a preserved specimen to digitize the anatomy, including all the cartilages, muscles, and ligaments of the skull. I then fabricated a physical model first using ribbons for ligaments and then replacing most of the ligaments with magnets. I also added hooks for attaching rubber bands, representing the cranial muscles. Our physical model can be manually manipulated to reproduce all of the described motions

of the dogfish skull (e.g., jaw protrusion-retrusion, jaw opening-closing, hyoid depression). The weak force of the magnets relative to the rubber bands does make motion with the rubber bands attached more difficult. However, it makes assembly and disassembly far easier in a classroom context. Our model shows that physical models, even with several layers of abstraction (e.g., magnets, rubber bands), can be an accessible tool for estimating and teaching animal form and function.

Intraspecific Cranial Variation In *Amphisbaena vermicularis* (Squamata: Amphisbaenidae)

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Amphisbaenians are highly specialized burrowing reptiles possessing robust skulls adapted for digging. We employed microcomputed tomography and geometric morphometrics to analyze cranial variation in 26 specimens (10 females, 16 males) of *Amphisbaena vermicularis*, a species distributed across northeastern and central-western Brazil, collected from various locations in Piauí and Maranhão states. Our findings revealed conserved cranial morphology that remained stable regardless of snout-vent length or geographic origin. Procrustes analysis showed no significant relationship between skull shape and size ($R^2=0.0244$; $p=0.6582$), suggesting strong biomechanical constraints associated with fossorial habits. While males exhibited slightly larger skulls than females (Procrustes ANOVA of centroid size, $p=0.0183$), we found no shape differences between sexes, indicating a potential trade-off between sexual selection pressure and digging functionality. PCA demonstrated that 83% of morphological variation was concentrated in the first two principal components, with subtle population-level differences that may reflect local adaptations to distinct soil types. The Guadalupe specimens ($n=17$) displayed a tendency toward narrower skulls, possibly associated with more compact soils. These results highlight the morphological stability of *A. vermicularis* skulls, reinforcing their subterranean specialization. The absence of sexual dimorphism in skull shape contrasts with patterns observed in other squamates, suggesting that functional demands of digging outweigh other evolutionary factors. Our study emphasizes the importance of integrated approaches combining morphology, ecology, and genetics to understand cranial evolution in these unique reptiles.

Hindlimb Morphology and Locomotor Ecology of the South American Notoungulate *Miocochilius anomopodus*

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South American notoungulates were a diverse group of mammals representing a large proportion of endemic South American faunal diversity before the Great American Biotic Interchange, with no modern analogues. Among them, *Miocochilius anomopodus*, a late-diverging Colombian interatheriid, stands out for its potential cursorial adaptations atypical of other Interatheriidae. Studying *M.*

nomopodus offers insights into the selective pressures behind these adaptations and how phylogeny may have constrained convergence with other cursorial mammals, particularly artiodactyls and perissodactyls. We used three-dimensional geometric morphometrics of the femur and calcaneus in *M. anomopodus*, comparing it with approximately 25–50 extant small-bodied mammals. Calcanei from three fossil Perissodactyla species were used to assess morphological convergence on ‘intermediate’ fossil perissodactyls. Principal component analyses reveal that femoral morphology places *M. anomopodus* at the intersection of fossorial, arboreal/scansorial, and semi-aquatic species, with broader and shorter femora than cursorial taxa. Calcaneal morphology places it between fossorial and cursorial groups, with differences in shape and orientation of the talar facets. These contrasting reconstructions suggest that *M. anomopodus* did not fully converge on any single modern ecological niche and potentially retains varying degrees of phylogenetic inertia from its reconstructed fossorial ancestry. This highlights the complexity and challenges of reconstructing locomotor behavior in extinct taxa and the unique evolutionary trajectories within extinct South American endemic fauna.

Toward a Phylogenetic Framework for *Rhinella* (Anura: Bufonidae): Integrating Ct-Scanned Fossils and Extant Species

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Toads of the genus *Rhinella* are small to medium-sized bufonids widely distributed across the Neotropics, exhibiting significant morphological and biological diversity. The genus is recognized as monophyletic and is divided into two major clades: *R. marina* and *R. margaritifera*. Traditionally, osteological characters have been used to study the taxonomy and evolutionary relationships within the group. However, conventional techniques have limitations in capturing the full extent of morphological variation in both extant and fossil specimens, making their classification challenging. To address this, the present project aims to use microcomputed tomography (CT scanning) to build a comprehensive osteological atlas of *Rhinella*. This will allow for a detailed assessment of intraspecific variation in skeletal traits and improve taxonomic resolution. In this context, a primary goal of the project is to develop a phylogenetic hypothesis for *Rhinella* using Total Evidence, to phylogenetically place all known fossil specimens related to the genus. Currently, more than 30 extant species of *Rhinella* and two fossil specimens — which are currently being described — have been CT scanned. This approach has already revealed morphological features that had not been previously considered, and a morphological matrix is being developed as a foundation for the upcoming phylogenetic analyses.

Post-Mortem Age Determination of Two South American Wild Canids (*Lycalopex vetulus* and *Cerdocyon thous*)

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Although South America is the most speciose continent for canids, with 11 extant species, few studies focused on the age estimation of their skeletal remains, which is key to several types of morphological analysis and population dynamics inferences. Previous studies showed that diet directly affects dental wear, as more abrasive items wear down teeth more rapidly. In addition, recent studies showed that *Lycalopex vetulus* and *Cerdocyon thous* share numerous food resources, which raises the question of how overlapping diets impact the dentition of different species during their ontogeny. Here we aimed to investigate the relationship between the diet and post-mortem age determination for adult specimens of *L. vetulus* (n = 24) and *C. thous* (n = 20). We compared cranial and dental age categories, which are the most widely adopted proxies of age for mammals, using skull base sutures (presphenoid, basisphenoid and basioccipital) and superficial teeth wear for age estimations. Cranial and dental age groups of both species did not match in 40,90% of the cases; for many specimens of both species, middle-aged skulls exhibited higher dental age. This inconsistency was more noticeable in *L. vetulus* (60%), which presented a higher degree of dentine exposure, suggesting its greater consumption of insects, especially ground termites, resulting in an abrasive diet due to the accidental consumption of sand and other minerals.

Ontogenetic Development of Pneumatized Cervical Vertebrae in Flagellicaudatan Sauropods

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A key factor allowing gigantism in sauropod dinosaurs was their bird-like lung with pneumatic diverticula that permeated the body. In addition to elevating lung efficiency, these air-filled diverticula resulted in a comparatively low body density and increased the body-air contact surface for heat exchange, which is particularly important for large-sized animals. Diverticula growth from the lung towards the body's extremes during ontogeny has been inferred from external vertebral morphology, but the exact process of internal pneumatization remains poorly understood. We assess the ontogenetic development of internal cervical vertebral pneumaticity in a sample of flagellicaudatan sauropods from the Jurassic Morrison Formation of Wyoming, representing a hatchling, juvenile, and subadult ontogenetic stage. We used micro-CT scanning to examine internal bone structure and produce 3D models of the vertebrae and their internal pneumatic chambers. Crenulated bone texture in the hatchling indicates that diverticula reached the anterior-most cervical vertebrae very early in ontogeny. However, in this individual, penetration of diverticula only occurred in middle and posterior cervical neural arches, with left-right asymmetry. Older juveniles show internal pneumaticity in anterior cervical neural arches. Penetration of the centra was only observed in

the vertebrae of a subadult individual. Hence, cervical diverticula first penetrate the neural arches and only later in ontogeny the centra. The functional and developmental implications of this observation remain to be explored.

Exploring the Snout of Pseudosuchians: The Unexpected Sensibility of the Ornithosuchid *Riojasuchus tenuisiceps*

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The snout of amniotes has numerous bone correlates that can be associated with neurovascular structures for heat exchange sites and sensory function. Here we present an unusual bone correlate on the surface of the premaxilla of *Riojasuchus tenuisiceps* (Pseudosuchia: Ornithosuchidae), a medium-sized tetrapod from the Argentine Upper Triassic Los Colorados Formation. Two almost complete and articulated skulls are known for *Riojasuchus*, PVL 3827 (holotype) and PVL 3828. Both show a pattern of neurovascular bone correlates formed by a curved groove, with an irregular edge that runs down the lateral surface of the premaxilla from the prenasal process. Anteriorly, this groove has a parallel line of rounded equidistant foramina near the contact between the premaxillae, which continues ventrally with a disrupted distribution. This combination of features on the premaxilla is uncommon because extant and extinct crocodylomorphs and some theropods usually have a beehive or linear foramina pattern. Foramina concentrated in the distal part of the premaxilla are registered in some pterosaurs and birds. This unique groove and foramina pattern in *Riojasuchus* shows a greater diversity than expected for pseudosuchians. It may indicate the presence of high heat exchange and an enhanced mechanoreception function in its snout. The latter hypothesis would be consistent with the recently proposed wading hunter habits, allowing *Riojasuchus* to perceive its prey better when dipping its head under water to catch it.

Muscle Diversity of the Sacroiliac Joint in Scinaxini (Anura: Hylidae)

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The musculature associated with the sacroiliac articulation in anurans is essential to locomotor behaviors such as burrowing, swimming, jumping, and walking by enabling pelvic rotation and sliding. While the osteological components—sacral diapophyses, sesamoids, and ilia—have been extensively studied, the

corresponding musculature remains comparatively underreported. Muscles such as the *m. longissimus dorsi*, *m. coccygeosacralis*, *m. coccygeiliacus*, and *m. iliolumbaris* are fundamental to sacroiliac function, yet detailed anatomical descriptions, particularly beyond *m. iliolumbaris* are lacking. This gap is especially evident in the hylid tribe Scinaxini, which includes 133 neotropical treefrog species across the genera *Julianus*, *Oedipoda*, and *Scinax*, and where some species of the first genus shows distinctive osteological features—such as medially elongated sesamoids and reduced sacral diapophyses. We analyzed in detail the sacroiliac musculature in nine Scinaxini species, including *J. camposseabrai* and *J. pinimus*. Our findings reveal that muscle origin and insertion sites are generally conserved across species; however, notable interspecific differences exist in the fiber orientation of the *m. coccygeosacralis* and in the degree of separation between branches of the *m. iliolumbaris*. These variations may reflect functional adaptations linked to the unique osteological configurations in this clade.

3D Digital Modelling of the Giant Rhinocerotoid *Paraceratherium bugtiense* and What was the Largest Land Mammal Ever?

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Despite potentially being the largest land mammal, the extinct rhinocerotoid *Paraceratherium bugtiense* remains poorly studied regarding its biomechanical adaptations to gigantism. We designed three 3D digital models of a composite skeleton of *Paraceratherium* with different bone scaling ratios and used these to estimate body mass. We also estimated its limb joint ranges of motion in flexion/extension to test whether *Paraceratherium* exhibited a columnar stance or retained a more flexed posture. Importantly, we applied the same methods to its extant relative the white rhinoceros, *Ceratotherium simum*. Convex hulls were generated for body segments to estimate total body mass. We conducted sensitivity analyses for the three models comparing them with estimates obtained via the scaling of femoral and humeral circumferences with body mass. We estimated a body mass range of a large *Paraceratherium* specimen between 12,000 to 13,900 kg compared to 21,900 kg from scaling equations. Body mass estimation of *Ceratotherium* was 1,307 kg versus 2,900 kg from a scaling equation, overlapping an empirically measured mass for a similar-sized individual at 2,160 kg. Our results from limb joint range of motion estimates suggest more restricted limb joint mobility compared to *Ceratotherium*. These findings are consistent with graviportal adaptations, meaning that *Paraceratherium* likely adopted a columnar stance to support its huge body mass.

Gbx2 in Mammalian Cranial Development: Roles in Neural Crest-Derived Peripheral Nerve Patterning and Craniofacial Connective Tissue

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Mice with reduced Gbx2 expression show subtle craniofacial and head muscle defects, including delayed development and

underdeveloped muscle connective tissues, such as tendons. Although cranial ganglia and peripheral nerves form, they appear nonfunctional, evidenced by lack of muscle contraction. These results suggest *Gbx2*'s importance for guidance and differentiation of CNCCs and their derivatives, impacting cranial ganglia, peripheral nerves, and craniofacial connective tissues, therefore impacting also pharyngeal arch musculature. This study sheds light on how modulation of axial patterning genes like *Gbx2* contributes to the emergence of diverse mammalian cranial morphologies and functions.

Comparative Morphology of Turbinal Bones in Akodontini Rodents (Muroidea, Cricetidae)

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Turbinates are bony structures within the nasal cavity of most mammals, playing essential roles in conditioning inhaled air—regulating temperature, humidifying it, and facilitating odor detection. Here, we examined the turbinates of Akodontini, a Neotropical rodent tribe within the Sigmodontinae (Cricetidae), known for ecological diversity including omnivores, herbivores, and insectivores specialized in capturing live prey. To investigate morphological variation possibly linked to prey detection and capture, we segmented the eight turbinates of the herbivore *Necomys lasiurus* and the insectivores *Blarinomys breviceps* and *Oxymycterus delator*. The anterior nasoturbinates and maxilloturbinates are primarily involved in respiration, showed notable differences among species: *Oxymycterus* had the largest anterior turbinates, while *Necomys* had the smallest. Additional variation appeared in the number and degree of curvatures, which were most pronounced in *Oxymycterus*. The remaining six turbinates, primarily related to olfaction, are smaller and located in distinct regions: two in the frontal recess, three near the ethmoid bone, and one internally between the frontal and ethmoid turbinates. Although their sizes were relatively similar across species, curvature patterns differed. *Oxymycterus* showed more highly curved turbinates, possibly increasing the surface area for olfactory epithelium and suggesting enhanced olfactory capability. Further quantitative analyses are underway to provide deeper insights into these morphological adaptations.

Symposia

Recent Advances In the Macroevolutionary Morphology of Rodents

Skull and Encephalon of *Acarechimys* (Rodentia, Hystricognathi) from the Early-Middle Miocene of the Argentinian Patagonia

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Acarechimys is an extinct South American hystricognath rodent (Caviomorpha) from the late Oligocene-Late Miocene. Skulls and encephalons highlighted the relevance of cranial characters

in understanding the evolution of the group. In this study, we describe the skull and encephalon of *Acarechimys* from the Santa Cruz Formation (Early-Middle Miocene), southern Argentina, through direct observation and high-resolution tomographies. *Acarechimys* has brachydont cheek teeth, enlarged auditory bullae, a middle ear with malleo-incudal complex, a cochlea with 2.5 turns and a specialized vestibule. The encephalon is lissencephalic, with antero-posteriorly aligned elements, and an exposed mesencephalon. Cheek teeth and encephalon are primitive, while the basicranium, middle and inner ears have derived characteristics related to enhanced low-frequency sounds and agile head movements. The evolutionary implications of this curious combination of character require further study.

Rodent Brain Diversity as a Reflection of Evolutionary History and Ecology

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Before the broad use of X-ray computed tomography, few natural endocasts were known for rodents. Over the last decade, virtual endocasts of extant and extinct species have been published. The study of brain regions is progressively replacing the use of brain size alone. Specifically, the link between the size of brain structures and behavior is being studied using the fossil record. I present some examples of what endocasts can tell us about the behavior of extinct rodents. The Oligocene caviomorph *Incamys* has exposed caudal colliculi, which might be related to enhanced auditory capabilities and may have been crucial in the evolution of group-living in Chinchillidae. Modern arboreal and terrestrial squirrels have relatively large neocortices. This trait was likely acquired during the transition to arboreality 33 million years ago. Terrestrial squirrels have smaller visual cortices and larger somatosensory areas in contrast to arboreal squirrels suggesting a reorganization of the neocortex in Sciuridae influenced by ecology. I also explain the challenges in linking ecology, function and associated brain structures. Based on decades of research, there are clear correlations between ecology and the brain; however, they might not always represent causations. The next frontier will be to more accurately define ecological categories as a reflection of brain functions. This step will allow us to more confidently link behavioral ecology to the brain and its plethora of functions.

Dental Dimension and Body Mass Evolution in Chinchilloids (Rodentia: Caviomorpha)

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Although the Chinchilloidea are not a species-rich clade today, they show astonishing past diversity, including the largest rodents of all time. Our goal is to infer the evolution of the first

molar dimensions and the body mass in this group and to assess whether changes in these characteristics were related to diversification rates. We assembled a matrix of 11,575 characters, including both extant and extinct species. Bayesian total-evidence dating phylogenetic analyses were performed. We measured or collected from literature the length, width, and area of m1/M1, and we computed the body mass of extinct species using recently published equations. We applied Bayesian comparative phylogenetic methods to estimate trait evolution and diversification through time. Regarding body mass, the rate of evolution accelerates slightly from the origin of the crown group (ca. 35Ma) and increases abruptly around 19-18 Ma with the emergence of the large/giant chinchilloids, until a slowdown from 9 Ma. Large body mass would have suddenly emerged in the lineage leading to the common ancestor of (Dinomyidae, †Neopiblemidae) between 35.6 and 33.6 Ma. This suggests an absence of medium- to large-bodied ancient taxa in the fossil record. As expected, dental dimensions exhibit a similar evolutionary trend compared to body mass. Diversification analyses show that the Chinchilloidea underwent extensive early diversification. The large variation in body mass may have facilitated the initial diversification of the crown group.

Influence of Food Constraint on Craniofacial Ontogeny and Covariation In Rodents

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The craniofacial complex is an intricate 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, to acquire and/or to maintain certain functions. During post-natal development, the different tissues making up the head will have to coordinate their spatialization to accommodate to food weaning (transition from sucking to chewing movement). These mechanical constraints can be modulated by the consistency of the feed from weaning onwards. We have raised house mice, golden hamsters and Mongolian gerbils applying either a hard or a soft diet as soon as weaning begins. This difference in consistency may reflect variations in the hardness of feed available in nature, depending on environmental conditions at the time of weaning. We follow the ontogeny of cranium and mandible shapes and their covariation. Although the mandible is more plastic than the skull, covariation of these two units throughout postnatal development is maintained. Mandible plasticity therefore appears to be a rapid adaptive response during development to the availability of food resources, without jeopardizing the functionality of the entire craniofacial complex.

Limited Cranial Shifts in City-Dwelling Rodents after a Century of Urbanization

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Examining how urbanization and climate change affect various species is important for understanding how wildlife adapts to human modifications on the environment and can aid in mitigating damage to the well-being of local populations going forward. Properly documenting these effects requires samples covering long, evolutionarily relevant time spans. Using museum specimens covering 100 years of urbanization in the greater Chicago area, we quantified the shape of the skulls of two ecologically distinct rodent species: eastern chipmunks (*Tamias striatus*) and eastern meadow voles (*Microtus pennsylvanicus*). Through linear and geometric morphometrics, we investigated the effects of urbanization and climate on skull variation through time. We recovered a significant albeit limited effect of urbanization and climate on skull morphological changes in both species. We attributed these shifts to nondirectional selective pressure caused by heterogeneous urbanization and oscillating climate. Chipmunks showed a weak association between skull characteristics and urbanization and climate, although their size increased throughout the study era. They also showed a decrease in toothrow length, indicating a possible dietary shift. Vole cranial morphology had a stronger association with degree of urbanization and showed a clearer shift in morphospace occupation between urbanization categories. These different patterns between chipmunks and voles reveal species-specific responses to the same human-induced habitat changes and the need for nuanced conservation plans in the face of continuing change.

Evolutionary Musculo-Skeletal Integration in the Skull of Rodents

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Rodents are characterized by their unique skull morphology, related to the specialization of their masticatory apparatus for chewing and gnawing. Despite these commonalities, rodent skull anatomy also displays a wide diversity of forms, which carries both phylogenetic and ecological signals. Indeed, while the classification of rodents was previously built on qualitative skull osteological morphotypes, the advent of molecular phylogenies has demonstrated many instances of convergent skull shapes. However, it remains to be shown whether these morphotypes can be detected quantitatively, and whether the changes in skull shape are integrated with muscle changes and are also functionally convergent. To tackle these questions, we gathered through μ CT-scanning and

dissections a large data set (c. 200 species) covering all three main lineages and most families, combining skull 3D geometric morphometrics and associated masticatory muscle data. Our results show that the Ctenohystrica can generally be clearly separated from the other two main lineages, notably their much larger superficial masseter muscle proportionally to other muscle complexes. The mouse-related clade displays a wide disparity in the masticatory apparatus, including some convergences towards a Ctenohystrica-like morphology, while the squirrel-related clade appears less disparate. Finally, our results show strong integration between skull muscles and bones, which is surprisingly strongest for the temporal and pterygoid muscle groups, while the masseteric and zygomaticomandibular musculatures, specialized in rodents, have less impact on bone shape.

Hypsodonty in Rodents: Definition, Prevalence and Future Prospects for the Study of a Highly Convergent Dental Trait

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Evolutionary convergences, where distantly related lineages independently evolve similar traits, have long fascinated biologists. A textbook example in mammals is hypsodonty, or high-crowned teeth, widely interpreted as a specialisation to withstand abrasive items. Rodentia is the most speciose mammalian order, presenting diversified herbivorous feeding strategies across varied ecological niche. While hypsodonty has been documented across numerous mammalian clades, its prevalence within rodents, remains under-quantified. To address this gap, we undertook a comprehensive examination of the literature on crown height in more than 400 extant and extinct rodent genera providing a detailed record of the trait's evolution. We recognized inconsistencies and ambiguities in the definition and description of hypsodonty that arose. We then conducted original measurements and calculations of the hypsodonty index on a selected sample, specifically chosen to target lineages exhibiting convergent evolution of hypsodonty. Our approach combines literature synthesis and morphometric analysis, and allows us to document at least 35 independent acquisitions of hypsodonty within the rodent crown-group. Furthermore, our review highlights the lack of a consistent framework for the concept of hypsodonty, which impedes direct comparisons across studies. To mitigate this, we propose specific recommendations for the standardised definition and utilisation of this character. Finally, the resulting comprehensive database of hypsodonty in rodents offers a powerful tool for future investigations into the evolutionary dynamics and ecological drivers of this highly convergent dental trait.

Impact of Allometry, Phylogeny and Ecological Traits on Skull Roof Bone Microanatomy in Rodents

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With substantial variation in habitat, lifestyle, and diet, rodents offer valuable insights into the evolution and adaptation of cranial bone microanatomy. However, the internal morphology of the rodent skull roof remains largely unexplored. In this study, we investigated how the inner structure of the skull roof is influenced by environmental factors, phylogeny, and body size. We analysed micro-CT scans of 119 skulls representing 72 species across 25 rodent families. A standardized region of the skull roof was selected in each specimen, and three parameters were quantified: compactness (C), cross-sectional area (CSA), and thickness (Th). We then examined their relationships with skull size, phylogeny, and ecological traits such as locomotion, digging behaviour, and diet. Our results show that skull roof microstructure is primarily influenced by skull size. Thickness and CSA exhibit positive allometry, while compactness shows negative allometry. Phylogeny had no significant effect on any of the structural parameters. Similarly, general lifestyle and dietary categories did not correlate with skull roof microanatomy. However, rodents that use their heads for digging—chisel-tooth and head-lift diggers—consistently exhibited thicker skull roofs with reduced compactness. These findings suggest that body size, rather than phylogenetic history or broad ecological categories, is the primary factor shaping skull roof microstructure in rodents, with specialised behaviours exerting additional localised influence.

Rodent Olfaction: An Integrative Perspective

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Olfaction is a critical sense for tetrapods, playing a central role in survival and reproduction by aiding in food detection, predator avoidance, and social interactions such as finding a mate. Different olfactory capabilities are therefore hypothesized to be associated with specific ecological lifestyles and behaviors. However, strong statistical evidence supporting these associations remains scarce. Among mammals, rodents represent an exceptional group for studying the link between ecology and olfaction, as well as potential patterns of convergence. Rodents have independently colonized a wide range of habitats (including aquatic environments, subterranean systems, deserts, high-altitude regions, and forest canopies) and exhibit a wide spectrum of ecological traits. These include diverse diets, varied activity patterns (e.g. nocturnality vs. diurnality), and contrasting social systems ranging from highly solitary to eusocial species. Here, we reviewed recent advancements in the field of olfaction from an integrative perspective, including morphology, behavior, and genomics, with a particular focus on rodents.

Masticatory Muscle Configurations and Functional Performance of Rodent Morphotypes

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Rodents can be categorised into four ‘morphotypes’ based on cranial musculoskeletal characteristics. These anatomical categories are quantitatively compared in this study using mechanical advantage. 27 extant rodent taxa from across the tree, representing all four morphotypes, were compared using lever-arm mechanics, assessing the variance in mechanical advantage of homologous muscles at a range of gape angles. The results show that the morphotypes’ group means are not significantly different, and each morphotype shows substantial mechanical variation. However, the full story is nuanced. Individual muscles (such as the infraorbital zygomaticomandibularis, or anterior deep masseter) can be significantly different in mechanical advantage between morphotypes, whilst the superficial masseter is only significantly different during molar biting. The IOZM of myomorphs is significantly different to the IOZM of hystricomorphs and to the ADM of sciurormorphs, but the hystricomorph IOZM is not significantly different to the ADM of myomorphs and sciurormorphs together. The ADM is significantly different to the undifferentiated DM of hystricomorphs. Bathyergid protrogomorphs appear more similar to extant hystricomorphs than to *Aplodontia rufa*, the non-bathyergid protrogomorph. Individual rodent taxa can be distinct from others of their morphotype, or even from all other rodents. The upper and lower extremes of the gape range studied are typically responsible for the majority of the variance. Overall, morphotypes show some patterns in mechanical advantage, with variation within each category and overlap between them.

Evolution of Squirrel Tooth Morphology and Diversification during North American Grassland Expansion

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The expansion of North American grasslands during the Cenozoic has long been associated with mammalian adaptive evolution. However, the timing of evolutionary responses to new environments, such as morphological change and diversification pulses, has received comparatively little attention in small mammals. Here, we integrate geometric morphometric analyses of dental morphology across extinct and extant taxa with phylogenetic and biogeographic frameworks to dissect these dynamics. Our analyses reveal that grassland-adapted squirrels (*Cynomys*, *Urocitellus*, *Marmota*, *Paenemarmota*) evolved distinct dental morphologies during the Late Miocene and Pliocene, establishing new adaptive peaks. These morphological shifts occurred after the initial spread of grasslands but coincided with periods of intensified aridity. Diversification rates peaked shortly after these morphological changes. This temporal sequence suggests that initial phenotypic innovation

in response to climatic stressors facilitated subsequent taxonomic diversification. These findings suggest that this squirrel evolutionary radiation occurred in stages: (1) colonization of new habitats, (2) rapid morphological adaptation driven by abiotic climatic pressures (e.g., aridification), and (3) lineage diversification following the stabilization of new phenotypes.

“Rules of Thumb” In Rodent Evolution

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The pentadactyl hands of tetrapods are adapted for diverse environmental interactions, for which the digits’ unguis are often crucial. Among mammals, the first digit and its unguis can be distinct and have unique specialized functions. Across Rodentia, we find that as a general rule most extant genera and ancestral lineages bear D1 nails. Exceptions follow specific structure-function associations that arose independently multiple times: the gain of D1 claws with subterranean habits, and the loss of D1 unguis with oral-only feeding behavior. We hypothesize that the ancient origins of both the D1 nail and oromanual behavior in rodents are fundamentally linked to their unique cranial adaptations for biting hard food items, such as nuts. Although the rodent thumb is routinely disregarded as “vestigial” and “nonfunctional”, we propose that the ability to gnaw was probably enhanced by structure-function adaptations enabling food items to be held stably as free objects in the hands and manipulated for efficient ingestion. These findings offer new insights into the evolutionary significance and structure-function relationships of postcranial structures in vertebrates, particularly highlighting the role of the unguis in rodent evolution.

Convergence to Fossoriality on the Way

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The adaptation to a subterranean lifestyle among mammals is a classic example of convergent evolution. However, little we know about how this process emerges among closely related lineages. In this study, we explore the morphological diversity of fore- and hindlimbs of the main subterranean hystricomorph families adapted to burrowing and living underground, which evolved independently in South America (Ctenomyidae, Octodontidae) and Africa (Bathyergidae). Multivariate and ordination analyses of eight species (183 individuals) were performed on 18 morpho-functional indices aimed to reflect the most relevant traits involved in digging. Ctenomyids (*Ctenomys maulinus*) and octodontids (*Spalacopus cyanus*) differ considerably from bathyergids by having a less specialized fossorial limb phenotype; e.g. proximally located deltoid tuberosity, smaller olecranon process, thinner femoral and tibio-fibular diaphyses, less symmetrical

limb proportions and more distally “fused” tibio-fibulae. Despite *C. maulinus* and *S. cyanus* are proficient diggers, they still show a tendency to maintain a more surface-dwelling limb phenotype, with relatively higher crural index and a not-ossified tibio-fibulae, probably as a reflection of their “bimodal” use of terrestrial and subterranean environment for foraging. Despite all bathyergids assessed here (except *Bathyergus suillus*) are chisel-tooth diggers, they showed higher degrees of bone specialization than caviomorph diggers. A discussion including factors such as the comparatively recent evolutionary history of Ctenomyidae and *Spalacopus* and a gradual transition to life underground are proposed as the factors explaining such disparate limb morphology.

Convergent Trajectories In the Evolution of Bipedality in Desert Rodents

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Bipedal desert rodents have long been a textbook example of convergent evolution. Australian hopping mice (Muridae), Kangaroo rats (Heteromyidae), and Jerboas (Dipodidae) are all capable of bipedal locomotion, construct underground burrows, do not need to drink water, and are crepuscular foragers. However, upon closer inspection, there are significant differences in diet, locomotion, and physiology that have led some researchers to propose that they are not convergent after all. To better understand how the concept of convergence relates to this clade, I collected morphological data on members of each group, closely related quadrupeds, and other rodents, totaling 158 species. Performing a phylogenetic Principal Components Analysis revealed that increase in metatarsal length paired with decrease in humeral length (pPC2) provides a reliable indicator of bipedal locomotion ability. I found that the best fit to the data was an Ornstein-Uhlenbeck model with multiple optima: one for quadrupedal and another for bipedal species. I then found that in each lineage, the maximum value of pPC2 is correlated with time since bipedal locomotion first evolved. In fact, when aligned by acquisition of bipedal locomotion, the pattern of trait variation is nearly identical across all three groups. I conclude that, instead of convergence being a binary designation with a specific threshold similarity, the bipedal desert rodents represent different timepoints on convergent trajectories of adaptive evolution in response to desert environments.

Rodents: A Model Group for Studies of Ecomorphological Change and Community Evolution Through Time

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Rodents are the most species rich group of extant mammals, distributed globally, and occupy nearly every terrestrial habitat on Earth. The group is characterized by incredible morphological and ecological diversity, including specialized forms that have evolved independently within multiple families. Recent ecomorphological studies have improved understanding of

rodent form and function, and facilitate research into processes responsible for their impressive diversity. Combined with recent advances in phylogenetics and an extensive fossil record, these efforts provide an outstanding comparative framework for understanding the tempo and mode of evolutionary change within and across rodent lineages. The rodent fossil record offers ample opportunities for studies of convergent or parallel evolution of dietary and locomotor specializations through time. Evidence indicates rodent diversity and disparity increased as climate became cooler, more arid and seasonal through time, and habitats became more heterogeneous. Studies document early and rapid in situ responses to environmental changes in rodents, reflecting greater sensitivity to environmental changes and generally more rapid evolution than larger mammals. Regional and local scale studies of rodent communities reveal clear shifts in structure that correspond to the timing of climate and habitat changes. Through time, rodent communities shifted to be dominated by species with higher tooth crowns, and open habitat adapted burrowing and saltatory taxa diversified. In sum, these records reveal dynamic evolution within lineages and communities driven by changes in environments.

The Macroevolutionary Dynamics of Rodent Morphology

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Rodents are the most speciose order of mammals, but many aspects of their body plan are highly conserved. This tension between high species richness and low morphological disparity has been studied from many angles, but new global morphological and behavioural datasets, as well as modern phylogenetic comparative methods, can now facilitate a fresh return to this apparent conflict. This talk will begin by examining the ecological, social, and environmental drivers of a trait that does vary widely across Rodentia – tail morphology (i.e., length, colour, and texture). I will then broaden the scope to the overall rodent body plan, highlighting differences between population-, order-, and class-wide correlations. These results emphasize the gap between micro- and macro-evolutionary studies, particularly the role of local ecological context in shaping rodent morphology.

A Generalist Bauplan? Locomotion-Driven Morphological Specializations in Neotropical Rodents

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Most rodents, especially small-bodied ones, are often perceived as terrestrial generalists, partly because of the assumption that small body size limits morphological specialization and requires efficient performance across multiple functions, given the structural heterogeneity of most environments. However, recent studies challenge this view by revealing locomotion-associated specializations even among small species. In the Neotropics,

Echimyidae and Sigmodontinae represent diverse rodent clades that occupy distinct ecological niches and display varied locomotor behaviors. Echimyidae includes lineages that have been diversifying since the middle Miocene, whereas Sigmodontinae experienced a more recent and rapid radiation, primarily during the Pliocene and Pleistocene. Using phylogenetic comparative methods and both linear and geometric morphometrics, our research has demonstrated that multiple postcranial structures, including the femur, pelvis, scapula, and vertebrae, exhibit clear morphological patterns associated with substrate use and locomotor strategies. These specializations are especially pronounced in Echimyidae, while in Sigmodontinae they tend to be more subtle, although still detectable. Our findings question the widespread assumption of a universal generalist bauplan in small rodents and underscore the importance of functional morphology for understanding the evolutionary and ecological success of these clades.

Island Effect on the Brain Evolution of Rodents: The Case Study of the Giant Rats of the Canary Islands (Canariomys, Muridae, Rodentia)

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Islands are complex ecosystems, and specific biological rules have been described for animals inhabiting them. One of the most spectacular patterns is the gigantism of small animals and the dwarfism of large animals relative to their mainland relatives. Here, we describe the first virtual brain endocast of two giant rats from the Canary Islands: *Canariomys bravo* (Tenerife) and *Canariomys tamarani* (Gran Canaria). We compare them with 10 extant mainland and insular Murinae. After segmenting the virtual endocasts, we measured the endocranial volume and the relative size of brain regions. Our results indicate that *C. bravo* and *C. tamarani* had a relative brain size in the low range of the *Arvicanthis* genus, which includes their closest extant relatives. The olfactory bulb and petrosal lobule ratios are relatively low, while the neocortex is within the range of variation of extant arvicanthin species. The relatively small size of the olfactory bulbs in *Canariomys* might be related to a decrease in olfaction linked to a lower risk of predation on the island compared to the mainland. The relatively smaller petrosal lobules in *C. tamarani* and insular extant rodents could result from a shift to slower locomotion compared to their mainland relatives. Ultimately, living on islands may have a strong influence on brain evolution as animals need to behaviorally adapt to potentially different environmental conditions compared to their ancestors.

Patterns of Epiphyseal Fusion in the Limb Long Bones of Rodents

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Epiphyseal fusion of skeletal elements is often used as an indicator of maturity in mammals. However, it is known that its pattern and timing in different skeletal elements can vary immensely across phylogeny. According to a study from 1925, the epiphyseal fusion sequence in limb long bones of laboratory rats is interrupted by more than 2 years. Follow-up studies on selected rodent species provided further evidence that epiphyseal fusion is partly delayed or perhaps completely halted throughout life. To understand epiphyseal fusion patterns in rodent limb long bones, we here adopted a clade-wide statistical approach. Drawing information from CT-data of hundreds of specimens and species, we quantified the relative frequencies of fusion at 15 epiphyseal sites. Using only specimens with at least one fused site, we found that, for example, whereas the humeral trochlea always fuses, the distal epiphyses of the radius and ulna were almost never fused. We used the frequency of fusion as an indicator of fusion sequence (the most fused site fuses first, etc.) and found contrasting patterns of frequency and sequence between the major rodent clades. This suggests a phylogenetic pattern, whereas fusion does not appear to be associated with lifestyle or body size. These preliminary findings raise the question of how evolutionary constraints on epiphyseal fusion affected the function and adaptability of the trabecular structures in the limb bones of rodents.

Phenotypic Variation and Development of Mammalian and Avian Voice Boxes

Comparative Anatomy and Development of the Vocal Apparatus In Bats and Implications for the Diversity of Laryngeal Echolocation

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Most of the over 1400 extant bat species produce high-frequency pulses with their larynx for echolocation. However, the debate about the evolutionary origin of laryngeal echolocation in bats remains unresolved. The morphology of the larynx is known to reflect vocal adaptation and thus can potentially help in resolving this controversy. However, the morphological variations of the larynx are poorly known in bats, and very little is described about their development. Here, we compare the 3D adult laryngeal morphology of 23 extant bat species of 11 different families and the laryngeal development for selected representative taxa. We find that, contrary to previously thought, laryngeal muscle hypertrophy is not a characteristic of all bats and presents differential enlargement. The larynges of pteropodids are morphologically similar to those of non-bat mammals. Two morphotypes are described among laryngeal echolocating bats, illustrating morphological differences

between rhinolophoids and yangochiropterans, with the main variations being the cricothyroid muscle volume and the shape of the cricoid and thyroid cartilages. For the first time we detail functional specialization for constant frequency echolocation among rhinolophoids. Lastly, the nasal-emitting taxa representing a polyphyletic group do not share the comparable laryngeal form, which raises questions about the potential modular nature of the bat larynx.

Laryngeal Adaptations to Underwater Vocalizations in Whales

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The larynx originally evolved to separate the airways from the esophagus, preventing choking during breathing. Later, vertebrates developed vocal folds or similar structures within the larynx or syrinx to harness airflow for sound production. As a result, acoustic signaling became a vital form of communication in most vertebrate clades. The return to the sea by ancestral whales posed fundamental adaptive problems for their vocal communication. These included managing large volumes of air during explosive surface breathing, preventing water from entering the airways, and conserving air for underwater vocalization. This obligate aquatic lifestyle demanded fundamental physiological changes to efficiently produce sound. Odontocetes (toothed whales) evolved a novel system that drives air through nasal passages, functionally similar to laryngeal or syringeal sound production. Vibrating tissues in different vocal registers allow them to produce distinct echolocation and communication signals. The vocal fry register is used across species—from porpoises to sperm whales—to create powerful, air-efficient echolocation clicks. In contrast, baleen whales retained their larynx for vocalization, developing unique structures that allow them to emit low-frequency, frequency-modulated calls efficiently. However, these adaptations limit their vocal range and depth. Consequently, baleen whales cannot escape interference from human-generated vessel noise, which severely reduces their active communication range and may hinder key behaviors like navigation and social interaction.

One, Two, or Three Sound Sources in the Syrinx – Evolutionary Perspectives

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The avian vocal organ, the syrinx, is located near the tracheo-bronchial junction and, depending on the exact position, it can house one or two pairs of vocal folds ('labia' or 'membranes'). The first syrinx likely consisted of two sound sources, one in each bronchus. A bipartite syrinx is present in many taxa, among them the Passeriformes, the most speciose order. Less frequent is a tracheal syrinx with one sound source. Remarkably, parrots, the sister group to passerines, have such a syrinx. Additionally, some suboscines (tracheophones) possess a third pair of vibratory tissues, membranes that are situated on the

ventral and dorsal surface of the trachea right above the syrinx. These membranes serve a modulatory role in that they interact with the two syringeal sound generators. Neuromuscular control of these sound sources differs between avian taxa. Parrots and passerines evolved additional muscles that play a major role in regulating airflow through the syrinx and control of acoustic parameters. Interestingly, suboscines, despite having intrinsic syringeal musculature, show less direct muscular control of sound features and syringeal gating of airflow than oscines. Independent and elaborate control of the two sound sources appears to be linked to vocal production learning. This hypothesis requires thorough testing across phylogenetically distant groups. In general, the evolution of syringeal morphology and the resulting consequences for acoustic behavior still remain poorly understood.

Evolution and Development of the Avian Syrinx

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The avian voice box, the syrinx, varies immensely among taxa. The origin and the functional consequences of differences in number of sound sources, the presence of intrinsic muscles, and the presence of sexual dimorphism—both within and between species—represent a set of critically important questions in avian evolution. Here, we explore the origin of these traits in a comparative context and show how changes in development have led to differences in the number of syringeal sound sources. Additionally, we examine the origins of the unusual sexually dimorphic left-right asymmetry of the duck syrinx. The syrinx of female ducks is symmetrical, while male ducks possess a hollow bulla on the left side of the organ. We show how asymmetric tissue identity develops via maintenance of epigenetic state from the early embryo through organogenesis and we support a hypothesis for the bulla's function in the duck courtship whistle. Together, these results describe the molecular and developmental origins of inter- and intraspecific variation in functionally relevant syrinx morphology.

Courtship Vocalizations in Male Ducks: Spectral Composition and Resonance of the Syringeal Bulla

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Ducks display a unique and dramatic sexual dimorphism in their vocal organ, the syrinx. Males have a left-sided bulla that is not present in females and that has been long hypothesized to play a role in courtship vocalizations, though this connection has never been tested. The large, hollow morphology of the bulla and its proximity to the sound-producing vocal folds introduce the possibility that it may work as a Helmholtz resonator, which makes it possible to predict the resonance frequencies enhanced by this structure. We find that during early ontogeny, the distribution of energy across the harmonic spectrum of contact calls is not different between males and females. We then used μ CT scans of duck syringes to estimate resonance

frequencies of the bullae and compared these to spectral features of their vocalizations. This comparison overall supports the idea that the bulla resonance may specifically enhance aspects of courtship vocalizations, especially in species that have a tonal courtship whistle. This was further supported when air was blown through 3D printed bullae. In species with tonal courtship whistles, frequencies produced by models matched those predicted and recorded in courtship vocalizations. We observed that in general bulla size is positively correlated with male bird body mass. This study provides support for the long-held hypothesis that the adult male duck bulla influences resonance frequencies, in particular in courtship vocalizations.

Embryonic Development of the Syrinx: Insights into the Evolution of the Vocalization In Birds

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Acoustic information plays a central role in courtship and species recognition, making it one of the most important signals for species diversification. In vertebrates, the water-to-land transition brought major shifts in auditory and vocal systems, including the evolution of middle ear ossicles and tympanic membranes for airborne sound reception, and laryngeal cartilages and muscles for vocalization. While reptiles and mammals use the larynx to produce sounds, birds have established a novel vocal organ—the syrinx—at the tracheobronchial junction. This voice box unique to birds, mainly controlled by lateral tracheal muscles, enables diverse vocalizations used in mating and alarm calls. Remarkably, parrots and passerines (Psittacopasserines) possess intrinsic syringeal muscles that allow for a wide vocal repertoire. Despite extensive research on the ecological significance of bird song, the development of the syrinx remains poorly understood; therefore, little is known about how complex vocalization has occurred in each lineage. This also complicates our understanding of the homology of the syringeal musculature between psittacopasserines and others. In this study, we examine the embryonic development of the tracheobronchial musculo-skeletal and nervous systems across birds using histology and immunohistochemistry. Our study resolves the evolutionary and developmental origin of the intrinsic syringeal muscles, which resulted in the diversification of the sound signals in birds.

Posterior Phonatory Protection in Perissodactyls

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The perissodactyl larynx was examined for anatomy that protects from choking. Four horse specimens, *Equus caballus*, were dissected. Photos of rhinoceros and tapir larynges were also studied. Larynges were compared with prior dissections of cetartiodactyls: cattle, sheep, goat, deer, llama, alpaca, camel, giraffe, pig, hippopotamus, and whales. The perissodactyl epiglottis overlaps the soft palate caudally, interlocking to form a

bridge. Air is channeled over this bridge, while swallowed food is diverted laterally into the piriform sinuses (lateral food channels). This adaptation ensures breathing (including olfaction) occurs during feeding. Protecting olfaction enhances survival advantage, as the warning scent of approaching predators is detectable while foraging. Perissodactyl corniculates are elongated and curl caudally to interlock with a fold (plica) of the dorsal pharyngeal wall. Together with the rostral interlock, the laryngeal inlet is well protected rostro-caudally. The reason for posterior protection is unclear. Artiodactyls also have caudal laryngeal protection. This adaptation prevents choking during rumination. The cud is diverted laterally around the laryngeal inlet by the posterior interlock. Perissodactyls, however, don't ruminate! So why do they need posterior protection? Perissodactyls, like artiodactyls, are head-down feeders with a relatively long neck. That places them at risk for choking when drinking/feeding against gravity. The tall hooked corniculates interlocking with the posterior palatal shelf prevent water/food in the esophagus from sliding backwards into the larynx.

Postnatal Phenotypic Variation of the Mouse Larynx

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The larynx performs multiple roles, ranging from essential functions like breathing and swallowing to those involved in vocal signal production. This study examined how the cartilaginous structure and airway of the mouse larynx change after birth. Specifically, it asked whether factors such as body size, genetic background, obesity, exercise, or social housing—absent any direct selection for vocal behavior—can drive morphological changes in the larynx that impact vocal communication. Using geometric morphometrics, the laryngeal structures of different mouse models were quantified. The results indicate that selective breeding has led to structural differences in the larynx. Outbred CD1 mice showed greater phenotypic variation than inbred C57 mice, while sex had only a minor or negligible effect on laryngeal size and shape. Additionally, factors like obesity, physical activity, and social environment influenced laryngeal morphology. In conclusion, laryngeal structure is shaped by a combination of stochastic effects, functional demands, and endocrine signals. Some of these structural changes were linked to differences in acoustic parameters of vocal communication signals. This study underscores the importance of often-overlooked factors in the evolution of vocal communication.

Wnt5a and Notum Control the Temporal Dynamics of Cartilaginous Mesenchymal Condensations in Developing Airways

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Congenital and acquired tracheal diseases frequently affect the cartilage, causing the collapse of the central airways during breathing. In Notum-deficient tracheas, chondrogenesis is delayed, with mis-patterned cartilage and narrower airway lumen. At the

molecular level, Notum mediates the de-acylation of Wnt ligands, thereby attenuating the canonical branch of the pathway. It is unknown whether Notum can also attenuate Noncanonical Wnt signaling. Notably, we observed premature tracheal chondrogenesis after mesenchymal deletion of the Noncanonical ligand Wnt5a, a phenotype opposite to that observed after Notum deletion. Hypothesis: Notum and Wnt5a are required to mediate the timely formation of tracheal cartilaginous mesenchymal condensations. Results: In the air-liquid interface culture of mouse embryonic tracheal tissue, inhibition of the Noncanonical Wnt signaling pathway promotes premature cartilaginous condensations, while Notum inhibition results in delayed condensations. Further, Noncanonical Wnt signaling induction delays cartilaginous mesenchymal condensations' formation. RNAseq analysis identified a subset of genes essential for chondrogenesis and extracellular matrix formation upregulated at E11.5 in Wnt5a mutants, while downregulated in E13.5 Notum mutants. In genetic and pharmacological studies, attenuation of Wnt5a-mediated signaling rescued the abnormal mesenchymal condensation process in Notum-deficient tracheas. Conclusions: Noncanonical Wnt5a signaling is required as a checkpoint to prevent premature mesenchymal condensation, while Notum balances levels of canonical and noncanonical Wnt signaling necessary for the timing of tracheal mesenchymal condensations. Partially supported by R01HL144774 and HL156860.

Single Cell Transcriptome Dynamics during Murine Vocal Fold Injury and Repair

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Vocal fold (VF) scarring is characterized by alterations in the extracellular matrix of the LP, a reduction in the integrity of the surrounding epithelium and an overall reduction in vocal fold pliability. Here we characterize single cell gene expression in the adult, murine vocal fold during wound healing using single cell RNA sequencing (scRNA-seq) to identify the subpopulations of cells present during hemostasis, inflammation, proliferation/re-epithelialization, and remodeling phases. The resulting atlas of injury-induced subpopulations of immune, fibroblast and epithelial cells generated by this study will be a key resource to better understand injury and repair in the vocal fold with clinical relevance towards future efforts to promote VF repair. Comparison of our work to other animals will be offered.

Anatomical Foundations of the Mammalian Biodiversity

Evolution of the Shrew Skeleton and the Discovery of a Novel Element: The Nuchal Sesamoid

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Shrews (Soricidae, Lipotyphla) comprise a diverse group of holarctic and paleotropical insectivore-grade mammals. Despite their ubiquity in many habitats, study of their comparative anatomy still yields surprises. One of these is a large sesamoid we found among

mysoricins, extending cranially from the second thoracic neural arch, which can approach the humerus in overall length. Small sesamoids dorsal to thoracic vertebrae are common in crocidurine shrews and appear sporadically in other groups. However, the T2 nuchal sesamoid of mysoricins is particularly robust, elongate in *Myosorex* and *Congosorex*, and short but wide in *Surdisorex*. The function of the sesamoid remains unclear. Nuchal sesamoid length in our sample exhibits no sexual dimorphism. Although the distal tip of the sesamoid is needle-like, it appears entirely embedded in soft-tissues and lacks a groove or lumen. The sesamoid provides an attachment site for several muscles of the upper back and neck, and a function in head mobility appears likely. Other derived aspects of the soricid skeleton include overlap of the nasal capsule with the double-jaw joint, the elongate cranial base in soricines, and the relatively large petrosals in crocidurines. Far from being “primitive insectivores”, shrews have evolved many unique adaptations throughout their skull and skeleton.

Ecological, Phylogenetic, and Intrinsic Effects on Skeletal Shape in Didelphid Marsupials (Didelphimorphia: Didelphidae)

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The diversity of skeletal shape in mammals is influenced by phylogeny, ecology, and intrinsic factors generating covariation between structures. Geometric morphometrics has enriched shape studies, though typically limited to single structures. This study assessed the effects of phylogeny, diet, locomotion, size, and morphological integration across 11 cranial and postcranial elements in 44 didelphid species, using 14 2D landmark configurations. We applied multifactorial analysis, PCA, a multivariate adaptation of Blomberg's K for phylogenetic signal, phylogenetic ANOVA for ecological and size effects, and an exploratory integration analysis of all element pairs. Morphospaces showed overlap between taxonomic groups, with partial separation of Didelphini, frugivores, and arboreal versus terrestrial species. Most configurations showed significant phylogenetic signal, except for the femur and tibia. Phylogenetic ANOVA revealed that only locomotion significantly affected anterior structures (skull, cervical vertebrae, forelimb). Integration analysis identified the atlas and axis as central elements, but less expected was the centrality of the tibia and fibula. In contrast, the skull (dorsal view), mandible, and scapula were the least connected. Most covariations occurred between different body regions, with scarce integration within regions such as the forelimb. Results suggest a strong phylogenetic influence on shape, but also highlight the role of locomotion in anterior structures—contrasting with placental mammals, where hindlimbs are often more specialized. This may reflect divergent functional evolution between marsupials and placentals.

From Womb to Maturity: Prenatal and Postnatal Cranial Growth in the Goat, *Capra hircus*

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The skull is a key marker of morphological diversity in ontogeny and phylogeny, yet prenatal growth patterns remain poorly understood in mammals. Changes in skull growth from embryonic to postnatal stages are influenced by multiple factors, including the offspring's maturity at birth within the altricial-precocial continuum, dietary transitions during the postnatal period, and the development of secondary cranial structures such as horns. In this study, we analyze pre- and postnatal skull growth in goats (*Capra hircus*) using three-dimensional geometric morphometrics and linear allometry. Our results indicate that prenatal growth follows the same ontogenetic trajectory as postnatal juveniles, whereas adults exhibit a markedly distinct cranial configuration. Furthermore, prenatal and postnatal ontogenetic allometry differ significantly, with the prenatal phase displaying a comparatively higher growth rate in cranial variables associated with the splanchnocranium and neurocranium. These findings suggest that goats exhibit prenatal and postnatal growth strategies consistent with precocial mammals. The development of horns profoundly alters cranial morphology, placing adults in a distinct position within the multivariate morphospace.

How Functional Constraints Shape Microanatomical Diversity in Mammals

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The skeleton adapts to the functional constraints it is subjected to. If bone outer shape responds to these functional constraints, in addition to the historical and structural ones, so does bone inner structure. Throughout the evolutionary history of amniotes, bones have jointly adapted their morphological and microanatomical structures. Since bone microanatomy is more plastic, microanatomical changes generally occur before significant morphological evolution, which then relieves or modifies some constraints, resulting in a further change in the inner structure. In addition, bone microanatomy can change over a lifetime, engendering intraspecific variation linked to ontogeny as well as ageing or movement restrictions. Various examples from the evolutionary history of mammals, as well as from studies on modern mammals, will highlight the co-evolution between bone morphology and microanatomy, as well as the great diversity of microanatomical specializations within mammals, while also addressing the relative extent of intraspecific versus interspecific variation.

Timing Variability in the Development of Limb Length

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The growth plate drives endochondral growth in developing long bones, contributing to its length and shape. This process is one mechanism by which much phenotypic diversity in limbs is

explored, regulating limb proportions through growth rate and the size of the discrete zones within the growth plate. Understanding how each zone varies through development would provide insight into the evolutionary potential of the cellular mechanisms – proliferation and hypertrophy in this context – that contribute to the great diversity of vertebrate limbs. Here we assess the variability of each zone of the mouse growth plate to understand their differential contributions toward final limb length and proportion. We train an image classifier to discriminate between growth plate zones from basic histological stains, allowing for a broader sample size to be taken to achieve a more accurate picture of variability through the tissue's development. Our findings show that the hypertrophic zone displays the greatest variability in size, consistent with observations of growth plates in taxa with extreme limb lengthening, which show disproportionately large hypertrophic zones. We investigate if this variability is due to timing of growth plate progression or an effect of cell hypertrophy. Our results suggest that timing plays the most significant role in this bias toward hypertrophic zone variation.

Bone Microstructure of Small Mammals: A Morphogenetic Perspective for Paleobiological Inference

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Over the past 20 years, there has been a significant interest in understanding the bone microstructure of extant and extinct tetrapods. This offers an excellent opportunity to reassess the factors influencing skeletal phenotype and its relationship to bone growth. This study reviews the latest information on osteogenesis and osteohistology of a wide range of extant mammals (small and medium-sized), establishing a morphogenetic theoretical framework for its analysis. The sample includes monotremes, marsupials, xenarthrans, afrotheres, eulipotiphans, rodents, chiropterans, carnivores and primates, and multiple methodological approaches (histomorphometry, polarized microscopy, in-vivo bone labeling) of different bone elements. The examined taxa cover a wide range of lifestyles (e.g. cursorial, fossorial, semiaquatic, volant), allowing microstructural characterization of their ecomorphological/locomotor modes. The data demonstrate that most mammalian orders present a conserved histomorphogenetic pattern involving three bone layers, periosteal, intracortical and endosteal, regardless of their ecomorphological adaptation. Microstructural adaptations are developed by well-established morphogenetic pathways linked to particular selective regimes of adulthood (locomotion), which results in phenotypic differentiation (divergence) among taxa, while others share analogous phenotypes, probably due to similar selective pressures (convergence). Most mammals analysed here showed cyclical bone growth, supporting the hypothesis of a plesiomorphic growth strategy. A review of the paleohistological literature on Mesozoic mammals and their most emblematic nonmammalian cynodont ancestors demonstrates that cyclical growth and other features are widespread traits during mammalian evolution. This morphogenetic approach contributes to understanding the development and evolution of both simple and complex mammalian traits, which leads to more precise paleobiological inferences of extant and extinct tetrapods.

Comparative Bone Morphology of the Hind Limbs In Bats (Chiroptera: Yangochiroptera) and its Relationship with Trophic Guilds

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Bats are a morphologically and ecologically diverse order. While wing morphology has been widely studied, the hind limbs, despite their key roles in roosting, locomotion, and foraging, have received comparatively less attention. This study presents a comparative osteological analysis of the hind limbs of 11 Yangochiroptera species representing diverse trophic guilds: frugivores, nectarivores, insectivores, carnivores, and hematophages. Specimens from scientific collections were cleared and double-stained to visualize bone and cartilage structures, and examined using stereoscopic microscopy. A matrix of osteological characters was developed, including bony processes, and sesamoid bone presence and position. Results show clear morphological differentiation linked to ecological function. Hematophagous bats share femoral and tibial grooves, robust fibulae, and short calcars traits facilitating terrestrial locomotion and stable feeding. Nectarivores display comparatively fewer bony processes and elongated, slender calcars, enabling brief flower landings. Carnivores exhibit pronounced femoral crests and sesamoid-rich autopodia, possibly related to prey handling. Frugivores have well-developed sesamoids and metatarsal processes, likely aiding in fruit manipulation and arboreal landing stability. Insectivores vary by habitat: open-space foragers as *Molossus molossus* show ossified calcars and tibial crests, while forest foragers like *Micronycteris minuta* lack these features. These findings underscore how ecological pressures, especially those tied to tropical guilds, have driven diverse functional adaptations in hind limb morphology among bats, expanding our understanding of their ecomorphological evolution.

Patterns of Prenatal Ossification and Sequence Heterochrony in Yangochiropteran Bats, Developmental and Evolutionary Basis of Morphological Adaptations

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Using Parsimov-based genetic inference (PGi), a comprehensive prenatal ossification sequences data-set of the skeleton (cranium + postcranium) from 15 species belonging to Phyllostomidae (ingroup), Molossidae, Vespertilionidae, and Emballonuridae (outgroups) families was optimized over a well-resolved phylogeny. Using 2D geometric morphometric analyses (14 landmarks in lateral view), prenatal cranial morphology development of *Artibeus lituratus*, *Sturnira lilium*, *Pygoderma bilabiatum* (Stenodermatinae), and *Carollia perspicillata* (Carollinae) were analyzed concerning heterochronies found. Heterochronies suggest a relationship with extant species ecology: Vespertilionidae + Molossidae consecutive early ossification onsets for the calcar (insects capture and manipulation), Desmodontinae early and late ossification onsets for hind and fore-limb elements (terrestrial locomotion), and Stenodermatinae with various consecutive late ossification onsets

for rostral and occipital cranial elements (differential bite performances at this frugivorous clade). Geometric morphometric analyses showed shared trends of developmental neurocranium compression and rostrum enlargement for the analyzed species (a common mammalian trend related to the brain and sensory capsules development). However, interspecific differences at the fetal stage exhibit reduced occipital and rostral cranial regions for Stenodermatinae regarding Carollinae species, corresponding with the adult morphology of those Phyllostomid frugivorous species. We confirm the mediation of peramorphosis mechanism at the evolutionary acquisition of extreme cranial morphologies in Stenodermatinae, supported by consecutive late ossification onset heterochronies for the rostral and occipital cranial regions, related to different food resource (fruit) exploitation capabilities of species.

Cracking the Case: Biomechanically Convergent Adaptations to Hard Biting in Morphologically Divergent Rat-Kangaroos (Genus *Bettongia*)

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Understanding the biomechanical basis of mammalian cranial feeding adaptations can provide insights into the evolutionary processes driving mammalian cranial diversity, and support palaeoecological interpretation of extinct mammals. However, cranial shape does not necessarily reflect habitual feeding behaviours. Instead, crania of two species with different feeding habits can be similar or even appear convergent if they need to masticate similarly hard food to survive. We employed geometric morphometrics to analyse shape variation among four bettong species (n=161). Of these, two crack the extremely hard seeds of sandalwood (*Santalum*), but feed mostly on soft truffles (*B. penicillata* or brushtail bettong) versus mechanically resistant grass, roots, and seeds (*B. lesueur* or burrowing bettong). We indeed found adaptations consistent with hard biting in both *Santalum*-cracking species, but based on different morphologies: the burrowing bettong has a shorter face with higher mechanical advantage, whereas the brushtail bettong has a reinforced area of bone behind a shorter, chisel-like third premolar. This suggests functional, but not morphological, cranial convergence related to hard biting, possibly involving a biomechanical trade-off with a large nasal cavity for the truffle-feeding *B. penicillata*. This indicates substantial variability in how mammals with different diets adapt to foods with similar biomechanical demands, and furthermore emphasizes that analysis of the entire cranium is required to yield insights into the dietary range of a species beyond just the hardest food.

Patterns of Ontogenetic Evolution Across Extant Marsupials Reflect Different Allometric Pathways to Ecomorphological Diversity

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In mammals, a group that shows spectacular adaptive diversity, there exist many lineages that have generated a remarkable amount of morphological diversity, whereas others have produced many anatomically and ecologically similar species. One such striking and poorly understood example is the relatively high level of morphological diversity in Australasian marsupials compared to that observed among American marsupials. In this study, we undertake a comprehensive macroevolutionary analysis of ontogenetic allometry of American and Australasian marsupials, to examine whether the contrasting levels of morphological diversity in these groups are reflected in their patterns of allometric evolution. We collate ontogenetic series for 62 species and 18 families of marsupials (n=2091 specimens), spanning across extant marsupial diversity. We combine analyses of allometric disparity and convergence with the application of macroevolutionary models that incorporate major phylogenetic and dietary partitions present in marsupials. Our results demonstrate significant lability of ontogenetic allometric trajectories among American and Australasian marsupials, yet a phylogenetically structured pattern of allometric evolution is preserved. Here we show that species diverging more than 65 million years ago, converge in their patterns of ontogenetic allometry under animalivorous and herbivorous diets, and that Australasian marsupials do not show significantly greater variation in patterns of ontogenetic allometry than their American counterparts, despite displaying greater magnitudes of extant ecomorphological diversity.

Paleo-Evo-Devo: A Pilgrimage into the Past Through the Lens of the Present

Evolutionary Origin of the Brachial Plexus

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The brachial plexus is morphologically well conserved in extant tetrapods, whereas the fishes lack a comparable pattern of spinal nerves, thereby representing an evolutionary novelty in the tetrapod lineage. In conventional paleontology and evo-devo, studies of the evolution of fins to limbs have focused mainly on skeletal morphology, showing that the evolution of skeletal morphology from fins to limbs proceeded gradually. However, it is unclear whether the acquisition of the brachial plexus occurred as a similarly gradual change. There is an old hypothesis by Fürbringer in the 19th century that the “narrowing” of the limb bud led to the evolution of the brachial plexus, but this has not been verified. There are two main questions regarding the evolutionary origin of the brachial plexus. The first is the evolutionary origin of the plexus mesenchyme, namely the embryonic environment in which the anastomoses of the brachial plexus are formed. Our ongoing developmental research into the lobed fin of the Australian lungfish is expected to be key to this. Another question is why limbs with the brachial plexus evolved only once. To answer this question, it is necessary, with the assumption that the

evolvability of the ancestors in deep time and descendants may have been different, to understand the evolutionary process of morphology, developmental plasticity and developmental constraints of the pectoral fin from its evolutionary origin.

Evolutionary and Developmental Patterns of Carpus and Tarsus in Salamanders and Basal Tetrapods Shed New Light on Fin to Limb Transition

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The metapterygial axis is the cornerstone in tracing homology across the fin-to-limb transition. This axis is widely believed to go through the ulnare/fibulare and distal carpals/tarsals (dc/dt) IV-III-II-I because it follows well the postaxial dominance of distal carpals/tarsals in anurans and amniotes. However, recent studies demonstrate that the postaxial dominance is a derived developmental pattern originated in amniotes, anurans and derived salamanders, and the carpals/tarsals are evolutionarily reduced in tetrapod lineages. Here we CT-scanned salamander specimens and compared them with early tetrapods and their fish ancestors to investigate primitive configurations of tetrapod carpal/tarsal. Centralia (c) 3 and 4 are found stably positioned postaxially to c2 and c1, respectively, in the primitive salamander clade Cryptobranchioidea and basal tetrapods (Tulerpeton, Greererpeton, Proterogyrinus), and collectively form series of bifurcations along the central column, where the intermedium (i), c1, c2 and dc/dt1 each has a 1:2 ratio between proximal and distal components. Loss of supernumerary elements occurs in a stepwise order of c1+c4, c2+c3, dc/dt1+2 and i+u/f during evolution, and these fusions is associated with a decelerated ossification of the central column and an accelerated ossification of the postaxial column (ulnare/fibulare and dc/dt4). The metapterygial axis is argued to go through the central column in salamanders and basal tetrapods, and is transferred to go through the postaxial column in amniotes and anurans with the loss of supernumerary carpals/tarsals.

Elucidating the Genetic Basis of Loss of Flight in the Emu, *Dromaius novaehollandiae*

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Determining the genetic underpinnings of phenotypic diversity is an enduring problem in evolutionary biology. Convergent evolution of regulatory regions is thought to drive independent losses of flight in the ratites, the group of flightless birds at the base of the avian tree. Comparative genomics, together with functional testing of enhancer elements, are powerful tools to determine noncoding genetic variants that may underlie loss of flight. We used a massively parallel reporter assay (MPRA) to test enhancer activity of

232 pairs of putative enhancers in chicken and emu, because chicken is capable of powered flight whereas emu is flightless. We tested this library of enhancers in the forelimb, hindlimb, and flank of chick embryos, and compared activity between paired chicken and emu enhancers. We found multiple examples of elements accelerated in emu that show differential activity in chicken forelimbs and hindlimbs. Strikingly, we also find conserved elements exhibiting differential activity between the chicken and emu elements. Finally, we report two regulatory regions located near genes upregulated in the emu forelimb relative to the early chick forelimb in which each emu enhancer has a higher activity than the corresponding chicken enhancer in chick limb buds. Using multimodal genomic data (RNA-seq, ATAC-seq, phyloACC, MPRA) in chicken and emu, we have identified two loci that may explain reduction of the forelimb, and hence loss of flight, in emus.

Evolution of Extrinsic Eye Muscles

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Extrinsic eye muscles (extraocular muscles) form a virtual constant in vertebrate anatomy. All living vertebrates have six extraocular muscles, and within gnathostomes there is little to no variation in the number and innervation pattern. However, lampreys have different innervation (two rectus muscles innervated by the abducens nerve). Placoderms are inferred to have seven muscles, two of which were controlled by the abducens nerve. The challenge remains to establish the homology of the six muscles across extant vertebrates. Here we present an alternative hypothesis based on new reconstruction of the orbital cavity in a jawless stem gnathostome, the osteostracan *Norselaspis glacialis*. Osteological correlates in *Norselaspis* resemble the placoderm pattern, once more indicating the presence of seven extraocular muscles. Two rectus muscles received the innervation by the abducens nerve in *Norselaspis* as in lampreys and placoderms. The trochlear-innervated oblique muscle sat in an intermediate position between lampreys and crown gnathostomes. Given this new evidence from *Norselaspis*, we argue that the seven extraocular muscles represent a primitive condition for all vertebrates. From this ground pattern, lampreys and crown gnathostomes lost one muscle each independently: the medial rectus and the posterior rectus, respectively. These independent loss events explain why the previously proposed homology requires elaborate changes in innervation and spatial arrangement. Our new scenario offers an altogether simpler solution within which the relationships between nerves and muscles remain conserved.

The Cellular and Genetic Changes Underlying the Pectoral Girdle Transformation from Water to Land

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The mechanisms of the pectoral girdle transformation at the origin of terrestrial locomotion in vertebrates remain an

outstanding problem. The loss of intramembranous bones and the enlargement of endochondral bones resulted in the disarticulation of the pectoral girdle from the skull and the formation of the neck during the fish-to-tetrapod transition. Despite the functional implications of this skeletal shift in the emergence of terrestrial vertebrates, the underlying genetic-developmental alterations have remained enigmatic. We recently found that the pectoral girdle in zebrafish develop as an amalgam of osteoblasts derived from various embryonic progenitor cell populations. We also found that mesodermal cells expressing gli3, a transcription factor gene in the Hedgehog signaling pathway, differentiate into both intramembranous and endochondral bones. Intriguingly, Gli and Hedgehog compound knockout fish exhibited an unexpected combination of actinopterygian fish and stem-tetrapod pectoral girdle characteristics. These ontogenetic and anatomical data suggest that a trade-off between the two distinct ossification pathways is a deeply embedded developmental program in bony fishes and that tuning of cellular heterogeneity and Gli signaling can generate novel pectoral girdle akin to those of stem-tetrapods at the dawn of vertebrate terrestrialization.

Reconstructing the Evolution of Limb Regeneration in Lissamphibians: New Clues from Paleozoic Fossils

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Unlike amniotes, salamanders and frogs (i.e. limbed lissamphibians) can fully regenerate their limbs. It has been shown that this capacity was also present in temnospondyls, the lissamphibian stem group. Based on fossil individuals showing skeletal abnormalities that are distinctive of irregular limb regeneration in living salamanders, regeneration capabilities have been inferred for *Micromelerpeton credneri*, a 300-million-year-old temnospondyl. However, limb regeneration has not yet been reported in any other stem lissamphibian. In this study, we show that limb abnormalities indicative of regeneration are also present in two additional temnospondyl species that coexisted with *Micromelerpeton*: *Apateon pedestris* and *Sclerocephalus haeuseri*. Interestingly, whereas *Micromelerpeton* and *Apateon* are closely related to lissamphibians, *Sclerocephalus* diverged from them very early in the temnospondyl evolutionary history. Therefore, in this phylogenetic context, our data not only support the idea that limb regeneration is ancestral to lissamphibians, but also show that it was likely a widespread phenomenon in temnospondyls. In light of our findings and the rich evidence available on the paleobiology of these fossil amphibians, we revisit different hypotheses that have been proposed on why salamanders and frogs are the only living tetrapods with limb regeneration capabilities, including the putative relationship between regeneration and metamorphosis, cell size, and preaxial polarity in limb development.

Comparative Functional Morphology of Elasmobranch Fishes

What Drives Differences in Chondrichthyan Ear Geometry?

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The inner ear of vertebrates functions both in hearing and equilibrium. In some groups of tetrapods, habitat and locomotion appear to be important factors governing shape change in the skeletal labyrinth, rather than labyrinth geometry being primarily influenced by phylogenetic history. However, to date, the drivers for inner ear variation have only been explored in cartilaginous fishes using the membranous labyrinth of the inner ear, which requires magnetic resonance imaging (MRI) or destructive dissection. We have recently embarked on a study of the comparative morphology of the skeletal labyrinth in chondrichthyans, aiming to test the relationship between habitat and locomotion and the shape of the inner ear. We share preliminary descriptive findings in a handful of taxa, grouped both by taxonomy and by shared ecology, and we compare these findings with prior studies of the skeletal labyrinth in tetrapods and with studies of the membranous labyrinth of sharks and their relatives.

Modernizing Morphology: Advances in the Study of Mineralized Tissues of Rays and Sharks

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The mineralized tissues of sharks and rays—tooth, denticle and skeleton—differ fundamentally from those of mammals, in composition, architecture and development. Such natural variation is exceedingly valuable for understanding how nature mineralizes and structures materials, yet nonmammalian mineralized tissues remain understudied. Recent directions in elasmobranch functional morphology are changing this: following a previous heavy focus on the kinematics of shark and ray feeding and swimming, the advent of more accessible laboratory-based tools for studying finescale anatomy, tissue mechanics and materials characterization have ushered in a new era for form-function research. Here, we discuss these advances, drawing on examples from diverse species and size scales to offer perspectives on the evolution of mineralized tissues and growth-mechanics trade-offs (both inside and outside the body), while reflecting on the value of cross-disciplinary bridges to invigorate the study of biological tissues and inform the design of bioinspired materials.

To Glow or not to Glow: The Evolution of Eye and Photophore Aize, and the Function of Bioluminescence in Lantern Sharks (Squaliformes: Etmopteridae)

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Bioluminescence (the production and emission of light by living organisms) has evolved on numerous occasions in diverse radiations of terrestrial and aquatic animals. Bioluminescent taxa are particularly abundant in the mesopelagic zone (200–1000 m) of marine environments, where levels of ambient light diminish exponentially with depth resulting in complex sensory-environmental gradients. In many marine animals, the specific function of bioluminescence remains poorly understood. Lantern sharks (Etmopteridae) are one such group. Bioluminescent flank markings in Etmopterids have been suggested to play a role in predator evasion and/or intraspecific communication, either during group hunting or reproductive events. However, empirical behavioural and physiological data are limited to a small number of species, and ecologically unrealistic ex-situ experimental designs. Here, we apply classical ecomorphological theory and cutting-edge comparative phylogenetic methods to interspecific and intraspecific datasets (n=52 and n=14 species, respectively) of Etmopterid eye and photophore morphology. We provide multiple tests of the hypotheses that lateral flank markings function 1) as a counterillumination adaptation for predator evasion, 2) as a sexual signal, and 3) as a nonsexual intraspecific communication signal. Cumulatively, these tests give unparalleled insight into the functional role of bioluminescence in sharks, and the mechanism(s) by which it influences taxonomic diversity.

From Armor to Art: The Coloring Role of Blue Shark Denticles

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Sharks' skin is armored with tiny, tooth-like placoid scales called denticles. While their fluid dynamics are well-studied across species and body regions, our research reveals a new optical role for denticles. Although often perceived as grey, some shark species display diverse hues and camouflage strategies, including countershading and bioluminescence. The blue shark (*Prionace glauca*) exemplifies striking countershading, with a vibrant blue dorsal side fading through silver-grey laterally to white ventrally. μ CT showed that the pulp cavity in blue shark denticles is expanded, occupying about 25% of the volume. Z-stack imaging from polarized and bright-field microscopy uncovered a densely filled cavity with light-absorbing and scattering cells. FIB-SEM revealed that guanine crystals (1500 x 600 x 60 nm) are stacked within reflecting cells above melanosome-filled absorbing cells (~500 nm) in blue and silver denticles. These absorbing cells are absent in white denticles, and larger, square crystals (600 x 70 nm) are chaotically arranged within the reflecting cells. We propose that color diversity across the body depends on guanine crystal morphology and architecture, shaping broadband light scattering, while melanin variably absorbs specific wavelengths. The interaction of these domains results in vibrant colors visible through transparent denticle walls, revealing a previously unrecognized role for denticles as micro-scale color-producing "laboratories." Understanding these mechanisms provides insights into shark optical ecology, social signaling, conservation, and the development of bio-inspired, structurally colored materials.

Against the Grain: Exploring the Unique Skin Denticle Patterns of Basking Sharks

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In contrast to other sharks, the slow swimming basking shark (*Cetorhinus maximus*), a high-volume suspension filter feeder is covered by massive, curved tooth-shaped denticles. Despite shark denticles are effectively little teeth embedded in the skin, most examples, however, consist of a wide basal plate anchored in the skin, tapering towards a pointed crown, often covered by ridges. In streamlined arrangement on the skin with cusp tips pointing towards the trailing edge of the body they enable drag reduction. Antithetical to that, basking shark denticles are densely clumped together to form ‘paver blocks’ separated by unscaled folds. I found that the denticles within the blocks are circularly arranged with tips covering all azimuthal directions and the folds by bordering denticles of adjacent paver blocks horizontally. The wrinkling, which resembles the folded skin of elephants, made possible by this deviating arrangement of denticles, benefits the deforming of the skin. Using high-resolution μ CT scans, histology, mechanical tests and large-area laser scanning, I characterized how significant shape and orientation of denticles differ from other species and display variations of denticles and skin alignment along the body to discuss how this unique arrangement promotes increased stretching of the head skin for oral volume enlargement. These investigations provide much-needed insights for more in-depth studies of basking shark anatomy and understanding the evolution and ecological constraints of large marine suspension filter feeders.

Kings and Queens of the Air: How Archosaurs Grew Wings and Controlled the Skies

New Information on the Hind Limb Feathering, Soft Tissues and Skeleton of *Microraptor* (Theropoda: Dromaeosauridae)

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Microraptor has one of the most characteristic extensive leg feathering among extinct and extant paravians. Its distinct hind limb features differentiate it from most other paravians, leading to a variety of hypotheses regarding the function of its

elaborate feathering. Although recent research has attempted to clarify its evolutionary role, the anatomy of *Microraptor* has only been described based on a relatively small number of fossil specimens. In this study, we analyse 16 *Microraptor* specimens, including 8 that have not been previously described, with details on their bones, soft tissues and feathers. We revised the hindwing morphology, with feathers that cover the entire hind limb except the pedal digits. We detail six specific feather types: metatarsal remiges, long metatarsal coverts, long femoral feathers, and for the first time, long tibial feathers, anterior coverts, and minor coverts. Our examination of specimens BMNHC PH881 and STM 5-5, 5-75, 6-62, and 6-86 partly correspond to observations in previous studies, but importantly, we observe a more proximal position of the triangular wing area formed by long tibial feathers and metatarsal coverts. This distinctive configuration, outlining the tibiotarsus-metatarsus junction, is unknown in any other bird or non-avian paravian. Furthermore, the asymmetrical, close-vanned metatarsal coverts remind of forewing feathers and are new for the leg feathering. These findings provide new insight into *Microraptor* locomotion and behaviour, suggesting some complex ecological implications.

From so Humble a Beginning: Ways Forward in Archosaur Wing Analysis

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Modeling how ancient organisms learned to fly has long occupied a special place in paleontology. But modeling needs to be anchored, or its just recreating our favorite monsters from the big screen with better Latin nomenclature. Here I will discuss how we bridge the gaps from the past to the present and set a path forward to better understand how and why archosaurs have dominated the airways for over 220 million years. From looking at how atmospheric changes, physiology and cost of transport have influenced patterns of evolution, to linking trackways and other underexplored lines of evidence to squeeze new blood from old stones, we are moving into an age where questions that have been plague use for decades may finally be addressed. As a capstone on this session, we will also flesh out the points of debates and consensus we need to move towards to grow beyond old dichotomies and better understand the diversity of wing-based behaviors across archosaurs. Just like the organisms themselves, new ideas and methods most beautiful and wonderful have been, and are being, evolved.

The Role of Atmospheric Density in the Emergence of Flight

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It is extremely unlikely that atmospheric mass has been constant over time. Crustal productivity and outgassing of both CO₂ and N₂ are known to vary, as does the geomagnetic field of the Earth, influencing atmospheric retention and loss. Flight aerodynamics and thermal engineering are universal and can be used as proxies for air density. Animal respiration and metabolism are also useful indicators of oxygen availability. The simplest form of flight, gliding, evolved several times in reptiles living in forested areas, such as the late Permian *Coelurosauravus* and the late Triassic *Kuehneosuchus*, both relatively large at about 200 g. Simulations suggest that airspeeds, launch drop and energy conservation were viable at an atmospheric density equivalent to ~1.7 bar, a value also found for the flight and thermoregulation of giant Permian griffenfly species, all of which became extinct at the end Permian. During the late Triassic, other giant dragonfly bauplan and titanoptera insects emerged, along with small, early pterosaurs and bony ‘flying’ fish, again indicating a denser air. The end Triassic and early Jurassic witnessed the loss of gliding lizards and ‘flying’ fish, as well as a Large Volant Insect Gap, suggesting a cold low density atmosphere incompatible with large animal flight. We reconstruct atmospheric mass for the Mesozoic showing the close correlation and between air density and the development of animal flight.

Modeling the Origins of Pterosaur Flight

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Animals evolved aerial locomotion—whether parachuting, gliding, or powered flight—over thirty separate times. While the origin of bird flight has been extensively studied, less is definitively known about how bats and pterosaurs developed this ability. The biology and ecology of pterosaur ancestors have long been a mystery, but recent fossil discoveries of early pterosaur-omorphs are finally unraveling this mystery. Building on these new finds, we used computer modeling, similar to methods used for early bats and birds, to understand how pterosaur ancestors might have moved. These models incorporate fossil data from close pterosaur relatives, early pterosaurs, and flying dinosaurs, along with ancient atmospheric density values. Our goal is to create testable ideas about how pterosaurs transitioned from climbing to gliding to powered flight. This study aims to advance the study of early pterosaur evolution, much like how bird evolution research has progressed over the past two decades.

Do What You Can, with What You Have, Where You Are: Locomotory Wing Use Diversity In Non-Avian Theropods

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Powered flight is a rare and extraordinary thing, and thus it is not surprising that much of the work on the origins of wing-

based locomotion in theropods has focused on it. Yet flying isn't the only possible locomotory use of wings. Studies of living birds have shown wings to aid in facilitating escape behaviors in pre-flight capable juveniles (W.A.I.R., controlled flapping descent), increasing maneuverability in terrestrial locomotion (turning, braking) as well as aiding in terrestrial stability during prey capture. Given the recent discovery of physical evidence of wing assisted running amongst non-avian theropods, the topic of how wings were used in non-flight capable taxa deserves more investigation. Here, using a large data set compiled originally to estimate flight potential across the theropod to bird transition, we look at the evolution and diversification of locomotory functions for wings amongst feathered theropods. We discuss how integrating shoulder morphology with wing metrics opens new possibilities for behavioral morphospace reconstructions within theropods. The old question of “what use of half a wing” may lead not just to stepping stones on the pathway to flight, but a greater understanding of the behavioral diversity of that feathered forelimbs can provide.

Investigating Wing Muscle Attachments Across Early Paravians Through Soft Tissue Reconstruction

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Understanding the flight stroke is essential for studying aerodynamic motion through air. Wing muscles and ligaments are indispensable for modern birds to optimize wing shape during flight. Studying the soft tissues in feathered dinosaurs, including *Microraptor*, *Anchiornis*, *Archaeopteryx* and *Confuciusornis*, is thus key towards further understanding early flight in theropods. Limb musculature in fossil theropods has been reconstructed through analyzing and applying soft tissue data of extant archosaurs (especially birds) to recreate muscle attachment sites. Recognizing and mapping the shape, size and position of wing muscle groups would greatly aid in studying flight strokes in early paravians. Preliminary muscle reconstructions focus on the forelimb and shoulder. Origins and insertions of muscles are determined based on preserved landmarks, previous fossil reconstructions, and referencing the musculature of modern birds and crocodilians. Early results primarily show similarities and few differences in muscle attachment sizes and relative locations among the observed taxa. The size of the attachment sites at the humeral head shows the most variation, possibly due to differences in arm motions. Larger attachment sites could indicate increased muscle usage, influencing flight stroke motions. These results provide a platform for further work to better understand these observations and their implications for early flight.

New *Microraptor* Specimens Bring Insight into the Forewing Anatomy and its Impact on Flight Behavior and Ecology

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Microraptor is an essential animal for understanding the evolution of flight in birds and their closest relatives. Recent studies have uncovered evidence of its powered flight potential and details of its diet and ecology. However, we are still missing a thorough description of the anatomy of *Microraptor*, which connects feathers, soft tissues, and osteology. Past reconstruction of the forewings relied on brief descriptions of the primary and secondary feathers. Observed under white light and Laser-Stimulated Fluorescence, ten new specimens from the Shandong Tianyu Museum of Nature and previously studied specimens (e.g., IVPP V13352 and BMNH PH881) were used to reconstruct the wing shape from the tip of the digits to the proximal end of the ulna, with the different layers, number and characteristics of each feather type. New information was recovered from the humerus, radius and wrist bones, which, with the description of the shoulder muscles, propatagium and postpatagium, help us understand the role of *Microraptor's* forewing anatomy in wing cohesiveness and lift generation. Results suggest *Microraptor* was a moderately-fast, high-agility, flying forager engaging in short-range ambush within cluttered environments. Comparing *Microraptor's* wings with other key early paravians (e.g., *Anchiornis*, *Archaeopteryx* and *Confuciusornis*) and modern birds expands our knowledge of flight origins and early diverging paravian theropods, as well as opens new perspectives for future locomotion simulation work.

Specialisations in *Microraptor* Towards the Utilization of Low Reynolds Flow Features

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Modern agile flyers, such as birds and insects, employ complex aerodynamic mechanisms—including leading edge vortices, tip vortices, rapid pitch rotations, and wing-wake interactions—to enhance performance. However, the evolutionary origins of these traits remain unclear. Early birds and their relatives, like *Microraptor*, possessed a unique multi-winged design with flight feathers on their arms, legs, and tail, a configuration absent in modern species. The flight capabilities of these early flyers have long been debated, particularly regarding the evolutionary drivers behind their multi-winged anatomy and its loss in favour of the modern wing pair configuration. Here, we investigate the aerodynamics and wing-wing interactions in *Microraptor*, characterizing their flight benefits. Our findings reveal flow patterns similar to those observed in extant flying species, including leading edge vortices on both forewings and hindwings, beneficial wake interactions between wings, and tip vortices on the distally flared hindwing. These results suggest that *Microraptor's* wings were evolutionarily specialized to exploit these aerodynamic features, indicating that such adaptations were already present—to varying degrees—in early theropod flyers.

Feathered Dragons: An Historical Review of Questions of the Origins of Birds and of Avian Flight

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Living birds (Aves/Neornithes) are among the most transformed of extant tetrapods. Their diverse adaptations result in a profound morphological gulf from other extant forms, rendering early attempts to place them in an evolutionary context problematic. Superficial similarities with turtles were among the few potential connections to other living forms accessible in the early 19th Century. However, as the fossil record of vertebrates were more fully revealed over the course of the 19th and early 20th Centuries, it became clearer that bird origins lay among the archosaurian reptiles, with Crocodylia as their closest living relations. Continued work in the mid-20th Century onward clarified that birds are deeply nested among coelurosaurian theropod dinosaurs, and that numerous adaptations previously interpreted as having evolved in the context of flight (post-cranial pneumaticity, furculae, laterally oriented glenoid fossae, pennaceous feathers, among many others) originated stepwise among terrestrial forms. While the phylogenetic position of birds as paravian coelurosaurs is firmly established, the functional and behavioral situations in which avian flight originated remains a matter of debate. Early models of arboreal “trees-down” and cursorial “ground-up” models have been found to be oversimplifications and indeed not mutually exclusive as originally conceived. Indeed, while flight as manifested in extant birds seems to be a singular evolutionary origin, various interpretations suggest this is just one case of volancy evolving among the branches of the paravian tree.

Laser Stimulated Fluorescence Reveals Delicate Membranes in the Early Volant Reptiles

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Pterosaurs, the avemetatarsalian pioneers of flight, vanished in the K-Pg extinction. Given the lack of extant relatives, our understanding of their behaviour and anatomy relies on the fossil record. The soft anatomy of pterosaurs can be inferred from fossilised tissues preserving elements varying from the gular pouches to cranial crests, and importantly, flight membranes. For this project, we have amassed soft tissue instances corroborated with novel surface screening techniques deploying Ultraviolet (UV) and Laser Stimulated Fluorescence (LSF) to existing international collections. The screening recovered previously unseen soft tissues in multiple non-pterodactyloid pterosaurs. Noted pterosaurs stand out from other volant vertebrates by sporting an elongate ossified tail with an elaborate membrane at its terminus. The fluorescence helped to delineate the unique membrane and recover its delicate internal supportive structure. The structures show two different morphologies that intersect, creating a fluid lattice. We suggest the lattice supported a sophisticated dynamic tensioning system,

used to maintain vane stiffness, allowing the tail to augment flight control. The application of new surface screening techniques helps to reveal key anatomical-functional features otherwise unseen in the visible light.

Falling with Style: Evaluation of Glide Capability in Maniraptoran Theropods

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Only three lineages of tetrapods are known to have evolved powered, flapping flight, while a much more common form of aerial locomotion is gliding flight or parachuting. Given its frequent occurrence and relative ease of achievement, gliding has been suggested as a prerequisite intermediate on the path from terrestrial non-avian theropods to flying early birds, followed by repeated occurrences of derived flightlessness. If accurate, previous suspected “stepping stones” to powered avian flight are actually vestigial remnants of a gliding ancestor. Here we investigate the claim that gliding flight using a feathered aerofoil can be plausibly reconstructed outside of Paraves and could this be a crucial intermediate stage explaining the origin of the avian wing. We find that wing loading values greatly exceed those of any known extant or extinct gliding tetrapod until we reach Paraves, and then it is still at the upper end of the range for most taxa within that clade. Even assuming a parachuting behavior with a feathered wing would be unlikely in non-paravian taxa or those above 3 kg. Descent velocity estimates for non-paravian taxa are exceedingly high, often greater than 20 m/s. Even accounting for estimates of different atmospheric densities in the Late Jurassic and Early Cretaceous, this is not enough to overcome these deficiencies.

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