



UNIVERSITY OF  
LINCOLN



The 69<sup>th</sup> Annual Symposium of  
Vertebrate Palaeontology and  
Comparative Anatomy





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### **About the Paleontological association**

The Palaeontological Association (Est 1957) is a charity which funds and promotes the study of paleontology. The support provided by the charity includes sponsorship of meetings and events (such as SVPCA), and gifting of awards. Additionally, the association are involved in publication of research in the journal *Paleontology*.



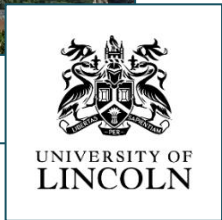


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### Venue information

Situated in the heart of a historic city on the beautiful Brayford Pool Waterfront, the University of Lincoln is proud of its reputation for putting students at the heart of everything it does. We are ranked in the top 30 UK universities for student satisfaction in the Guardian University Guide 2023, listed in the world's top 130 universities in the Times Higher Education's (THE) Young University Rankings 2022, and hold a top five-star score overall in the QS Stars rating system of global universities.



UNIVERSITY OF  
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## Code of Conduct for SVPCA & SPPC meetings

The SVPCA and SPPC meetings welcome all those who are interested in vertebrate palaeontology, comparative anatomy, and care of fossil collections. Symposium organisers and the steering group are committed to maintaining a meeting environment that encourages the free expression and exchange of scientific ideas through open and respectful dialogues at oral and poster presentations, workshops, fieldtrips, and associated social events. Diversity in all its forms is celebrated and meeting attendees are expected to be respectful and considerate of fellow attendees, meeting organisers, and facility staff.

### **Behavioural expectations**

Throughout the meeting and associated events, attendees are expected to behave in a courteous, collegial, and respectful manner to each other, volunteers, exhibitors, and facility staff. Attendees should respect common sense rules for professional and personal interactions, public behaviour (including behaviour in public electronic communications), common courtesy, respect for private property, and respect for the intellectual property of presenters. Demeaning, abusive, discriminatory, harassing, or threatening behaviour will not be tolerated, in either personal or electronic interactions.





## Social media and digital images

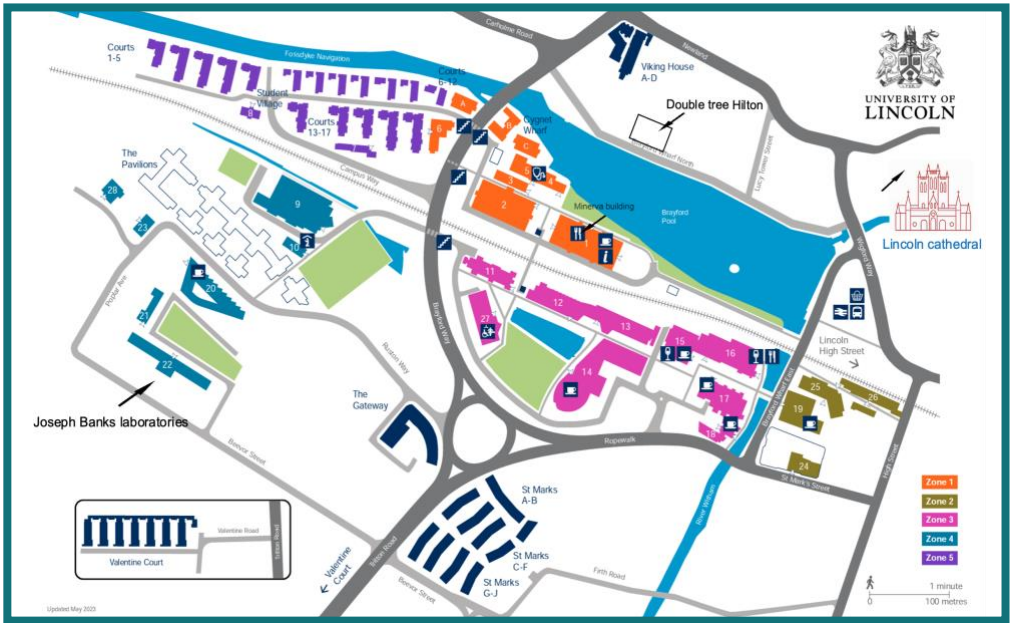
At the time of the meeting, open discussion on social media and other outlets is encouraged. While the default assumption is to allow discussion of presentations on social media, attendees are asked to respect any request by an author to not disseminate the contents of their talk or poster. Authors should use the icons available on the SVPCA website to clearly express when content from their talks/posters should not be recorded, photographed, or posted online.

Any attendee who believes that an incident of scientific or ethical misconduct has taken place, or who experiences/witnesses any form of harassment is encouraged to contact the lead Symposium organiser or designated members of the steering group. All reports will be treated seriously and in the strictest confidence. Reports of such incidents will be investigated by the Symposium organiser with support from the Steering Group and, if a complaint is upheld, appropriate action will be taken. This action may include the banning of individuals found to have behaved inappropriately from giving presentations at future meetings, and in the most severe cases, individuals may be banned from attending SVPCA and SPPC meetings in the future.





## Maps



Scan (or click) the QR code for help navigating around the university!

The Double Tree Hilton (LN1 1YW), site of the conference dinner (08/09/2023).

Highlighted (on the right), location of The Lincoln Hotel (LN2 1PN) where the auction will be hosted. (07/09/2023)

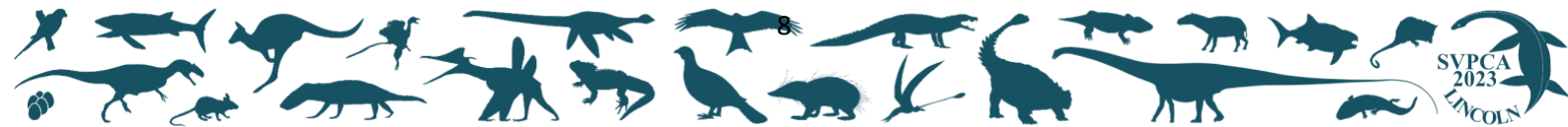






06/08/2023

Time start	MB1019	MB1020	MB0302
09:30 – 10:00	Registration	Tea/Coffee	
10:00 – 10:10	Posters	Workshop	<b>Allington-Jones</b> SPPC: Opening remarks
10:10 – 10:30		Workshop	<b>Kieran Miles</b> Removing plaster and bulap from Triceratops
10:30 – 10:50		Workshop	<b>Allington-Jones</b> Solvent Gels
10:50 – 11:10		Workshop	<b>Vervenioutou</b> Conservation and display of highly fragmented fulgurite
11:10 – 11:40		Tea/Coffee	
11:40 – 12:00		Workshop	<b>Ragni</b> How to become a fossil preparator in Europe
12:00 – 12:20		Workshop	<b>Vervenioutou</b> Diprotodon at the NHM
12:20 – 12:40		Workshop	<b>Nicholls</b> Megalosaurus moulds
12:40 – 13:30		Lunch	
13:30 – 13:40			<b>M. Sakamoto</b> SVPCL Special Symposium: Opening remarks
13:40 – 14:00			<b>M. Sakamoto</b> Big Data in vertebrate palaeontology
14:00 – 14:20			<b>O. Price</b> Avian flight evolution
14:20 – 14:40			<b>W. Deakin</b> Evolutionary constraint in big datasets
14:40 – 15:00			<b>E. Green</b> Understanding the evolution of biological complexity
15:00 – 15:30		Tea/Coffee	
15:30 – 15:50			<b>A. Shipley</b> Trait-based model of marine food webs
15:50 – 16:10			<b>A. Lanzetti</b> Feeding in heterostracans jawless “fishes”
16:10 – 16:30			<b>S. Singh</b> Megacarnivore functional morphology
16:30 – 17:30		<b>J. Bright</b> What can Big Data tell us about bird evolution?	

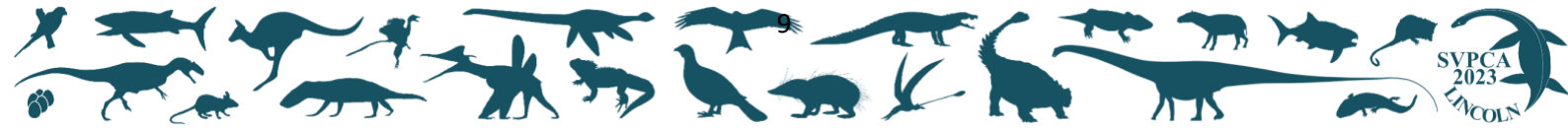






07/08/2023

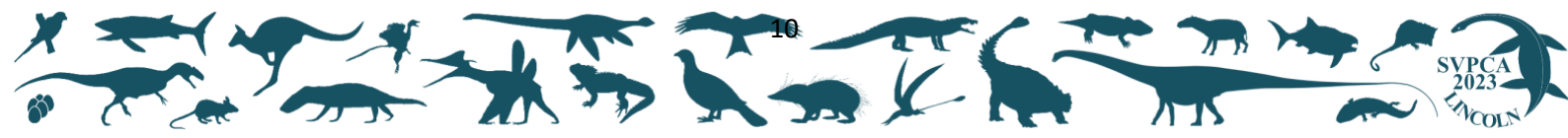
Time	MB1019	MB1020	MB0302
08:30 – 09:15	Registration	Tea/Coffee	
09:15 – 09:30	Posters		<b>M. Sakamoto</b> Opening Remarks
09:30 – 09:45			<b>M. Sakamoto</b> Integrating form and function
09:45 – 10:00			<b>E. Newham</b> Cementochronology reveals evolution
10:00 – 10:15			<b>J. Liston</b> Pachycormids, Palaeontologists and Pandemics
10:15 – 11:00			Tea/Coffee
11:00 – 11:15			<b>D. C. Deeming</b> Egg shape in birds
11:15 – 11:30			<b>A. Brinkworth</b> Bird appendicular skeletons
11:30 – 11:45			<b>E. Webb</b> Thoracic cage morphology
11:45 – 12:00			<b>K. Starczewski</b> FEA tenrec mandible
12:00 – 13:30			Lunch
13:30 – 13:45			<b>E. Hunt</b> Galloanserae skull evolution
13:45 – 14:00			<b>M. Howgate</b> Furcula of Allosaurus
14:00 – 14:15			<b>M. Dempsey</b> Limb muscle masses predicted from skeleton
14:15 – 14:20			<b>S. Wheatley</b> Theropod hindlimb shape
14:20 – 14:25			<b>J. Bestwick</b> New anklyosaurian osteoderm
14:25 – 14:30			Q&A (Lightning)
14:30 – 15:15			Tea/Coffee
15:15 – 15:30			<b>M. Taylor</b> Carnegie Diplodocus
15:30 – 15:45			<b>R. Forrest</b> Lincoln plesiosaurs
15:45 – 16:00			<b>A. Lister</b> Proboscidean dental evolution
16:00 – 17:00		Cold refreshments	
19:00 – 22:00	Annual auction at the Lincoln Hotel	Annual auction at the Lincoln Hotel	





08/08/2023

Time	MB1019	MB1020	MB0302
08:30 – 09:15	Registration	Tea/Coffee	
09:15 – 09:30	Posters		<b>M Sakamoto</b> Announcements
09:30 – 09:45			<b>R. S. H. Smyth</b> Pterosaur palaeoecology and evolution
09:45 – 10:00			<b>D. Henderson</b> Cranial steering in pterosaurs
10:00 – 10:15			<b>D. Unwin</b> Ontogenetic niche partitioning in pterosaurs
10:15 – 11:00			Tea/Coffee
11:00 – 11:15			<b>L. Muscott</b> Understanding Plesiosaur Locomotion
11:15 – 11:30			<b>P.G. Gill</b> Tooth replacement in the Brazilian cynodont
11:30 – 11:45			<b>Stockdale</b> Species Distribution Modelling in Dinosaurs
11:45 – 12:00			<b>Gernelle</b> Cenozoic Laurasian marsupials
12:00 – 13:30			Lunch
13:30 – 13:45			<b>Harrison</b> Bite force in parrots
13:45 – 14:00			<b>Ballell</b> Mandibular disparity in Lepidosauria
14:00 – 14:15			<b>Wagstaffe</b> Cranial kinesis in birds
14:15 – 14:30			<b>O'Driscoll</b> Mandibular Mass Distribution
14:30 – 15:15			Tea/Coffee
15:15 – 15:30			<b>Butler</b> New leptopleuronine procolophonid
15:30 – 15:45			<b>Pereira</b> Fish assemblage of the Lower Cretaceous of Portugal
15:45 – 16:00			<b>Sakamoto</b> Closing Remarks
16:00 – 18:00		Cold refreshments	
19:00 – 19:30	Reception drinks	The Double Tree Hilton	
19:30 – 21:30	Annual dinner		





09/09/2023

Field trip to Ketton quarry, area of coach departure to be communicated during the conference. Please email M. Sakamoto if you have yet to sign up for the field trip.

**About the site:**

Ketton quarry is fossiliferous active quarry situated about an hour away from Lincoln. It is currently under management of the Leicestershire and Rutland wildlife trust, who's aim is to encourage the re-wildification of the area. Within its 28 hectares of land, Ketton quarry is home to a variety of wildlife including a wide range of flies and moths, nightingales and even adders.



Ketton quarry

Pit Lane, Ketton, Stamford

PE9 3SZ

Coach leaves at 08:00 and returns at 16:00





Special symposium: Big data in vertebrate palaeontology and comparative anatomy.

We live in the age of “big data”. We generate and use vast quantities of ever-complex data in our daily lives, from browsing the internet to navigating routes abroad while on holiday. Vertebrate palaeontology and comparative anatomy are no exception. This symposium highlights and showcases how big data have transformed and advanced our understanding of vertebrate palaeontology and comparative anatomy.

Phylogenetic comparative analyses reveal a directional temporal trend in avian forelimb length.

Olivia Price, School of Biological Sciences, University of Reading

The evolution of flight across many organisms has captured the imagination of researchers for decades. Recent evidence supports the notion that the evolution of modern avian flight was a gradual accumulation of features over time. However, despite intense efforts and theoretical expectations, no temporal trend in relative forelimb length has been found in early birds. Here we use Bayesian phylogenetic comparative methods to test for a temporal trend in relative forelimb length whilst simultaneously accounting for the known allometric relationship of the avian forelimb. Our results provide the first evidence of a long-term trend in increasing forelimb length in Mesozoic birds. Selection towards longer forelimbs in early birds may be associated with increased flight experimentation and the beginnings of increasing flight efficiency, which ultimately led to birds’ domination of the skies.





Using theoretical morphology to investigate evolutionary constraint in big datasets

**William Deakin<sup>1</sup>**

<sup>1</sup>University of Bristol

Theoretical morphology has been employed as an analytical tool for over 50 years. Its benefits lie in generating control samples of form, allowing us to compare the morphological pathways that a clade could have evolved through with the specific trajectory it followed through time. This comes at the cost of extremely inefficient sampling of morphospace. As the number of morphological axes increases, the volume of empirical morphospace increases exponentially, and so too does the number of theoretical morphologies required to adequately sample it. This heavy cost has rendered theoretical morphology infeasible in the past, especially with the increasing number of dimensions in morphological analyses over time. However, with the increased processing power of modern computers, the use of theoretical morphospace has become practical when describing the variety of emergent properties of morphology (such as mechanical function or complexity) within a dataset. It is even efficient when investigating these properties in big datasets, which is increasingly popular in palaeobiological studies. In this talk, I will discuss how theoretical morphology, a framework that has remained relatively static for over half a century, can be adapted to ask questions of large, modern datasets.





## Biological Complexity in Perissodactyla

**Emily Green**<sup>1</sup>, Marcello Ruta<sup>1</sup>, Andrew Brinkworth<sup>2</sup>, Yimeng Li<sup>3</sup>, Jack Oyston<sup>4</sup>, Matthew Wills<sup>2</sup>

<sup>1</sup>Department of Life Sciences, Joseph Banks Laboratories, University of Lincoln, <sup>2</sup>Milner Centre for Evolution, Department of Life sciences, University of Bath, <sup>3</sup>Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences, <sup>4</sup>Centre for Integrative Anatomy, Department of Genetics, Evolution, and Environment, University College London

Biological complexity is a key but understudied facet of macroevolution, but neither its adaptive role nor its relationship with key innovations are known. Using Perissodactyla as a model group, we test whether complexity increased over time following a driven trend, and whether its evolutionary trajectory was comparable across different skeletal structures. We use vertebral and appendicular data to derive indices of complexity from vertebral counts, and limb bone measurements, respectively. These indices are subjected to a variety of tests for detecting driven trends. We find that complexity changes did not follow a driven trend in perissodactyls, and that vertebral and appendicular complexity followed divergent patterns. For all tested indices, increases and decreases in complexity values along ancestor-descendant pairs do not differ significantly. In addition, changes in minimum complexity values conform to a stasis model or random walk models throughout the Cenozoic. Despite variation within genera, changes occur gradually along individual lineages. We find multiple instances of reversals in complexity, e.g., in the appendicular skeleton following the emergence of cursoriality in some lineages.





## Reconstructing food webs using a trait-based model: insights into a marine megafaunal extinction

**Amy E. Shipley**<sup>1</sup>, Tracy Aze<sup>1</sup>, Catalina Pimiento<sup>2,3</sup>, Andrew P. Beckerman<sup>4</sup>, Jennifer A. Dunne<sup>5</sup> and Alexander M. Dunhill<sup>1</sup>

<sup>1</sup> University of Leeds, UK, <sup>2</sup> University of Zurich, Switzerland, <sup>3</sup> Swansea University, UK, <sup>4</sup> University of Sheffield, UK, <sup>5</sup> Santa Fe Institute, USA

Despite increasing threats of extinction, it is not well understood how vertebrate communities in marine ecosystems may be impacted following losses of taxa in different trophic levels. Reconstructing extinct ecosystems can inform on how community dynamics shift following extinction events. An end-Pliocene marine extinction resulted in global losses of megafauna, including the giant apex predator *Otodus megalodon*.

Using a trait-based model, we constructed metacommunity webs of ~300 nodes for pre- and post-extinction North Atlantic communities. Vertebrate occurrences were collated from fossil data and assigned the traits of body size, spatial distribution and preferred prey (inferred from known feeding interactions). As modern food webs exhibit a standard link distribution across trophic levels, we additionally enforced this distribution on the metacommunity webs by randomly removing links, producing 50 iterations of these ‘realised’ webs for both time bins. Our analyses indicate consistency in structure across the extinction in both the metacommunity and realised webs, suggesting this ecosystem was robust to losses of taxa in higher trophic levels (even the giant generalist *O. megalodon*). However, a slight decrease in vertical complexity and increase in generalism in the Pleistocene could indicate a drop in primary productivity, a potential driver for this extinction event.





No jaws? No problem. High-density morphometrics characterizes the diversity in the feeding apparatus of heterostracans jawless fish (Agnatha: Heterostraci)

**Agnese Lanzetti**<sup>1,2</sup>, Richard Dearden<sup>1,3</sup>, Andrew Jones<sup>1</sup>, Sam Giles<sup>1</sup>, Zerina Johanson<sup>2</sup>, Stephan Lautenschlager<sup>1</sup>, Emma Randle<sup>1</sup>, Ivan Sansom<sup>1</sup>

<sup>1</sup> University of Birmingham, UK; <sup>2</sup> Natural History Museum, UK; <sup>3</sup> Naturalis Biodiversity Center, The Netherlands

The evolution of jaws is thought to mark a dramatic shift in vertebrate evolution. However, jawless fish diversified and dominate the Middle Palaeozoic vertebrate record. Constraints of preservation and investigative techniques have previously hampered the acquisition of high-quality quantitative data from these fossils, limiting our understanding of their evolution and ecology. Here, for the first time, we use CT scanning and landmark-free 3D morphometrics to characterise the anatomical and functional diversity of the heterostracan oral region. Heterostracans were a morphologically diverse group of armoured, jawless stem-gnathostomes that were a major component of vertebrate ecosystems in the Silurian and Devonian. By sampling across the phylogenetic range of the group, we delimited three main functional groups based on the number and morphology of the oral and post-oral plates. These functional groups are obtained when performing landmark-free shape analyses on the post-oral plate, while the oral plates display a convergent morphology. Ancestral state reconstruction points to similar morphologies of the oral apparatus having evolved multiple times in several lineages, likely to occupy similar feeding niches and environments. We are also able to estimate the ancestral morphology, which likely consisted of multiple oral plates with a reduced post-oral plate.







## Megacarnivore functional morphology reveals novel ecosystem restructuring during the rise of the dinosaurs.

**Suresh A. Singh**,<sup>3\*</sup>, Armin Elsler<sup>1</sup>, William Deakin<sup>1</sup>, Thomas L. Stubbs<sup>2</sup>, Emily J. Rayfield<sup>1</sup>, and Michael J. Benton<sup>1</sup>.

<sup>1</sup>School of Earth Sciences, University of Bristol, Life Sciences Building, Tyndall Avenue, Bristol, BS8 1TQ, United Kingdom, <sup>2</sup>School of Life, Health & Chemical Sciences, The Open University, Walton Hall, Milton Keynes, MK7 6AA, United Kingdom.

Dinosaurs emerged from the End-Triassic mass extinction as the predominant large tetrapods on land, supposedly mirroring the earlier opportunistic diversification of their archosauromorph ancestors following the End-Permian mass extinction. However, ongoing study has shown that patterns of faunal change across the Triassic-Jurassic transition are more complex and differ between different ecological guilds. Large carnivores can exert great influence over their ecosystems through their interactions with prey and competitors and are positioned at the top of their trophic networks, making them useful indicators of wider ecosystem change. Therefore, we use morphometric and phylogenetic comparative methods to chart the ecology and evolution of carnivorous dinosaurs, pseudosuchians and other archosauromorphs, using their ecological utility as large terrestrial carnivores to dissect patterns of faunal turnover and ecological diversification through the early Mesozoic. We show that dinosaurs began to specialise as apex carnivores in the late Norian and pursued a trophic strategy unlike that of either their pseudosuchian or more basal archosauromorph relatives. Predatory dinosaurs were adapted to feed on relatively small, fast prey and remained unsuited to tackling larger prey until much later in the Early Jurassic, demonstrating an interesting shift in predator-prey dynamics through the Triassic-Jurassic transition.





## What can Big Data tell us about bird evolution?

**Jen Bright**<sup>1</sup> \*Keynote speaker

<sup>1</sup>University of Hull

Birds are a classic evolutionary model organism. However, despite (or perhaps because of) their enormous diversity of over 10,000 species, most studies have historically focused on only a few, small, well-known clades where either: the key variables are long established (e.g. Galapagos finches); the group is of domestic importance (e.g. fowl); or the group is phenotypically unusual (e.g. hummingbirds). For most birds, therefore, we only loosely understand how different intrinsic and extrinsic factors shape the course of their evolution. Recently, several large efforts have been made to capture and share vast databases of phenotypic, phylogenetic, ecological, and biogeographic information on modern birds. In addition to evolutionary insights, this wealth of data has allowed us to better understand the importance of scale on study datasets, both in terms of the number of species considered and the number of variables measured from them. In vertebrate palaeontology, similar data are often severely and unavoidably limited by the quality of the fossil record. Through a case study of the Cretaceous bird group, Enantiornithes, I will show how comparative examination of extinct species within the Big Data framework of modern birds can help our understanding of fossil ecosystems, and the evolutionary dynamics within them.





## Talk abstracts

### Integrating form and function in a multi-variate phylogenetic regression framework

Manabu Sakamoto<sup>1</sup>

<sup>1</sup>Department of Life Sciences, University of Lincoln

A core objective of functional morphology is to reveal how form (morphology) relates to function, and whether morphology can predict function, particularly in extinct or exotic species for which behaviours cannot be directly observed. Function is thus often the trait of interest with morphology being the explanatory/predictor variable. However, in terms of observable anatomical traits, morphology is the set of traits that are changing through evolutionary time in response to selection resulting from physical demands of function. Here, I focus on how morphology can be explained by function in an evolutionary context using a statistical phylogenetic modelling framework. The challenge here is that morphology is often quantified as multivariate data, and multiple-response models are not very common. To this end, I employ a multivariate phylogenetic regression approach, using Bayesian generalised linear mixed models (GLMMs), to test how six linear skull morphometrics in theropod dinosaurs relate to biting performance measures, bite force at three biting positions. Results reveal that two morphometric variables, the height of the skull posterior to the orbit and the length of the antorbital fenestrae, can be explained by bite force.





## Cementochronology reveals the evolution of life history amongst the earliest mammals

**Elis Newham** \* 1,2, Pamela Gill 3,4, Philippa Brewer 4, Julia Schultz 2, Kai Jaeger 2, Ian Corfe 2, Thomas Martin 5,6

1Queen Mary University of London, 2Rheinische Friedrich-Wilhelms-Universität, 3University of Bristol, 4Natural History Museum London, 5University of Helsinki, 6Geological Survey of Finland

The Jurassic radiation of crown mammals has been linked to the acquisition of key physiological innovations, including the evolution of determinate patterns of rapid juvenile growth truncated at sexual maturity. These patterns are intrinsically related to the evolution of mammals' endothermic physiology, the timing and mechanisms of which remain under debate. We use synchrotron X-ray tomographic imaging of annual growth increments in the dental cementum of Early-to-Late Jurassic mammaliaforms to map the origin and evolution of mammalian determinate growth. Non-mammalian mammaliaforms exhibited slow growth-rates with relatively little change through life. Early crown mammals developed significantly faster juvenile growth-rates that reduced at the attainment of sexual maturity, showing distinct contrasts in structure between juvenile and adult cementum. Fossils studied retained lower growth-rates, longer estimated maximum lifespans, and delayed sexual maturity relative to extant mammals. Estimation of basal-metabolic-rates (BMRs) using lifespan also suggests that non-mammalian mammaliaforms retained low BMRs, while some fossil crown mammals had BMRs approaching the lowest values of extant mammals. These patterns suggest that the mammalian determinate growth strategy first evolved amongst early crown mammals during the mid-Jurassic mammalian adaptive radiation, although growth remained slower than in extant mammals.





## Pachycormids, Palaeontologists and Pandemics : A Sea of Surface Publishing Pressure Leads to Ethical Breaches

Jeff Liston \* <sup>1</sup>, Darren Naish <sup>2</sup>

<sup>1</sup>Royal Tyrrell Museum of Palaeontology, <sup>2</sup>University of Southampton

Pachycormids have been viewed as a marginal group of actinopterygia, substantively regarded as a curiosity with little intrinsic value, arising off the main line of teleost ancestry and thus attracting little research focus beyond descriptions of new specimens and occasionally consequent new taxa. Exceptions include Mainwaring's 1978 review and Lambers' 1992 revisions of the group. This changed midway through the 2000s, when this group were invigorated through rigorous re-examination, with particular emphasis on the suspension-feeders. The rise of research focus on these animals reflects a broader rise in the production of vertebrate palaeontologists and their being subject to the imperative to publish or perish. This means that researching in areas related to these animals has become remarkably competitive, with ethically questionable behaviour that might only have been associated with theropod dinosaurs over the last few decades. As a case study, this presentation will review some of the aspects of this transition and discuss how much it relates to the growth in palaeontologists competing over the same slice of major taxa, together with the prospects for expanding the range of research into new areas, for example behavioural, to keep ahead of or distinct from the competition.





## Factors determining persistent asymmetry and egg shape in birds: A hypothesis

D Charles Deeming \* <sup>1</sup>

<sup>1</sup>University of Lincoln

The various shapes of birds' eggs have fascinated scientists for many years. It is now possible to mathematically describe shape accurately, allowing exploration of the physical and ecological factors driving evolution of egg shape. However, there has been relatively little consideration of: 1) how egg shape is established in the oviduct, or 2) how eggs retain their shape, even without an external calcitic layer. Here I postulate a hypothesis that answers these questions. The hypothesis suggests that, as the egg mass (i.e., yolk and albumen) moves from the magnum into the isthmus, it is squeezed by the physical restriction imposed by the isthmus lumen and cannot easily move into the isthmus. As the leading edge of the egg mass enters the isthmus, the egg mass in the distal magnum is forced to bulge outwards, resulting in an asymmetrical shape. The various egg shapes observed in birds are hence, produced by the interaction between the size of the egg mass relative to female body mass, and the degree of the restriction of the isthmus. Thus, a large egg mass, i.e., relative to female body mass, entering a narrow isthmus will produce a pointed egg shape. If the egg mass is relatively small, and the isthmus lumen wide, more of the egg mass could enter the isthmus and the degree of asymmetry is reduced. It is further proposed that egg shape is fixed by the formation of the shell membranes in the isthmus because the constituent protein fibres permanently stick together as they are deposited in the isthmus. The implications of the hypothesis for the diversity of egg shapes in birds (and reptiles), and for the deposition and characteristics of the calcitic egg, are wide-ranging.





## Bird clades with less complex appendicular skeletons tend to be more diverse

Andrew Brinkworth \*<sup>1</sup>, Emily Green<sup>2</sup>, Yimeng Li<sup>3</sup>, Jack Oyston<sup>1,4</sup>, Marcello Ruta<sup>2</sup>, Matthew Wills<sup>1</sup>

<sup>1</sup>University of Bath, <sup>2</sup>University of Lincoln, <sup>3</sup>Nanjing Institute of Geology and Paleontology, <sup>4</sup>University College London

Species richness is unevenly distributed across clades of all taxonomic ranks. Based on a body of theoretical work, and our own empirical findings, we propose that uneven species richness may be partially determined by varying morphological complexity between groups. While it is impossible to measure complexity directly, it is possible to derive proxies based on the morphology of particular structures. Specifically, the number of parts comprising a structure, their relative differentiation from one another, and the relative disorder of their arrangement, can be used to derive useful proxies. In this work, we derived an index of complexity for 983 extant species of bird, based on serial differentiation of bones in the limb skeleton. We showed that the mean complexity exhibited by extant bird clades correlates negatively with their species richness. Further, we showed that mean complexity correlates negatively with the ecological niche diversity for each clade. This simple proxy for ecological specialisation is also correlates positively with clade species richness. We suggest that these findings demonstrate complexity mediated ecological constraint, which in turn limits the ability of clades to diversify.





## Thoracic cage morphology coadapts with aerobic capacity in artificially selected High Runner mice

Elizabeth Webb \*<sup>1</sup>, Theodore Garland<sup>2</sup>, Nicole Schwartz<sup>2</sup>, Katrina Jones<sup>1</sup>

<sup>1</sup>University of Manchester, <sup>2</sup>University of California, Riverside

Cursoriality, fast and sustained running, is a specialized behavior that has evolved numerous times in mammals. However, it is challenging to disentangle skeletal adaptations for cursoriality from other potentially correlated factors. The High Runner (HR) project is an experiment in which mice were selected based on voluntary wheel running, resulting in four replicate lines that run three times further than four control lines. These mice have myriad cursorial adaptations, including increased endurance and maximal oxygen consumption during forced exercise ( $VO_{2max}$ ). However, the role of thoracic morphology in facilitating increased  $VO_{2max}$  of HR lines is unclear. Here, we examine thoracic cage morphology in HR mice, and test the hypothesis of increased rib cage volume relative to controls. We postulate that ventilatory capacity may be increased via increased thoracic count or changing rib shape. Thoracic count and rib shape was measured using 3D geometric morphometrics and compared between HR and control lines. We find that some replicate HR lines have increased thoracic count, but other lines have modified rib shape to increase rib curvature or length. Therefore, we find varying adaptive responses in thoracic cage morphology to similar selection pressures, suggesting many-to-one form-function mapping in mammalian ventilation.







## A case study investigating varying muscle input parameters on finite element models of the tenrec mandible

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Biomechanical modelling is a powerful tool for inferring functional performance in extinct animals and higher-level inferences such as macroevolution. Model accuracy is dictated by muscle input parameters such as fibre length and muscle volume. In fossils, muscle reconstructions are informed by osteological features in fossils and anatomical data from related extant species, which can yield errors in reconstructions and higher-level inferences. In this study, we assess how varying muscle input parameters influence finite element (FE) model results. We created a FE model from CT data of a *Hemicentetes semispinosus* (lowland-streaked tenrec) mandible, with adductor muscle forces calculated from muscle mass and fibre length measured via dissection. We compared the results of this model to FE models created by varying muscle input parameters estimated via two modelling techniques conventionally used on fossil animals – muscle volume sculpture and the dry skull method. We also assessed the impact of changing fibre length on stress and strain outputs. Quantitative results varied in the degree of accuracy compared to the specimen-specific models, but predominantly failed to capture absolute magnitudes. However, most qualitative differences in bone stress distribution and relative magnitudes across the models are retained. This emphasises the importance of muscle property datasets and validation studies.





## Elucidating the ecological and life history drivers of Galloanserae skull evolution using high density 3D geometric morphometrics

Eloise Hunt \* <sup>1,2</sup>, Ryan Felice <sup>1,3</sup>, Joseph Tobias <sup>2</sup>, Daniel Field <sup>4</sup>, Stephan Lautenschlager <sup>5</sup>, Anjali Goswami <sup>1,3</sup>

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Our research aims to elucidate the drivers of Galloanserae (ducks, chickens, and relatives) skull evolution. We generated a comprehensive 3D dataset of skull morphology for >230 species, including key extinct lineages, to uncover their morphological variation and quantify the factors driving this disparity. Extant Galloanserae only represent a fraction of the remarkable morphological and ecological diversity they attained over ~67 million years of evolution. We tested the hypothesis that extinct Galloanserae exhibit distinct cranial forms unrepresented in extant taxa. Additionally, we isolated the relative influences of ecological and life history traits on skull shape variation and evolutionary rates. Principal Component Analysis (PCA) revealed that extinct clades greatly expand the breadth of Galloanserae morphospace occupation beyond what could be inferred from extant taxa alone. Analyses show significant relationships between skull shape and ecology ( $P = 0.039$ ), habitat density ( $P = 0.001$ ), and migration ( $P = 0.0016$ ). Rate analyses demonstrate heterogeneous rates of evolution for different character states within habitat density, migration, diet, and developmental mode. Our results indicate that these factors are key influencers in the skull evolution of Galloanserae and highlight the importance of fossils to inform estimates of phenotypic disparity.





## On the alleged furcula of *Allosaurus*

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In the early 1970's, when the dinosaur-bird link was first propounded by Professor John Ostrom, there was a problem. Dinosaurs did not have clavicles, the precursors of the avian furcula, so theropod dinosaurs could not have been the ancestors of birds. A flurry of activity ensued in which any suitably curved bone found associated with a theropod dinosaur was 'shoe-horned' into becoming a furcula. Some of the first such bones were five obtusely V-shaped bones excavated from the Cleveland-Lloyd quarry between 1960 and 1964. They were identified by Jim Madsen, in his 1976 monograph '*Allosaurus fragilis*: a revised osteology', as conjoined median abdominal ribs (conjoined gastralia). Soon however the identification was revised to furculae in line with the then current 'revolution' in dinosaur taxonomy. The bones are however identical in shape with the conjoined median gastralia found in many modern reptiles and have similarly chamfered articulation facets. Thus, the most parsimonious identification of 'V' and 'U' shaped bones found in theropod dinosaur skeletons is that they are median gastralia not furculae.





## Can limb muscle masses be predicted from skeletal morphologies? A case study using extant archosaurs.

**Matthew Dempsey** \* <sup>1,2</sup>, Susannah Maidment <sup>2</sup>, Karl Bates <sup>1</sup>

<sup>1</sup>University of Liverpool, <sup>2</sup>Natural History Museum UK

Understanding musculoskeletal properties is essential to the study of tetrapod locomotion, the evolution of which underpins key morphological radiations across deep time. However, due to the lack of soft tissue preservation in most fossils, muscle reconstruction is often subjective, with different methods producing varying results. Collating data from dissections and CT-based models, we established a workflow for estimating limb muscle properties across extinct archosaurs through correlations between muscle masses and skeletal surface areas in extant taxa. We combined muscles into major functional groups and sought correlations with whole-bone external surface areas. Our results suggest strong relationships between multiple muscle group masses and whole-bone surface areas, particularly in the triceps femoris (thigh flexors and knee extensors) and gastrocnemii (knee flexors and ankle extensors). There are nuanced allometric differences between limb muscle groups, and so caution should be exercised when estimating muscle masses in any given fossil taxon from a single extant analogue. These relationships provide a quantitative baseline from which muscle mass properties can be predicted more broadly across Archosauria, further illuminating the anatomical changes associated with major functional innovations.





## Innovations in hindlimb shape throughout theropod phylogeny demonstrated using mosimann variables

**Matthew Dempsey** \*<sup>1,2</sup>, Susannah Maidment<sup>2</sup>, Karl Bates<sup>1</sup>

<sup>1</sup>University of Liverpool, <sup>2</sup>Natural History Museum UK

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## A new ankylosaurian osteoderm from the Middle–Late Jurassic Oxford Clay Formation, UK

Jordan Bestwick \*<sup>1</sup>, Martin Nunn<sup>1</sup>, Chloe Oliver<sup>1</sup>, Stuart Pond<sup>2</sup>, Adam Smith<sup>1</sup>

<sup>1</sup>Nottingham Natural History Museum, <sup>2</sup>Natural History Museum, London

Ankylosaurs are a characteristic group of dinosaurs recognised by their extensive covering of dermal armour (osteoderms) across their bodies. The Middle–Late Jurassic (Bathonian–Oxfordian) Oxford Clay Formation, UK, contains among the earliest known ankylosaur material, including osteoderms assigned to *Sarcolestes* and a few currently unidentified species. The formation is thus important for understanding early ankylosaur evolution. Here, we describe an osteoderm from the Oxford Clay of Peterborough that exhibits a different morphology to other osteoderms from this formation. The specimen, although incomplete along its transverse axis, measures 43 mm across its anteroposterior axis with a spine length of 52 mm. The osteoderm is subrectangular with a concave ventral surface and a low-lying spine on its dorsal surface that slightly extends beyond the posterior margin of the specimen base. This morphology is superficially more similar to the thoracic osteoderms of more derived Cretaceous ankylosaurs from North America (e.g. *Borealopelta*, *Edmontonia*), than to Oxford Clay specimens and other contemporaneous Jurassic ankylosaurs (e.g. *Tianchisaurus*). Although its isolated nature prevents reliable identification of the taxon and body part to which it belonged, the osteoderm nevertheless indicates a larger morphological diversity in the body armour of the earliest ankylosaurs than currently appreciated.





## The Untold Story of the Carnegie *Diplodocus*

**Mike Taylor** \*<sup>1</sup>, Matt Lamanna<sup>2</sup>, Ilja Nieuwland<sup>3</sup>, Amy Henrici<sup>2</sup>, Linsly Church<sup>2</sup>, Steve Sroka<sup>4</sup>, Ken Carpenter<sup>5</sup>

<sup>1</sup>University of Bristol, <sup>2</sup>Carnegie Museum of Natural History, <sup>3</sup>Royal Netherlands Academy of Arts and Sciences, <sup>4</sup>Utah Field House of Natural History, <sup>5</sup>University of Colorado Museum

The sauropod dinosaur *Diplodocus* is best known from the iconic Carnegie specimen, casts of which were sent around the world in the early 1900s. The original skeleton was mounted in 1907, but its composition was complex: it contained real bone from four individuals, with casts and sculptures from six further specimens — some of which were from distantly related camarsaurids. Cast/sculpted material includes the skull, forelimbs and forefeet. Published estimates of the skeleton's length have varied wildly: new measurements establish it at 26.1m. In 1957, a last cast was made, in concrete, by the Utah Field House in Vernal, Utah. It stood outside the museum for three decades. The molds, weighing three tons, were shipped to Rocky Rount, North Carolina, with the intention of casting another outdoor *Diplodocus*, but work eventually ground to a halt. The molds were probably lost or destroyed around 1965. However, in 1989, new moulds were made from the concrete cast. Second-generation casts have been made from these, and now inhabit Japan, Canada and several locations in Florida, as well as Vernal. Elements cast from these new moulds have also been incorporated into other mounts, such as the iconic rearing *Barosaurus* in the AMNH atrium.





## The Lincoln Plesiosaurs

Richard Forrest \* 1

<sup>1</sup>[plesiosaur.com](http://plesiosaur.com)

The Collection at Lincoln has on display a fine specimen of a plesiosaur. It was found at the beginning of the last century in a brick pit within the city at a site now occupied by a primary school, who use it as their logo. It was on display during the 1960s but was forgotten until it was rediscovered in the museum stores in the late 1990s. It has been identified as a member of the Microclididae from the Pliensbachian Lias and is one of the most complete plesiosaur specimens from this period. It is partly in a limestone nodule which gives some evidence for a history of predation by a large, torsion-feeding predator. Another substantially complete plesiosaur, unfortunately (and typically!) missing a skull in the museum collection is not on display. It is part of a collection passed on from Grantham Museum in the early 20s when they were no longer able to store their geological material. It has not been the subject of any research, and information on provenance is limited. It was found in the early part of the 20th century, and fortunately photographed in situ at the time using a large format camera. The glass plates have deteriorated over time but could still be scanned to give reasonably good images. It appears to be from the Middle Lias and is possibly a rhomaleosaurid plesiosaur.







## Evolutionary ratchet drives longterm trend despite fluctuating climatic driver

Adrian Lister \* <sup>1</sup>, Juha Saarinen <sup>2</sup>

<sup>1</sup>Natural History Museum, <sup>2</sup>Department of Geosciences and Geography, University of Helsinki

We present new data on proboscidean dental evolution in East Africa over the past 26 million years, tracking temporal patterns of morphological change in relation to proxy evidence of diet, vegetation and climate (aridity). Strongly directional trends in molar crown height (hypsodonty), enamel thickness, and the number of enamel lamellae in the molar, occur in parallel across several elephant genera. We partition traits by selective agent, showing that the acquisition of high-crowned, multi-lamellar molars was primarily a response to an increase in open, arid environments with high dust accumulation (quantified in offshore cores), whereas enamel folding was more associated with the amount of grass in the diet (quantified via dental mesowear). We further show that long-term trends in these features proceeded in a ratchet-like mode, alternating between directional change at times of high selective pressure and stasis (not evolutionary reversal) when the selective regime reversed. In this way a strongly directional trend can accumulate with each climatic pulse. This pattern provides an explanation for morphology adapted to more extreme conditions than current usage (Liem's Paradox) if the selective force is currently below its former maximum.





## *Pteraichnites* as a tool for understanding pterosaur palaeoecology and evolution

Robert S. H. Smyth \* <sup>1</sup>

<sup>1</sup>University of Leicester

The Upper Jurassic (Oxfordian-Tithonian) deposits of the western USA form one of the world's most extensively sampled Mesozoic sequences, yet skeletal material of pterosaurs is exceptionally rare. Despite a poor skeletal record, the region produces abundant pterosaur tracks, or pteraichnites. These tracks have significantly improved our understanding of pterosaur terrestrial locomotion, but their ecological and evolutionary implications remain largely unexplored. Here, extensive photogrammetric documentation of tracks has revealed a robust correlation between track morphology and pterosaur autopodial anatomy. Using both multivariate analyses and traditional diagnostic methodologies, tracks can be referred to specific pterosaur clades. Pteraichnites across multiple localities in the western USA represent ctenochasmatooid trackmakers. These ground-based feeders frequented intertidal flats surrounding the Sundance Sea. Trackways reflect specific behaviors, such as persistent walking parallel to the palaeoshoreline as well as foot-propelled swimming, an unusual locomotory mode that cannot be confidently inferred from skeletal morphology alone. The broad geographic and temporal distribution of ctenochasmatooid tracks demonstrates their early pervasiveness within marginal marine environments during the early Late Jurassic, much earlier than indicated by the body fossil record. Integrating pteraichnites into our understanding of the pterosaur fossil record holds great potential for enhancing our knowledge of pterosaur palaeobiogeography, evolution, and behaviour.





## Using your head – cranial steering in pterosaurs

Donald Henderson \* <sup>1</sup>

<sup>1</sup>Royal Tyrrell Museum of Palaeontology

The vast majority of pterosaurs are characterized by large, elongate skulls. Projecting out in front of the body, these large heads must have had an aerodynamic effect. The working hypothesis of the present study is that these oversized heads were used to control the left-right motions of the body during flight. Using digital models of six, long-tailed “rhamphorhynchoids” and six, short-tailed pterodactyloids, the turning moments associated with the head and neck showed an isometric correspondence with the rotational inertia of the whole body about a vertical axis in both groups. Turning moments come from calculating the lateral area of the head (plus any crests) and determining the associated lift coefficient as a function of flight speed. Rotational inertias were calculated from the three-dimensional mass distribution of the axial body, the limbs, and the flight membranes. Substantial tail fins at the end of the tail are only known from specimens of *Rhamphorhynchus muensteri*. Unlike other pterosaurs, the head moments of *Rhamphorhynchus* lagged behind their rotational inertias. However, the tail fins provide additional turning moments in *Rhamphorhynchus*, and suggest a flight style different from other tailed pterosaurs.





## *Rhamphorhynchus*: a model for ontogenetic niche partitioning in pterosaurs?

David Unwin \*<sup>1</sup>, Jordan Bestwick<sup>2</sup>, Charles Deeming<sup>3</sup>, Rab Smyth<sup>1</sup>

<sup>1</sup>University of Leicester, <sup>2</sup>University of Birmingham, <sup>3</sup>University of Lincoln

Ontogenetic niche partitioning (ONP) has recently been proposed for several pterosaurs, primarily on the basis of size distributions that, while suggestive, are not conclusive. Resolving this question is important as ONP has potentially profound implications for the taxonomy, systematics, ecology and evolutionary history of pterosaurs. This study focused on *Rhamphorhynchus muensteri*, utilised a large data set (130+ individuals) that represent an almost complete growth sequence and aimed to identify putative ontogenetic niches using multiple independent data sets: comparative morphology, morphometrics and tooth microwear. Three distinct ontogenetic niches were identified: small, highly immature, flight capable invertivores (wingspan 0.3-0.4 m; <1 year old); medium-sized aerial piscivores (wingspan 0.75-1.25 m; ~2 to 7 years old); and large, osteologically mature individuals (wingspans 1.25-1.9 m; >7 years old) that seemingly represent an extension of aerial piscivory to include prey of relatively large size. Key evidence such as tooth microwear, which directly reflects changes in prey preferences, skull shape and wing-configuration are strongly correlated, permitting a high degree of confidence in the identification of ONP in *Rhamphorhynchus*. This pterosaur could thus be of great utility for assessing ONP in other taxa and a preliminary analysis suggests that this phenomenon is widespread in pterosaurs.





## Advances in Understanding Plesiosaur Locomotion: Insights from a Free-Swimming Robot

Luke Muscott \* <sup>1</sup>

<sup>1</sup>Imperial College London

Plesiosaurs employed a distinctive four-flipper swimming method that granted them remarkable advantages in speed and endurance. Previous investigations primarily focused on elucidating the mechanisms and benefits of this propulsion method using flume tank experiments. However, these experiments had notable limitations, such as the absence of rotational movement around the articular socket, and the exclusion of the plesiosaur body, neck, head, and tail. We present recent developments that have significantly advanced our understanding of plesiosaur locomotion. Specifically, we have successfully developed a free-swimming plesiosaur robot that accurately replicates the body morphology and flipper kinematics of these extinct creatures. This innovative robot serves as a valuable experimental tool, allowing us to investigate various flipper shapes, kinematics, and the influence of head, neck, and tail morphologies. Our novel approach, employing an accurate plesiosaur robot as a test platform, provides unprecedented insights into the evolutionary adaptations and locomotor capabilities of these marine reptiles. By gaining a deeper understanding of the hydrodynamics of plesiosaur swimming, we can acquire valuable knowledge applicable to both biological and engineering contexts. This knowledge holds great potential for advancements in underwater robotics and the development of biomimetic design principles.





## Ontogeny and tooth replacement in the Brazilian cynodont *Brasilodon quadrangularis*

**Pamela G Gill** \*<sup>1,2</sup>, Agustin G Martinelli<sup>3</sup>, Heitor Francischini<sup>4</sup>, Nuria Melisa Morales Garcia<sup>1</sup>, Pedro H Fonseca<sup>4</sup>, Ian J Corfe<sup>5,6</sup>, Emily J Rayfield<sup>1</sup>

<sup>1</sup>University of Bristol, <sup>2</sup>Natural History Museum London, <sup>3</sup>Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, <sup>4</sup>Universidade Federal do Rio Grande do Sul, <sup>5</sup>University of Helsinki, <sup>6</sup>Geological Survey of Finland

*Brasilodon quadrangularis* is a probainognathian cynodont from the Late Triassic (Norian) of southern Brazil that is phylogenetically positioned close to Mammaliaformes. This taxon is based upon several skulls and isolated jaws, including the junior synonyms *Brasilitherium riograndensis* and *Minicynodon maieri*. To investigate the tooth replacement pattern in *Brasilodon*, several specimens were micro-CT scanned. We observed that: 1) postcanines vary from five to seven functional tooth positions, with the loss of at least four anterior postcanines during ontogeny (indicating at least 11 positions during life); (2) more than one tooth replacement occurs at anterior loci in juveniles, and diastema enlargement is a result of the loss of incisor-like canines of juveniles and the anteriormost postcanine teeth; (3) as the middle postcanines are replaced alternately, new posterior postcanines are added; (4) larger individuals have more disparate postcanine morphology. *Brasilodon* has not acquired a diphyodont tooth, which is a major apomorphy for mammaliaforms. Tooth replacement mechanisms amongst non-mammaliaform cynodonts are highly diverse, and *Brasilodon* indicates a unique replacement pattern among probainognathians, sharing resemblances with *Sinoconodon*.





## A methodology for Species Distribution Modelling in Dinosaurs

Max Stockdale \* <sup>1</sup>

<sup>1</sup>University of Bristol

Species Distribution Modelling is a versatile and robust tool for estimating the geographic range of organisms using environmental variables. It relies upon the assumption that the greatest concentration of species occurrences will be at the location where the environment is most optimal. This presents challenges to palaeontologists, because fossil data is expected to concentrate in places where the preservation and sampling potential is highest. Therefore, fossil data cannot be expected to satisfy the assumptions of species distribution models. This presentation proposes an alternative methodology for species distribution modelling with fossil organisms. This alternative methodology yields contrasting results to conventional approaches. It also suggests that systematic biases are introduced when traditional methods are used to model the geographic distribution of fossil organisms.





## European pouches weigh: new insights on the evolutionary history of early Cenozoic Laurasian ‘opossum-like’ marsupials

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Peradectidae and Herpetotheriidae are mostly Laurasian, superficially ‘opossum-like’ metatherians (marsupials and related fossils) known by their generalist dentition and frequently regarded as arboreal stem-metatherians and terrestrial stem-marsupials, respectively. A systematic revision of Early Eocene European Peradectes integrates new dental rows together with an analysis of dental polymorphisms. It allows us to define the oldest European Peradectes species and to further show that a unique dispersal event towards Europe occurred during the history of peradectids. We also report the first metatherian from the Paleocene of Europe and oldest undisputed herpetotheriid. It reveals the simultaneous independent acquisition of the same styler cusp features on upper molars in the European Eocene species of the coeval families. Finally, we carried out a cladistic analysis at the metatherian level based on a majority of newly defined dental characters. For the first time, a Laurasian monophyletic group Peradectidae including all Paleocene-Eocene species is recovered. Peradectidae are a part of a robust and resolved unnamed clade, emerging consecutive to the K-Pg boundary and encompassing ‘Notometatheria’ (all South American and Australian metatherians plus herpetotheriids).







## Take another bite: new in vivo and estimated measurements of bite force demonstrate exceptionally large bite forces in parrots

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<sup>1</sup>University of Lincoln, <sup>2</sup>CNRS

Bite force, which in part determines the diet of an organism, is a function of the force exerted by contraction of the jaw musculature, applied via the jaw skeleton. Bite force has been determined in a range of vertebrate taxa using direct measurements using force transducers, or by calculation from skull morphology or jaw musculature. Bite force in birds has received little attention and values for parrots, anecdotally renowned for strong bites, are rare. Bite force estimates for nineteen parrot species of differing sizes were calculated using a novel method that used areas of jaw muscles measured in situ and their masses. Bite forces were also separately recorded in vivo using force transducers, allowing for validation of the dissection-based models. There was a positive allometric relationship for bite force against body mass (measured slope of 0.95 vs an isometric prediction of 0.66) and against skull mass (0.83 vs 0.66). Macaws (*Ara* sp.) had the strongest bite recorded to date for a bird (539 N). Calculated values for bite force were not statistically different from measured values taken from birds. These results have implications for how parrots process food items and how bite forces are estimated in other taxa using morphology of the jaw musculature.





## The influence of jaw muscle architecture on mandibular disparity in Lepidosauria

**Antonio Ballell** \*<sup>1</sup>, Hugo Dutel<sup>1</sup>, Matteo Fabbri<sup>2</sup>, Christina Hammond<sup>1</sup>, Anthony Herrel<sup>3</sup>, Emily Rayfield<sup>1</sup>

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The interplay between skull morphology and architecture of jaw muscles remains understudied, despite its importance in identifying functional and developmental constraints shaping head evolution. Combining data on muscular and skeletal anatomy in a phylogenetic context can provide a clearer picture of the integration of the musculoskeletal system and the functional and ecological implications of morphological change. Lepidosaurs show outstanding variation in skull and jaw configuration, as well as a wide range of dietary habits, representing an ideal study case to investigate the relationship between osteology, myology and ecology. We quantify mandibular disparity across Lepidosauria using 3D morphometrics in over 80 species. The effect of muscular anatomy on mandibular shape is tested using phylogenetic comparative methods and different muscular parameters (muscle mass, PCSA). Mandibular shape is partly explained by phylogenetic relatedness, allometry and diet. Muscle architecture covaries with mandibular morphology, suggesting that the jaw and associated muscles have evolved as an integrated system in Lepidosauria, facilitating the acquisition of the remarkable ecological diversity of the clade.





## Cranial kinesis mechanics and feeding ecology among birds

**Amber Wagstaffe** \*<sup>1</sup>, Jen Bright<sup>1</sup>, Roger Benson<sup>2</sup>, Peter Watson<sup>1</sup>, Philip Anderson<sup>3</sup>, Gavin Thomas<sup>4</sup>

<sup>1</sup>University of Hull, <sup>2</sup>American Museum of Natural History, <sup>3</sup>University of Illinois, <sup>4</sup>University of Sheffield

Cranial kinesis in birds allows the rotation of the upper beak relative to the skull via displacement of the palate. This important mechanism tends to be overlooked in feeding studies, but the cranial kinetic system may provide new insights into the form-function relationships between bird skulls and their ecology. Using a simple 2D four-bar linkage model, we modelled cranial kinesis using lateral images of 308 extant bird species. Kinematic Transmission (KT) and gape measurements were compared with feeding categories. We also compared these metrics with link lengths and considered these results in the context of four-bar biological systems as a whole. Although KT did not demonstrate strong relationships with feeding ecology, the addition of the beak to the 4-bar system permits significant separation of dietary groups by accommodating gape differences within the models. Additionally, we find that body size appears to constrain the feeding method employed by birds. Analysis of link lengths revealed that the output link (beak depth) is more strongly correlated with KT than the input (quadrate). This is despite the fact that within birds, the output link is not the shortest link, which was the trait previously believed to drive mechanical sensitivity in other biological four-bar systems.





## External Morphology or Internal Anatomy – Assessing Determinants of Mandibular Mass Distribution

Adrian Maurice O Driscoll \*<sup>1</sup>, Nathan Jeffery<sup>2</sup>, Sam Cobb<sup>1,3</sup>

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Mammals have a distinctive masticatory system, and the distribution of bone in the mandible varies due to differences in form and function and remodelling in response to mechanical loading. Mass distribution and its functional significance have been well studied in mammalian limbs and locomotory biomechanics, but not in the mandibles and mastication. I investigated the degree to which material density variation influences centre of mass (CoM) to better understand the determinants of mandibular mass distribution and tested five estimation methods for agreement against an established standard. I estimated CoM for an interspecific sample of 40-adult-specimens (Orders Artiodactyla, Perissodactyla, Proboscidea) and an ontogenetic series of 15-individuals (*Diceros bicornis*), using analogue and CT-based methods. Mass distribution data estimated with, and without, specification of material density does not significantly differ. CoM may be accurately estimated using surface scans in adult specimens, and in the ontogenetic case, simple linear measurements. That CoM can be reliably approximated, across a functionally diverse group of taxa, implies remodelling of the internal architecture of the mandible does not meaningfully contribute to mass distribution. The tested methods exhibit high agreement, allowing datasets to be composed using a variety of approaches.





## A new leptopleuronine procolophonid from the Late Triassic of southwest England

**Richard Butler** \* 1, Luke Meade 1, Terri Cleary 1, Kai McWhirter 1, Emily Brown 1,2, Tom Kemp 3, Juan Benito 4, Nicholas Fraser 5  
1University of Birmingham, 2Natural History Museum, London, 3University of Oxford, 4University of Cambridge, 5National Museums Scotland

The fissure fill localities of southwest England and South Wales are well-known for preserving rich assemblages of predominantly small-bodied Late Triassic to Early Jurassic tetrapods, but many aspects of these assemblages remain contentious. The fissures have been hypothesized by some workers to have formed on an archipelago, with island effects invoked to explain aspects of the assemblages such as the abundance of small-bodied species. Procolophonids were a successful group of Triassic parareptiles, best known from Early to early Late Triassic assemblages, but are poorly known from the fissure fills. Here, we describe new procolophonid specimens from the Cromhall fissure that represent at least six individuals of different sizes, with much of the skeleton represented including well-preserved skull material. The Cromhall procolophonid shows strong similarities to Late Triassic procolophonids from Scotland, Brazil and North America, but both autapomorphies and a unique character combination demonstrate that it represents a new species. Phylogenetic analysis places the Cromhall taxon in a derived clade within Leptopleuroninae, together with *Leptopleuron*, *Hypsognathus* and *Soturnia*. The largest specimens of the Cromhall taxon demonstrate a body size that is similar to *Leptopleuron* and *Hypsognathus*, supporting other recent work questioning the insular dwarfism hypothesis for the fissure fill assemblages.





## The fish assemblage of the Lower Cretaceous (upper Barremian–lower Aptian) Arrifes section (Algarve Basin, Southern Portugal)

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The Arrifes coastal section – which is located approximately 2 km west of Albufeira (Central Algarve) – provides exposures of a sequence of late Barremian–early Aptian age. Bulk samples totalling 500 kg were collected from several horizons and were processed for the recovery of microvertebrate remains. The study and description of the collected material have permitted the identification of an unexpectedly rich and diverse vertebrate fauna. The fish assemblage comprises both chondrichthyans (Carcharhiniformes, Heterodontiformes, Lamniformes, and Rajiformes) and osteichthyans (Amiiformes, Elopiformes, Lepisosteiformes, Ionoscopiformes, Pycnodontiformes) and is represented mainly by fragmentary and isolated material (fragments of dental plates, teeth, ganoid scales, vertebrae, thorns and dermal denticles). The fish assemblage recorded in the Arrifes section corresponds to a mixture of freshwater, euryhaline and marine taxa. Some of these taxa are recorded for the first time in the Lower Cretaceous of Portugal. The fish remains are associated with benthic foraminifera, ostracods and other marine invertebrates but also with charophytes, numerous plant remains and insect coprolites, and disarticulated non-marine vertebrate remains (lissamphibians, lepidosaurs, turtles, crocodyliforms and dinosaurs). The new data presented here have considerable paleoenvironmental implications and provide additional insight into the environment of deposition and palaeoecology of the central part of the Algarve Basin during the Early Cretaceous.





## Poster abstracts

### The Evolution of Golden Moles and Tenrecs (Afrotheria, Mammalia)

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We undertook a phylogenetic analysis of genetic and anatomical data focusing on golden moles (Chrysochloridae) and tenrecs (Tenrecidae). Our results support the now well-resolved topology for extant tenrecids, and the paraphyly of "Chrysochlorinae" and the genera *Chrysochloris* and *Chlorotalpa* as traditionally used. The oldest divergence within crown Chrysochloridae is likely the node separating *Eremitalpa-Huetia* or *Eremitalpa* alone from the remaining species. A *Chrysochloris-Cryptochloris* root appears most frequently under equally-weighted parsimony, or with few or no sampled tenrecids, suggesting it is artefactual. The tropical genus *Huetia* is among the most widely distributed and anatomically polymorphic in our sample. *Eremitalpa* and *Huetia* have a relatively unspecialized hyoid apparatus and short angular process of the dentary. These elements in *Huetia* show a particular resemblance to those of the Namibian fossil *Namachloris*, which we reconstruct as a stem chrysochlorid. Crown chrysochlorids are geologically younger than crown tenrecids, and likely diversified in the Miocene around the same time as the tenrecid genus *Microgale*. Fossils of both groups from Eocliff in Namibia are probably late Eocene to early Miocene in age.





## The Congo Basin's Mysterious Hero: An investigation into vertebral mobility and the impact of tubercles in *Scutisorex*.

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The genus *Scutisorex*, also known as the Hero Shrew, possesses a unique vertebral morphology; The Transverse processes of its lumbar vertebrae, as well as some of its thoracic vertebrae, are dorsoventrally expanded and covered in numerous tubercles that project along the craniocaudal plane. Despite detailed documentation of *Scutisorex*'s skeletal and muscular anatomy (at least with regards to the first found species, *S. somereni*), as well as analyses of trabecular bone and research into *Scutisorex*'s biomechanical properties, the biological function of this extreme morphology remains unknown. This study attempts to rectify this gap in research through 'AutoBend', a novel program that offers an automated approach to estimating the mobility of vertebral joints. The mobility of *Scutisorex*'s vertebral column is compared to those of Shrew's with more typical Soricid morphology, and the impact of *Scutisorex*'s tubercles on mobility is assessed. The two key hypotheses tested are as follows; (1) That vertebral range of motion is lower in *Scutisorex* than in more typical Soricids and lower in the apparently more derived *S. somereni* than the apparently less derived *S. thori*, and (2) that in both species of *Scutisorex*, joints with higher tubercle counts will be less mobile.







## Understanding the mechanisms of polyphyodonty: insights gained from tooth replacement in fish

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Most jawed vertebrates exhibit lifelong tooth replacement (polyphyodonty), and there is a great drive to understand its developmental basis. Here, surface feature observations and X-ray micro-CT virtual sections are used to identify tooth replacement mechanisms in fossil and modern fish. Tooth replacement requires a 'dental lamina', an epithelial connection which enables only one tooth to be replaced by one successor, at any one time, and provides the putative stem cells required for long-term tooth renewal. However, 'one-for-one' replacement is not present in the crushing dentitions of an extinct group of fishes, the pycnodonts. Instead, tooth positioning suggests an opportunistic, gap-filling addition, where teeth fill any available space e.g. arising from tooth damage/loss. Contrastingly, in the modern fish specimens, tooth replacement mechanisms are recognisable, although seabream show unusual change in tooth size, shape, and positioning, over one tooth generation. Pycnodont, seabream and other crushing dentitions exhibit a close-packed, near-tessellating patterning. I hypothesise that in pycnodonts, gap-filling occurred by the oral epithelium retaining odontogenic potential throughout life, possibly facilitated by stem cells that generate taste buds. I also hypothesise that tooth patterning in crushing dentitions is an adaptive phenotypic response to mechanical strain at the crushing surface, a known phenomenon in cichlids.





## Interpretation of fossil embryos requires reasonable assessment of developmental age

D Charles Deeming \* <sup>1</sup>

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Dinosaur embryos cause a lot of excitement in the scientific literature and are widely reported in the popular press. Well-preserved, articulated oviraptorosaur embryos in eggs are usually interpreted as representing a stage of development close to hatching because of their large size and good level of skeletal ossification. Here we explore how the developmental stage of oviraptorosaur embryos can be estimated, rather than assumed. Using quantitative methods in comparison with modern crocodylian embryos, it was shown that articulated oviraptorosaur embryos are small relative to their egg length which suggests a stage of development equivalent to around 50%–60% of the developmental period rather than being close to hatching. Moreover, many elements of the crocodylian skeleton are well ossified at this point of development. Misunderstandings about the stage of the developmental biology of these and other well-preserved embryos hampers our understanding of the true nature of reproductive biology and development of extinct species. Palaeontologists should adopt a more conservative approach for initial interpretation of new specimens. This is important, because misunderstandings in the minds of the public about dinosaur biology are hard to counter once poorly evidenced ideas have been reported around the world.





## Surely long wings have more feathers? Numbers of primary and secondary flight feathers reflect underlying skeletal size but only in some orders of birds

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Bird wings vary in size and morphology in terms of both size and number of feathers and the underlying skeletal anatomy. The number of primary remiges does not seem to vary much between bird species but, by contrast, the number of secondary remiges ranges between 6–40 depending on bird size. Given that the primaries are attached to the manus and the secondaries are attached to the ulna, it was predicted that as bone lengths increased then feather count would increase. Data were collected for 251 species from 25 different orders and phylogenetically controlled analysis explored the allometry between feather count and bone size. Number of primaries did not vary with manus size but the number of secondaries increased with ulna length, but only in some orders. For example, in Gruiformes, the number of secondary feathers increased concomitantly with ulna length but in the Passeriformes almost all species had nine secondary remiges. It is unclear why birds with an ulna length of 70 mm can have between 9 and 24 secondaries. Further research is needed to explore size dependent variation in the breadth of the feather vane and its ability to withstand aerodynamic forces generated during a wing beat.





## A new Middle Triassic Tanzanian dicynodont species associated with strongly curved claws

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The Manda Beds of Tanzania have produced a diverse assemblage of Middle Triassic tetrapods including 6 dicynodont taxa. Recent examination of a death assemblage of multiple dicynodont species collected in 1963 by Charig and Cox and repositied in the Natural History Museum, London has identified a cranium and mandible clearly belonging to a single individual which is substantially different to the other Tanzanian dicynodonts. The presence of hypertrophied tusks, a squared off premaxilla tip, a triangular skull in dorsal view, and the lack of a ridge along the nasals indicate this individual has more similarities with the South American *Dinodontosaurus* than other taxa. However, it also has several unique features such as a bulbous posterior ridge on the premaxilla, incompletely fused splenials, and an anteroposteriorly short palatal area. This suggests this individual belongs to a novel taxon, and a phylogenetic analysis accompanied with statistical tests further support this hypothesis. Among the associated postcranial elements are strongly curved unguals never before reported in dicynodonts. If these unguals belong to the same taxon as the skull, the unique suite of adaptations would have facilitated a mode of foraging different to that of contemporary dicynodont taxa, allowing them to occupy separate ecological roles.





## Locomotion in Extinct "Giant" Kangaroos: Information from Finite Element Analysis of the Astragalus

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All modern kangaroos (Macropodidae) hop. It is likely that some extinct "giant " (i.e., larger than extant species) kangaroos likely did not hop, or hopped only rarely. Extinct short-faced kangaroos (Sthenurinae) were likely bipedal striders while Protemnodon species ("giant wallabies", closely related to modern large kangaroos, Macropodinae) were probably more quadrupedal than their extant relatives. The astragalus, comprising part of the ankle joint, plays a key role in transmitting locomotory forces. Using Finite Element Analysis we investigated astragalus stresses during different simulated types of locomotion to see if different stress patterns could be determined among large kangaroos, extinct and extant. We varied body mass (transmitted over two legs or one, whether hopping [5x body mass], bounding quadrupedally or bipedal striding [both 2x body mass]) and the tibia/astragalus angle (90° during hopping and bounding, 120° during striding) and compared pairs of taxa of similar body masses. Hoppers showed greater stress in striding simulations than hopping simulations; the striders performed well in both simulations but better in striding. The likely more quadrupedal Protemnodon performed poorly all simulations except bounding, where its low stresses were similar to the other kangaroos. Our results thus support prior hypotheses of alternative locomotion in extinct giant kangaroos.





## The Biomechanical Constraints on Hopping in Giant Kangaroo Hindlimbs

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Several Pleistocene kangaroo species greatly exceeded the size of the largest kangaroos alive today. With extant large kangaroos already experiencing unusually high stresses in their hindlimbs while hopping, the size of these extinct megafaunal kangaroos has prompted the question: were they able to hop at all? At what body size is a kangaroo too big to feasibly hop? Previous attempts to answer this question have mainly focussed on extrapolating the safety factors of the hindlimb tendons. Here, we use biomechanical calculations to test the assumptions of these studies, by investigating the strength of the bones, muscles, and tendons of the giant kangaroo hindlimb, and testing which is most likely to limit the hopping ability of these species. We also attempt to minimise the extrapolation of scaling patterns beyond extant data, instead referring to fossil measurements wherever possible. We found that the bones and muscles of the hindlimb were likely capable of supporting hopping in giant kangaroos. Meanwhile, the strength of the tendons was indeed the most likely limiting factor, supporting the assumptions of prior studies.





## Skull anatomy and paleoneurology of a new specimen of the von Huene's gomphodont cynodont *Traversodon stahleckeri* (Middle-Late Triassic of Brazil)

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Traversodontidae, a clade of gomphodont cynodonts, thrived during the Middle and Late Triassic, exhibiting a widespread distribution. *Traversodon stahleckeri* stands out as one of the earliest-known traversodontids. Discovered by Friedrich von Huene in 1936, the species is based on few remains found in the Chiniquá region, *Dinodontosaurus* AZ, Ladinian/early Carnian (Brazil). In more recent research, a new specimen (ULBRA PVT-049) was unearthed at the Bortolin Site (*Dinodontosaurus* AZ), offering invaluable insights into the skull anatomy and paleoneurology of the taxon. This discovery enabled the identification of previously unknown phylogenetic characters, enhancing our understanding of the species' evolutionary history. Additionally, the endocranial anatomy of *T. stahleckeri* was examined for the first time. Notably, the reconstruction of the cranial endocast revealed paleoneurological features consistent with non-gomphodontosuchine traversodontids, including the presence of an unossified zone and a pineal body. However, distinctively, the parietal foramen was closed in this specimen. The presence/absence of the parietal foramen in some traversodontids has been linked to ontogeny, with older individuals losing it while retaining the pineal body. These recent findings offer valuable contributions to understanding the evolutionary history and cranial characteristics of *T. stahleckeri*, shedding light on the diversity and adaptations of traversodontids.





## Claws- a new tool for understanding the terrestrial ecology of pterosaurs?

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Pterosaurs were a group of flying archosauromorph reptiles that appeared in the Late Triassic and became extinct at the end of the Cretaceous. While there have been numerous examinations of pterosaur flight capabilities, their modes of terrestrial locomotion remain poorly constrained. In this study, the terrestrial ecology of pterosaurs is reviewed using a novel methodological approach utilising ungual and claw sheath morphometrics. Amniote claws are complex structures that are intimately connected to lifestyle and locomotory habits, and therefore can, by extension, yield intriguing data on ecology and function. Claw morphology presents an understudied yet promising model system for the study of ecology in extinct amniotes through comparisons with the ecomorphospace occupied by extant taxa. To facilitate a comprehensive ecomorphospace comparison, a dataset of pterosaur claw photographs encompassing a large taxonomic diversity has been compiled. This data has revealed a hitherto unrecorded morphological diversity in pterosaur manual and pedal unguals, as well as variable relationships between ungual and claw sheath morphologies in different taxa. These valuable new insights further our understanding of pterosaur ecology and expand our knowledge of the morphological diversity present in amniote claws as a whole.







### 3D geometric morphometrics on Carboniferous *Polygnathus* conodonts suggests temporal and ontogenetic differences rather than two coexisting genera

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The diversified conodont genus *Polygnathus* has been proposed to be split into *Polygnathus* sensu stricto, and several new genera. Among them, *Neopolygnathus*, described from the Late Devonian / Early Carboniferous, differs from *Polygnathus* s.s. only by the presence of a depression on its aboral face posterior to the basal cavity. The morphological variation of *Polygnathus* s.l. has been quantified using 3D geometric morphometrics in ten levels from the Puech de la Suque section (France) where *Neopolygnathus* cooccurs with *Polygnathus* s.s.. Four successive groups of levels sharing similar patterns of morphological variation have been identified. Within these groups, if size-related variation is accounted for, the two proposed genera *Neopolygnathus* and *Polygnathus* s.s. do not differ significantly in shape. The degree of expression of the aboral depression varies as a continuous and coherent gradient within each group. The frequency of conodonts with well-expressed depression however varies between the four groups, due to differences in the shape of the platform and in ontogenetic growth patterns. The genus *Neopolygnathus* is therefore not supported by the 3D morphometric analysis. The conodont elements being tooth-like structures involved in occlusion, the functional consequences of the morphological differences observed along the section requires further investigation.





## Two new *Kimmerosaurus* specimens expand geographic range and morphological understanding of the genus

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Cryptoclidid plesiosaurs were widely distributed across the Northern hemisphere during the Late Jurassic, displaying regional endemism at a species level, with few genera shared between regions. We present two new specimens that offer new material from *Kimmerosaurus*, as well as the first recorded presence of this genus from the Boreal Region (Svalbard). The two new specimens are PMO 212.662 from the Slottsmøya Formation of Svalbard (Norway) and K2134 from the Kimmeridge Clay Formation (UK-Etches collection). K2134 includes a disarticulated partial skull and four cervical vertebrae. PMO 212.662 includes a partial skull with partially articulated axial and appendicular elements. CT of K2134 provides amazing imagery of the specimen – significantly adding details on the rostrum, palate, and cheek region for *Kimmerosaurus langhami*. K2134 is largely similar to the holotype of *K. langhami*, with some differences in the atlas-axis and braincase. PMO 212.662 shares the unique *Kimmerosaurus* trait lacking a sagittal crest, as well as aspects of braincase morphology. Additionally, this specimen provides insights into the morphology of the posterior cervical and dorsal axial skeleton. Phylogenetic analysis supports the close relationship of these two specimens with *Kimmerosaurus*.





## On *Ossirarus kierani*, a curious little tetrapod from Romer's Gap

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Tetrapods are rare in the early Carboniferous. Until recently, they were represented by a few disarticulated limb and girdle bones from Nova Scotia and the skeleton of *Perderpes* from Scotland. Discoveries in the Scottish Borders have greatly expanded our knowledge of post-Devonian tetrapods and six new taxa have been named and briefly described so far. One of these, *Ossirarus kierani*, represented by a single specimen from the coastal section of the Tournaisian Ballagan Formation at Burnmouth, comprises the disarticulated bones of the posterior half of the skull, the anterior portion of the axial skeleton, and parts of the pectoral girdle and forelimbs. Compared with *Pederpes* it is small, with an estimated skull length of 55 mm. Like *Acanthostega*, it has a preopercular and a lateral line system represented by pores. It shares with embolomeres, a tabular-parietal suture, an intertemporal and a long tabular horn. The gastrocentrous vertebrae resemble those of *Caerorhachis* and the brachial foramen pierces the humerus through the posterior edge, as in *Mesanerpeton*. Preliminary phylogenetic analyses place *Ossirarus* on the tetrapod stem-group, crownward of some – but not all – Devonian taxa. The topology of the tetrapod stem suggests that numerous lineages of Carboniferous tetrapods extended back into the Devonian.





## Tracing archosauromorph origins through space, time, and climate in the TARDIS

Joseph Flannery-Sutherland \* <sup>1</sup>

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The diversification of archosauromorph reptiles from the Late Permian to Late Triassic is a classic example of an adaptive radiation. It has received significant attention from phylogenetic, morphological, and ecological perspectives, but its spatial signature is understudied. I reconstruct the geographic origins of early archosauromorphs using a taxonomically updated, time-calibrated super tree. I then couple landscape connectivity analysis and high-resolution reconstructions of deep time climate and topography in a novel workflow (TARDIS – traversal and routes of dispersal in spacetime) to infer the phylogeographic structure of their radiation across the ecologically anachronous stage presented by Pangaea. Finally, I quantify their rates and routes of dispersal and rates of climate adaptation to examine the biogeographic constraints on their early evolutionary success. Preliminary results highlight that the deepest archosauromorph divergences took place in European Pangaea but later cladogenetic events were geographically disparate and frequently involved trans-equatorial dispersals. This indicates that that extreme climates across the supercontinent were not as robust biogeographic barriers as previously suspected and demonstrates the role that landscape connectivity analysis can play in reconstructing the spatial dynamics of evolutionary radiations.





## Variation in pedal morphology of kangaroos suggests different mechanisms drive digit reduction in hopping and 'giant' short-faced lineages

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Locomotory styles of extant kangaroos (Macropodoidea) include hopping, walking, climbing, and bounding; the extinct giant short-faced kangaroos (Sthenurinae) are proposed to employ bipedal striding. The pedal morphology of extant kangaroos exhibits variance in the relative robusticity of the 5th and 4th digits (other digits are lost or highly reduced). The role of the smaller 5th digit in weight bearing and locomotion remains unknown, as well as the reasons for its loss in Plio-Pleistocene monodactyl sthenurines. Here we employ linear measurements of 4th and 5th metatarsals from 86 macropod individuals (including two Miocene sthenurines which retain digit five), thus establishing patterns of variation in 5th metatarsal robusticity with the view to understand sthenurine digit loss. Morphometric analysis showed that within the extant subfamily Macropodinae 5th metatarsal robusticity depends on the length of the 4th metatarsal: elongate feet have thinner 5th metatarsals and short feet more robust ones. The large extinct macropodines *Protemnodon* and *Congruus* have short feet and robust 5th digits. The sthenurines do not conform to this macropodine pattern of digit reduction, retaining a robust 5th digit with an elongated 4th one. Thus the reasons and mechanisms of digit loss in Plio-Pleistocene sthenurines remain obscure.





## Duplicating a dead horse: recreating the lost Crystal Palace *Palaeotherium magnum*

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Eight of the original 37 Crystal Palace Dinosaurs sculptures have vanished in the last 170 years. Most of these constitute mammal reconstructions from the “Tertiary Island” and are poorly documented, frustrating efforts to understand their morphology and the circumstances surrounding their disappearances. An exception is the sculpture of the Eocene equoid *Palaeotherium magnum*, which was photographed and illustrated in relative detail before it was lost six decades ago. These records have allowed a replica *P. magnum* to be created in the first effort at replacing a lost Crystal Palace “Dinosaur” since 2003. Initiated by the Friends of Crystal Palace Dinosaurs charity, the replica was funded through public contributions and a grant from the Crystal Palace Park Trust and was sculpted by Robert Nicholls in his Bristol studio. We estimate that the original *P. magnum* model exceeded 2 m in length and, instead of the tapir-like form suggested by leading Victorian scholars, its anatomy was primarily informed by African elephant species. Recreated in durable fibreglass, the replica was unveiled alongside the two surviving Crystal Palace palaeothere sculptures in June 2023. Future restorative work includes plans to recreate another lost palaeothere component, the original head of the sitting “*Palaeotherium minus*”.





## It's all about the upstroke: allometric analysis of flight muscles in birds demonstrates that flight style is a function of variability in supracoracoideus mass

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Avian flight is powered by a downstroke force generated by the pectoralis (P) muscle and an upstroke force generated by the supracoracoideus (SC) muscle. This analysis explored the allometry of flight muscles to test for isometry with body mass in birds. Data for muscle masses for over 600 species, representing 28 orders, were used in phylogenetically controlled analysis of covariance to test for the effects of order on allometry of flight muscles. The pectoralis scaled isometrically with body mass, but the supracoracoideus muscle exhibited a slight but significant negative allometry. Both muscles showed significant effects of order, but this effect was greatest for the supracoracoideus. As well as wing-propelled diving birds, and hovering hummingbirds, tinamous, gamebirds, and pigeons, which exhibit burst flight, also had had a disproportionately large supracoracoideus. This is needed to generate a powerful upstroke to counter water-borne drag or gravity. Many other orders had a P:SC ratio around 10:1 but values of 20:1, recorded for raptors and owls, were associated with relatively small supracoracoideus muscle mass. Differing flight styles reflect variability in supracoracoideus mass, rather than pectoralis mass. The significance of this result will impact our understanding of how morphology impacts flight action of birds.





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