SPPC/GCG Conference

Controlled exsiccation of fossilised remains in waterlogged marl: Slowly Slowly Dryee Squiddie

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A fossil from a squid-like animal, preserved in Lower Jurassic argillaceous limestone or marl, was collected on the 8th March 2019 from Lyme Regis beach. The collectors kept the specimen wet by wrapping it in newspaper and plastic, and transported it to the Conservation Centre at the Natural History Museum in London (UK).

Conservators partially immersed the block in water, with a few drops of thymol to prevent mould growth, whilst tests on samples of the matrix were undertaken. Two consolidants were selected from the field of waterlogged archaeological artefact conservation: Primal WS24 and PEG 400. Untreated and consolidated samples were variously dried rapidly in ambient lab conditions or dried slowly within Dartek C-917 semi-permeable cast nylon film microenvironments. Both consolidation and slow drying proved beneficial but insufficient to prevent cracking entirely. A double layer of film was then considered, to slow the drying-time even further.

The entire specimen block was then consolidated by immersion in 10% and then 33% Primal WS24 before slow drying in a double-layer Dartek C-917 film microclimate. Primal WS24 was selected in preference to PEG 400 because the former would be compatible with Paraloid B72 in acetone (if future remedial conservation becomes necessary). After drying, parts of the surface of the block were prepared using a split-V ultrasonic tool, to expose more of the nacre layer, and the lower half of the block was removed using rotary tools to minimise vibration.

Palaeontological preparation facilities in UK universities: the north south divide?

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Palaeontological preparation facilities in university departments are sadly often lacking and where present unfortunately frequently do not have a permanent member of staff or a trained preparator to manage the facilities or conduct preparation. With micro CT-scanning becoming the preferred method of fossil analysis alongside ‘digital preparation’ the need, or perhaps desire, to actively maintain a program of physically preparing fossil specimens may not be regarded so importantly. Information from all UK universities involved in active palaeontological research shows that most institutions do have some form of rudimentary preparation facilities but those that do have an active palaeontological preparation program are not evenly distributed geographically. We announce a new palaeontology preparation facility in the University of Edinburgh, School of Geosciences that represents the only such facility in a Scottish university. As part of the PalAlba consortium of academic scientists, conservation specialists, and collectors working together to recover, record and research fossils from Scotland, and our aim is to provide a facility for students to develop palaeontological preparation techniques alongside the theoretical side of palaeontological research. We present some examples of material that has been processed in this new facility and describe the set-up for this preparation.

A combination of air abrasion and ultrasonic preparation reveals fine details ahead of scanning electron microscopy, in fossil ophiuroids

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Multiple well preserved fossil ophiuroids (brittle stars) within blocks of consolidated sandy clay from the Atherfield Clay Formation of the Isle of Wight, were fully exposed to facilitate taxonomic study by scanning electron microscopy (SEM).Their preparation required the removal of covering matrix; complicated by the entanglement of the arms of multiple specimens, the need to retain delicate taxonomically important spines and dermal plates, as well as exposing plate boundaries whilst minimising any damage to the plate surfaces (stereomes).

The specimens were also small; discs varied from 2mm to 10mm with arms up to 20 mm in length. Thus air abrasion was undertaken under a stereoscopic microscope with illumination. The optimal abrading set-up was sodium bicarbonate No.4 particle size (50 microns) delivered at 2.5bar/35 p.s.i. via a 0.75mm diameter air abrasive nozzle. The areas surrounding the specimens' arms were trenched by air abrasion to reveal the surfaces and sides; effectively mini-pedestalled in relief on the blocks. The central discs were air abraded to expose mouthparts, ossicles, spines and plate boundaries.

Industrial metholated spirit (I.M.S.) was applied to highlight surface detail during preparation; this evaporated after a couple of minutes and left no residue on the specimens, but enabled finer details to be developed.

In order to facilitate detailed SEM of individual arm plates, several pieces were removed from the blocks and placed in small, sealable plastic specimen bags with a few drops of water. The exterior of the bags were then touched with the tip of an ultrasonic pen, (Sonotec Split V) which removed the remaining matrix from the plate boundaries very effectively.

This combination of techniques fully exposed all the elements required for full taxonomic study without causing severe damage and should be more widely applied to other echinoderm fossils in order to retain as much taxonomic information as possible.

Cold climate collection of Cretaceous creatures in Canada

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1 - Royal Tyrrell Museum of Palaeontology

In February of 2016 staff at the Royal Tyrrell Museum of Palaeontology were informed about Early Cretaceous fossil bone that was recovered from drill core at a depth of 33.6m at the Suncor oilsand mine in northern Alberta, but were told to wait at least two years before the working face of the mine got to the drill hole. Finally, in February 2019 a crew of four was able to make the 800km drive from the Museum to the mine site. At the start of the work, daytime temperatures were in the -25C range so special precautions were going to be needed to safely and completely collect the as yet unidentified specimen. Large excavation machines were engaged for four days to dig a very large hole with the correct slopes for stability. The precise coordinates of the drill hole enabled a targeted excavation. Final exposure of the specimen was done with an electric jackhammer and hand tools. The drill hole had pierced almost the exact centre of a scattered and incomplete plesiosaur skeleton. A portable shed was temporarily used to trap warm air from a hot air source to enable plaster and glues to set and cure properly. After a week temperatures rose to around -10C, so the shed was removed. To provide daytime heat warm air was ducted directly down into the pit and blown directly on the fossil remains in the ground and the crew. At night a tarp covered the excavation and the warm air was directed and trapped under the tarp to keep the rocks and fossil warm enough for glues and plaster to behave and set properly, and to keep water warm for making plaster. The resulting plaster jackets were also kept insulated and warm during their curing process before being lifted out of the pit by heavy equipment.

13 years of preparing Danish fossils, a retrospective

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1 - Museum Salling, Conservation

I have had the privilege working with some of the most spectacular fossils found in the last decade in Denmark. Working at Museernes Bevaringscenter I Skive with specimens from Fossil og Molermuseet and Fur Museum I have had many lovely fossils on my prep. table.
Fishes, turtles, birds and a couple of whales, mostly originating from the Eocene Fur Formation in northern Denmark. Once in my lab, the usual procedure was used. Hammer and chisel, diamond rotating tools and heavy pneumatic tools, using "finer" tools when working closer to the fossil surface, dental tools, scalpels and so on. The preparation of the finest details would normally be with Acetic acid preparation buffered with Calcium orthophosphate. The preservation of the fossils often, with preserved soft tissues, would be a real challenge. I will talk about my techniques and give a broad view of my work over the years.

A new technique for sampling plant debris beds from the Early Cretaceous Wealden Group of southern England

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Sampling techniques of Wealden Group plant debris beds often target specific micro-vertebrate, invertebrate or palaeobotanical assemblages. This specific targeting of microfossils inevitably results in a bias and the potential

loss of important palaeontological data. A new method combining acid digestion, salt floatation and ultra-violet light illumination allows plant debris beds to be comprehensively sampled for their entire fossil assemblage. The use of traditional sieving techniques often leads to the abrasion and destruction of specimens. This multi stage method results in the retrieval of delicate, exceptionally preserved plant material, amber, plant cuticle and micro-vertebrates.

SVPCA Conference Abstracts

Neural Canal Ridges: A Novel Osteological Correlate of Post-Cranial Neurology in Dinosaurs

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Bony ridges occur on the walls of the neural canal in caudal vertebrae of numerous sauropod dinosaurs. These neural canal ridges (NCRs) are anteroposteriorly elongated but do not extend to the ends of the canal. To date, we have observed NCRs in caudal vertebrae of *Alamosaurus*, *Apatosaurus*, *Astrophocaudia*,*Brontomerus*, *Camarasaurus*, and *Diplodocus*. Numerous similar structures occur in extant vertebrates: (1) Neurocentral joints are ventral to NCRs in sauropod caudal vertebrae, and NCRs occur in unfused juvenile arches. Hypothesis rejected. (2) Attachment scars from ligamentum flavum occur at the ends of the dorsal roof of the canal, not the midpoint of the lateral edges, and this mammalian ligament was probably absent in dinosaurs. Hypothesis rejected. (3) Smooth ridges separate the spinal cord from the dorsal spinal vein and paramedullary airways in some crocodilians and birds, respectively. However, these septa persist to the ends of the canal, giving it an 8-shape, unlike the discrete NCRs of dinosaurs. Hypothesis rejected. (4) Bony attachments for denticulate ligaments occur in some non-mammalian vertebrates. The dura mater around the spinal cord fuses to the periosteum of the neural canal in non-mammals, so the denticulate ligaments that support the spinal cord can leave ossified attachment scars. These spinal cord supports have been identified in teleosts, salamanders, and a juvenile lizard, and they are the best match for the morphology of the NCRs in sauropod vertebrae. Functions of NCRs remain obscure. Denticulate ligaments are largest in regions of the vertebral column that experience strong lateral flexion. The hypothesis that NCRs supported the spinal cord of sauropods during lateral tail-whipping is attractive, but inconsistent with our recent discovery of NCRs in a hadrosaur caudal. NCRs are a new osteological correlate of the peripheral nervous system in dinosaurs, and highlight the need for more study in this area.

Quantitative taphonomy – they key to understanding the pterosaur bauplan?

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Quantitative taphonomy has huge potential for furthering our understanding of vertebrate palaeobiology. So far, however, it has been a neglected field with little development. Here we show how quantitative taphonomy can be used to determine the ‘bauplan’ of pterosaurs. With no descendants and a unique morphology, pterosaurs remain an enigmatic group despite a high degree of research interest for over 200 years. One aspect still debated is the basic construction and extent of the wing membrane, fundamental to locomotory abilities and other key aspects of their biology. Did the wing membrane connect all four limbs, bat-like, forming a single flight surface and single anatomical module? Were they bird-like, with separation of limbs to create four anatomical modules? Or were they a unique two or three module construction? Soft tissue evidence is patchy and found in only a tiny

number of species, and the insights it provides is limited. Quantitative taphonomy, through metrics of completeness, articulation, and joint geometry, can test limb association, and help identify anatomical modules. Over 100 pterosaurs have been analysed thus far, with an intended data set of 200+ individuals from more than 40 species representing all principal clades. This will allow different models to be mapped across the phylogeny. Fossil birds and bats will be similarly analysed in order to provide context and constrain the models, as their bauplan can be safely inferred from extant forms.

'*Pallisteria angustimentum*' from the Middle Triassic of Tanzania and the Triassic rise of archosaurs

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One of the most significant evolutionary radiations in terrestrial ecosystems occurred after the Permo-Triassic mass extinction, with the origination and diversification of archosaurs, including dinosaurs, pterosaurs and crocodylomorphs. Originating by the late Early Triassic, archosaurs diversified into a broad range of ecomorphologies through the Middle and Late Triassic, replacing previously incumbent lineages such as therapsids. Important data on the early archosaur radiation comes from the Manda Beds (Middle Triassic: Anisian) of Tanzania. Three phases of field expeditions have collected archosaur fossils from the Manda Beds: in the 1930s, 1960s, and over the last 15 years. Those archosaur fossils collected in the 1930s and 1960s were initially studied by Alan Charig, who created many nomina nuda but never published his research. Recent restudy of Charig's material has revealed a diverse assemblage of poposauroid (*Hypselorhachis*), paracrocodylomorph (*Mandasuchus*) and aphanosaurian (*Teleocrater*) archosaurs, and possibly the oldest dinosaur fossil (*Nyasasaurus*). Here, we describe the last unstudied 'Charig taxon': *Pallisteria angustimentum*. *Pallisteria* is known from a very large partial skull (basal skull length ~95 cm), including the premaxillae, maxillae and palate, several cervical vertebrae and a partial manus. Although poorly preserved, multiple autapomorphies and a unique character combination support identification of *Pallisteria* as a distinct species. Dental and jaw anatomy suggest a hypercarnivorous palaeoecology, with *Pallisteria* being the largest predator known in the Manda ecosystem. We analyse the position of *Pallisteria* among pseudosuchians using comprehensive phylogenetic analyses of early archosaurs. The Manda Beds contain at least nine crown archosaur species, including the earliest known representatives of several key groups, making it one of the most important sources of data for understanding the tempo and pattern of the archosaur radiation.

Determinate growth and diphyodonty of early mammaliaform *Morganucodon watsoni*

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The early mammaliaform, *Morganucodon*, has given us unique insights into the appearance of what we consider mammalian characteristics, and is often cited as the first in the mammalian lineage to possess the traits of diphyodonty (a mammalian condition of a single set of replacement teeth) and determinate growth patterns. Indications of potential dimorphism in M. watsoni led to this study, in order to reappraise earlier conclusions of determinate growth. An extensive dataset of measurements of over 850 jaw specimens has been collected and statistical analysis performed, showing only a single morphotype in the population and confirming determinate growth in this mammaliaform. Also, earlier statistical analysis of tooth sizes raised doubts about true diphyodonty existing in *Morganucodon*, and suggested a possible partial third wave of replacement teeth. However, there was a lack of evidence of actual teeth being replaced, so the study has also been revisited with this more extensive dataset, to try and fully establish the replacement pattern at this critical junction in mammalian evolution.

The Bristol Baby: a reassessment of a juvenile plesiosaurian from the Pliensbachian (Early Jurassic) of Dorset, UK

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The collections of the Bristol Museum and Art Gallery include a juvenile plesiosaurian which was collected in 1990 from the Pliensbachian of the renowned Jurassic Coast of Dorset, UK. Originally described as one of the smallest known individual plesiosaurians, it was nevertheless too large to be a neonate. Although taxonomically indeterminate, it was tentatively assigned to the genus *Plesiosaurus*. This specimen has now been reassessed in light of both an improved sample of Pliensbachian plesiosaurian diversity and an improved understanding of plesiosaurian ontogeny and reproductive strategy (K-selected vivparity).

The specimen comprises a partial axial skeleton with incomplete pectoral and pelvic girdles and gastralia. Despite the incomplete preservation and juvenile status it can be included in recent phylogenetic datasets. It forms a clade with other Pliensbachian specimens from the UK which represent separate species within an undescribed genus. The coracoids show a small median embayment which is only seen in the aforementioned Pliensbachian specimens amongst Jurassic plesiosaurians.

The specimen contains both inorganic (sand-grade gastroliths) and organic gastric contents. The majority of the latter are here identified as cephalopod hooklets with some minor fish remains. Identical gastric contents are seen in one of the other Pliensbachian specimens and as this was an adult this implies an ontogenetic continuity of diet and behaviour for the clade. Soft tissue structures are preserved in black and buff material, with a striated texture in places. This is similar to recently described soft tissue from the Toarcian of Germany, with a net-like appearance, and also the longitudinal rows of scale-like structures seen in the early Late Cretaceous polycotylid *Mauriciosaurus*.

A recently described foetus of the Campanian *Polycotylus latippinus* was approximately 40% of adult body length, indicating that the neonate was somewhat larger. This juvenile can be reconstructed at between 55% and 45% of adult size. However it is also clearly not a neonate having had sufficient time to acquire a collection of gastroliths which would have acted as a gastric mill. Neonates of basal Triassic sauropterygians were approximately 25-30% of adult length, and it is possible that those of Jurassic plesiosaurians were intermediate in size between these and derived Cretaceous taxa.

Yet *another* explanation for long necks in the Plesiosauria.

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1 - plesiosaur.com

Although long necks are known from several clades such as sauropod dinosaurs, azdarchid pterosaurs and oddities such as *Tanystropheus*, plesiosaurs are unique in that their long necks are created in part by a huge increase in the number of cervical vertebrae, reaching as much a 76 in the elasmosaur *Albertonectes*. Numerous explanations for this extreme length have been suggested both in the scientific literature and in popular media, but few stand up to critical scrutiny or yield predictions which can be tested by the acquisition of evidence. There is also a tendency to explain long necks in teleological terms.
A detailed study of vertebral proportions in plesiosaurs has shown patterns of variation which are remarkably consistent over 100 million years of plesiosaur evolution and hint at underlying mechanisms for extending the neck. I propose that the hyperelongation of plesiosaur necks is driven four-flipper propulsion found uniquely in plesiosaurs through a process of successive waves of cervicalisation of dorsal vertebrae. Plesiosaur skulls and dentition show a range of adaptations for feeding, which suggests that the long neck did not evolve in response to a particular feeding strategy but that the feeding strategy developed to accommodate the long neck.

Humeral Head Shape: A Predictor for Avian Flight Capability?

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Determining the flight capabilities of fossils is essential for understanding avian evolution. Humeral head shape may predict flight ability, because the wing pivots around the glenohumeral joint during flapping. If so, then the flight abilities of feathered fossils could potentially be determined from their humerii. Here, the hypothesis that humeral head shape relates to flight ability was explored. Geometric morphometrics (elliptical Fourier analysis) was used to quantify humeral head shape in three extant groups. A linear discriminant analysis (LDA) based on species was run on Group 1 (phylogenetically close species with similar flight ability) to determine if factors other than phylogeny and flight ability impacted humeral head shape. Only one species was statistically distinct indicating limited impact of other factors. Next, an LDA based on phylogenetic order was run on Groups 2 (phylogenetically close species with differing flight abilities) and 3 (phylogenetically distant species with similar flight abilities) to identify any phylogenetic effect. All orders were statistically distinct. Consequently,

following a cluster analysis to distinguish four statistically distinct clusters, a phylogenetically-controlled functional discriminant analysis (pFDA) was run on all groups to determine the effect of flight ability. This correctly classified 91% of taxa indicating flight ability impacts humeral head shape. The order of the four clusters in a subsequent cluster dendrogram suggested a trend towards better flight manoeuvrability. To test this, morphological/flight performance variables that may be linked to manoeuvrability (for example, wing loading) were ordered as the dendrogram. For all variables, clusters 4 to 2 showed a directional trend, but cluster 1 did not conform to the pattern. The explanation for this and implications for future work will be discussed.

Exploring hypotheses of Late Cretaceous Western Interior endemism using phylogenetically-corrected Biogeographic Connectedness

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During the Late Cretaceous, the Western Interior of the USA was divided into eastern and western landmasses by a large and long-lived epicontinental sea, the Western Interior Seaway (WIS). Dinosaurs inhabited lowland environments either side of the WIS, and their fossils are found in abundance in terrestrial sediments from the time. Campanian and Maastrichtian deposits from the Western Interior are particularly notable for the diversity and abundance of duck-billed hadrosaurs and horned ceratopsids, large-bodied herbivores that dominated terrestrial ecosystems at this time and in this geographic setting. Recent work has hypothesized that dinosaur faunas from the Western Interior show pronounced endemism, with distinct faunas evolving and radiating in the northern and southern parts of Laramidia, a large island that bordered the WIS to the west. Such hypotheses invoke a barrier of unknown origin dividing the island of Laramidia into two distinct provinces, either side of which evolution occurred independently. However, these hypotheses of endemism have not been rigorously or quantitatively tested. We used the recently developed technique of phylogenetically-corrected Biogeographic Connectedness (pBC) to examine the degree to which the faunas of Northern and Southern Laramidia were endemic during the Campanian and the Maastrichtian. We built supertrees of ceratopsids and hadrosaurs, and measured pBC between Northern and Southern Laramidia in two timeslices representing the Campanian and Maastrichtian. For hadrosaurs, low taxon sampling in Southern Laramidia meant that pBC could only be calculated for the Campanian. We then permuted the areas in which taxa lived to generate 1000 randomized pseudoreplicate datasets from which we calculated pBC and compared it to our observed values. We find lower pBC values, and therefore higher endemism, in the Campanian than in the Maastrichtian for ceratopsids. pBC is statistically significantly different from that of the randomized datasets in both the Campanian and Maastrichtian for ceratopsids, and in the Campanian for hadrosaurs. This indicates that Northern and Southern Laramidia contained endemic faunas, and appear to have been distinct geographic provinces during the Late Cretaceous. Geological evidence for a barrier to migration between Northern and Southern Laramidia remains elusive, suggesting that this barrier may have been ecological or climatic.

Twisting by (in) the Pool: the potential for twist feeding in pliosaurs

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1 - Royal Tyrrell Museum of Palaeontology

Pliosaurs were a clade of plesiosaurs distinguished by broad heads, short necks, and robust teeth. This indicates that they had a very different feeding style from those plesiosaurs that possessed longer necks, smaller heads, and slender, more numerous teeth. As a consequence of their more robust body forms and large size, there exists the possibility that pliosaurs made use of twist feeding to attack, dismember and ingest large prey items. Twist feeding can be observed in living crocodilians, and the analysis of this feeding style can be done with consideration of the physics of rotating bodies - rotational inertia (RI) and conservation of angular momentum. To investigate these properties in pliosaurs/plesiosaurs in relation to feeding styles, six, three-dimensional, digital models were constructed: *Nichollssaura*, *Cryptoclidus*, *Tatenectes*, *Rhomaleosaurus*, *Albertonectes*, and *Liopleurodon*. These animals/models range in size from the smallest 2.8m, 127kg *Nichollssaura* to the largest 12m, 9.6t *Lioleurodon,* and include short-, medium- and long-necked forms. Calculation of the rotational inertias about the longitudinal, transverse, and vertical axes of the models included the contributions from the limbs and the presence of a lung cavity. For comparison with living forms, rotational inertias were also computed for the American alligator (*Alligator mississippiensis*) and the saltwater crocodile (*Crocodylus porosus*). *Liopleurodon* (9.6t), *Albertonectes* (5.6t) and *Rhomaleosaurus* (2.7t) were found to have the highest relative rotational inertia (RI divided by body mass) about their longitudinal axes. The relative RI of *Liopleurodon* was found to be 10 times that of the saltwater crocodile, a known twist feeder. The smaller, longer necked forms had dramatically lower relative RIs. The unusually high value for the axial RI of the elasmosaur

Albertonectes is attributed to its exceptionally long limbs, but its long neck, narrow head, and slender teeth would heavily discount its potential for twist feeding.

What is a nyctithere? The relevance of Hampshire Basin finds to an answer

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Nyctitheres are a family of small insectivorous placental mammals that lived between the early Paleocene and middle Oligocene in North America, Europe and Asia. When known essentially only from teeth and jaws, they were initially thought to be related to bats (Chiroptera) and subsequently to shrews (Lipotyphla). Around the turn of this century, the first tarsal bones were found in the Hampshire Basin. They showed similarities to those of scandentian tree-shrews and indicated a scansorial lifestyle, unlike the terrestrial lipotyphlan true shrews. After more of the skeleton became known in the UK, a phylogenetic analysis strengthened their relationships to tree-shrews, colugos and primates, as stem members of the superorder Euarchonta. New finds in the USA revealed partial skulls with ear-regions, which led to a new phylogenetic analysis, but which included fewer postcranials than previously. This returned nyctitheres to having a close relationship with Lipotyphla. Recent finds of nyctithere ear regions in the Hampshire Basin allow a more comprehensive analysis, which once more finds nyctitheres to be stem euarchontans. Postcranial adaptations appear to be key to this relationship, whilst ear-regions retain largely primitive placental states. A high diversity of 17 nyctithere species in the Hampshire Basin, more than half of which now have postcranials attributed, demonstrates a variety of traits within the scansorial locomotor mode.

Cetiosaur diversity in the Middle Jurassic of the UK

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The Middle Jurassic *Cetiosaurus* of the UK is historically the oldest sauropod described, and numerous phylogenetic and osteological analyses build on its information. However, *Cetiosaurus* is a classic ‘wastebasket-taxon’, with many specimens traditionally assigned to it without having been examined in over almost a century. Next to the holotypic and associated material of *Cetiosaurus oxoniensis* from the Forest Marble Formation of Oxfordshire, currently housed at the Oxford University Museum of Natural History, several specimens are housed in museums in Leicester, Gloucester, Stroud, and Skye. The ‘Rutland *Cetiosaurus*’ from Leicester is already thought to consist of a different taxon and is currently being revised. The Gloucester material comprises ischia, coracoids and caudal vertebral material. Stroud has several axial elements, including cervical and dorsal vertebrae, a femur, and an ilium. The Skye material consists of dorsal and caudal vertebral centra, as well as appendicular elements. As the Gloucester and Stroud material originate from the Lower Oolite, underlying the Forest Marble, it is possible these represent different taxa. Indeed, when compared to the holotype material of *Cetiosaurus oxoniensis*, they present significant osteological differences in vertebrae and pelvic elements. A preliminary phylogenetic analysis retrieves the Gloucester specimen as nested within *Cetiosaurus*, and as sister-taxon to *Lapparentosaurus* from Madagascar. The Stroud specimen is retrieved outside and more basal to this node, and the Skye material shows potential to be more derived than the latter two. These results suggest a high diversity in both cetiosaurid and eusauropod taxa in the Middle Jurassic of the UK.

A new ichthyosaur (Reptilain, Ichthyopterygia) from the Late Jurassic Kimmeridge Clay Formation of Dorset, UK

MEGAN JACOBS * [1]& DAVID MARTILL [1]

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A new ichthyosaur specimen (K1885) from the Late Jurassic (Kimmeridgian) Kimmeridge Clay Formation of Dorset, United Kingdom is described. The specimen was found and expertly prepared by Mr Steve Etches MBE, a plumber by trade, and is now housed in a new purpose-built museum, The Etches Collection in Kimmeridge, Dorset. It is preserved on a slab of laminated coccolith limestone, and comprises a near complete skull, in articulation with the anterior vertebral column and associated thoracic ribs, complete pectoral girdle, fully exposed left forelimb, and some elements of the right side.

Aspects of the dentition, skull roof bones and the forelimb configuration distinguishes the new specimen from previously described Late Jurassic ichthyosaurs, and consequently it is referred to a new genus and species.

Unusually, an enlarge process on the supratemporal bones may have given the animal a ‘horned’ appearance in life. Aspects of the humerus and skull show the new taxon lies as a sister taxon to Ophthalmosauridae, and this is supported by a cladistics analysis.

The new specimen adds to the diversity of the Ichthyopterygia of the Kimmeridge Clay Formation, and also emphasis the important contribution of amateur collectors in Palaeontology.

Interpreting vortices inside Mesozoic suspension-feeding mouths: a total perspective extrapolation from gill raker evidence

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Many pachycormid problems result from their trend towards poor ossification with the increasing adult size of a given taxon. This entails that with increasing adult size, genera have increasingly poorly ossified sections of their post-cranial material (leading to a reduction in post-cranial material to code), and more poorly fused and fragile cranial material (leading to a lack of accessible skull characters to code). Both of these tendencies have the effect of reducing the quantity of comparable characters common across most of the taxa, and increasing the fog surrounding phylogenies, in particular the latter trend, when the standard matrix used to decipher interrelationships for pachycormids is a dataset of over 120 characters where 77% of them are cranial.

In 2007, it was argued that the use of gill raker characters for pachycormids was flawed, as they were only really known in the largest representatives from the group (specifically *Leedsichthys*, and more questionably at the time from *Asthenocormus*) and might simply be acting to overweight the suspension-feeding signal. However, ten years on, the discovery of rare examples previously unknown for some taxa, coupled with recent advances in CT-scanning making it possible to determine the structure of gill rakers deep within unprepared skulls, have meant that gill raker morphology may now be regarded as a credible and perhaps uniquely ubiquitous source of characters with which to examine pachycormid interrelationships across a breadth of taxa.

Furthermore, this new information on diversity of raker morphology across the group enables feeding models to be constructed for the first time, based on similarities to extant chondrichthyan and osteichthyan taxa.

Building a new approach to visualising the topology space of all possible phylogenetic trees

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Appropriate visualisation remains critical to sound data analysis and is more valuable than any summary statistic. However, oftentimes our data are high-dimensional, either because they are multivariate or due to some other intrinsic property, meaning simple bivariate visualizations are not possible. Phylogenetic trees – a special case of directed acyclic graphs that attempt to capture the relationships between a set of species – fall into this latter category. Typically, researchers only work with samples of optimal trees, choosing to visually summarise their variance using “consensus” methods that capture only very limited information. A more appropriate alternative might be to use tree “spaces” that visually summarise trees in the context of all possible topologies (arrangements of tips). Such visualisations have broad application in vertebrate palaeobiology. For example, by assigning numerical values to tips the space becomes a “landscape”, allowing identification of multiple tree “islands”. Unfortunately, there are multiple challenges to implementing treespace approaches, primarily the high numbers of all possible topologies – for 50 tips this number is equivalent to estimates for all the atoms in the observable universe. Here I attempt to derive a novel approach by drawing on mathematical tools from graph theory, geometry and topology. I conjecture that treespace can be first captured as a two-dimensional graph, with vertices corresponding to topologies and edges to adjacencies, and then projected onto the N-sphere (the hyperdimensional extension of the sphere), where the rich toolbox of map projections can be co-opted for subsequent visualisation. Critical to this approach is the consideration of not just fully bifurcating topologies, but also the multifurcating trees that are largely ignored by workers. Here I show practical solutions for the 1-, 2-, 3-, and 4-tip cases that both retain low dimensionality and Euclidean distances, in contrast to currently

available methods. Finally, I speculate on what needs to be achieved to generalize this approach to higher tip counts.

The first duckbill dinosaur (Hadrosauridae:Lambeosaurinae) from Africa and the role of oceanic dispersal in dinosaur biogeography

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The Late Cretaceous saw the evolution of endemic dinosaur faunas in the northern and southern hemispheres. The Laurasian continents of North America and Asia were dominated by hadrosaurid and ceratopsian ornithischians, with tyrannosaurs as apex predators. In Gondwanan communities, including Africa, South America and Indo-Madagascar, titanosaurian sauropods dominated as herbivores and abelisaurids as predators. These patterns are thought to be driven by the breakup of Pangaea and the formation of seaways, which limited dispersal between Laurasia and Gondwana. Here, we report a lambeosaurine hadrosaurid from Africa, the first Gondwanan representative of a clade previously thought to be restricted to Laurasia. The new animal, from the late Maastrichtian of Morocco, is recovered as a member of Arenysaurini, a previously unrecognized clade of lambeosaurines that are otherwise restricted to Europe. Biogeographic modelling suggests that hadrosaurs dispersed from Asia to Europe, and then Africa. Given the existence of large, persistent seaways isolating both Africa and Europe from other continents, and the absence of the extensive, bidirectional interchange that characterizes land bridges, these patterns suggest multiple dispersals across marine barriers, similar to those seen in Cenozoic mammals. Dispersal across marine barriers is also seen in other hadrosaurids lineages and titanosaurian sauropods, suggesting that oceanic dispersal played a role in structuring Mesozoic terrestrial faunas.

The radiation and biogeography of the Ceratopsidae (Dinosauria: Ornithischia)

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The Ceratopsidae (Dinosauria: Ornithischia) is a monophyletic group of marginocephalian dinosaurs. All ceratopsid taxa possess a hypertrophied nasal region, extensive cranial ornamentation (e.g. nasal and supraorbital horns and a caudally extended parietosquamosal frill) and dental batteries with vertical shearing dentition. Identifiable ceratopsid remains appear throughout a stratigraphic interval of approximately 79.0-65.5 Ma with the Late Campanian strata (i.e. 76.4-70.6 Ma) of western North America the most extensively sampled. Contemporary studies suggest ceratopsids represent a significant component (i.e. diversity and biomass) of Late Cretaceous vertebrate assemblages of western North America. Here, we present an analysis of the biogeographic history of the Ceratopsidae. We hypothesise that the evolution and radiation of the ceratopsids was regulated by the degree of isolation of the palaeolandmasses of North America (i.e. northern Laramidia, southern Laramidia and Appalachia) by the Western Interior seaway. To test ancestral state probabilities, analysis of phylogenetic and stratigraphic data was implemented in the R software package BioGeoBEARS using six biogeographic models; the Dispersal-Extinction-Cladogenesis (DEC) + jump dispersal maximum likelihood model presents as the optimum model for interpreting ancestral ranges. Our results indicate that the most recent common ancestor of Ceratopsidae was widespread throughout Asia and western North America with the basal split between chasmosaurine and centrosaurine taxa attributed to a peripatric speciation event at the upper boundary of the Mid Turonian approximately 90.4 Ma. The early evolution of the centrosaurines (e.g. nasutoceratopsins) is characterised by vicariance and subset speciation; intermediate and derived forms are restricted to Northern Laramidia by a single subset speciation event In contrast, chasmosaurine evolution is characterised by dispersal between the northern and southern Laramidia faunal regions.

Internal radial spoke-like trabeculae resist torsion and bending in hyper-elongate azhdarchid pterosaur vertebrae

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Azhdarchid pterosaurs are noteworthy for their highly elongate necks with seemingly limited scope for manoeuvrability. In some genera, neck length may exceed 2 metres, posing interesting questions for their posture and feeding capability. Lengthening of the neck occurred by hyper-elongation of the cervical vertebrae, especially CV3-7, rather than an increase in vertebral count. Lengthening of the neck was accompanied by elongation of the skull and the forelimb, potentially giving these pterosaurs an imposing, perhaps giraffe-like posture when on the ground.

Exceptionally well-preserved (3D) azhdarchid pterosaur vertebrae from the Cretaceous Kem Kem beds of Morocco provide an opportunity to investigate the internal histology of the hyper-elongate neck. Topographic and CT scanning reveals an intricate arrangement of thin, radially arranged trabeculae suspending a bony neural tube in a more or less central position within a near tubular centrum/neural arch complex. The ultra-thin wall of the centrum/neural arch complex suggests a very fragile structure; however, linking of the bony neural canal by multiple spoke-like trabeculae generates a double-tube structure that significantly increases the strength of the vertebra.

Chemistry and ultrastructure of feathers and skin in an ornithischian dinosaur

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The evolution of feathers and flight is a major research topic stimulated by spectacular discoveries of feathered dinosaurs from NE China, Siberia and Canadian amber. Many aspects of feather evolution remain poorly understood, including the origins of feathers, the nature of aberrant feather types in fossils and the coevolution of feathers and skin. These uncertainties relate in part to a relative paucity of studies exploring the ultrastructure and chemistry of relevant fossil soft tissues. The neornithischian dinosaur *Kulindadromeus zabaikalicus*, a basal neornithischian dinosaur from the Jurassic of Siberia, provides an ideal opportunity to resolve these issues as it preserves primitive feathers, including types not present in extant birds, in association with enigmatic soft tissue features and unequivocal scales. We analysed diverse integumentary structures, including scales, monofilaments, and compound feather-like structures, using scanning- and transmission electron microscopy, time-of-flight secondary ion mass spectrometry, synchrotron X-ray absorption spectroscopy and Raman spectroscopy. The results reveal the widespread preservation of tissue ultrastructure, including melanosomes plus associated organic matrix, in feathers and scales. Feathers can be discriminated from other integumentary tissues on the basis of melanosome geometry and, especially, trace element chemistry, sulfur speciation and Raman spectroscopy. These data reveal the morphology of new aberrant feather types transitional between simple monofilaments and divergent barb clusters and provide a new mechanism to determine the nature of evolutionarily important tissue types in feathered dinosaurs, constraining scenarios for the evolution of feathers.

Edentulous pterosaurs from the Cretaceous Kem Kem beds of Southern Morocco: a new genus and species and an upper jaw for *Alanqa saharica*

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The mid-Cretaceous (?Albian/Cenomanian) Kem Kem beds of Morocco have yielded the remains of several azhdarchoid pterosaurs, particularly rostral material. Currently, only two taxa of Kem Kem azhdarchids, Alanqa saharica and Xericeps curvirostris, have been described, with a tapejarid currently undergoing description. However, several other morphologies in known rostral material from the Kem Kem beds clearly distinct from the described species can be identified. This unnamed rostral material can be distinguished by the size range of

their lateral and dorsoventral angles, the shape of the dorsal surface, the shape of the occlusal surface, the thickness of the internal bone walls, and the shape and density of rostral foramina. Here we examine these rostral morphologies using surface and XCT scanning and digital. Using these methods, we are able to identify a possible new genus and species of azhdarchid pterosaur from the Kem Kem beds, in addition to two indeterminate azhdarchoids unique from the known taxa. We also identify material with extreme morphological similarities to Alanqa saharica but with a higher rostral angle and complimentary bony processes to known material. We regard this morph to be the upper jaw of *Alanqa*.

The Hydrodynamics of Plesiosaurs

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The four-flipper swimming method of plesiosaurs has been investigated using full-scale flume tank experiments, which highlight the advantages and mechanisms behind their novel propulsion method. Marked increases in thrust and efficiency of the rear flippers are caused by their interaction with the wake of the front flippers. These increases would have given plesiosaurs clear advantages in swimming speed and endurance, compared to if they had all their propulsion surface contained within one set of flippers as is the case with turtles. However, such increases in hydrodynamic performance only occur for certain kinematics of the flippers, so plesiosaurs would have needed to control their flipper phasing accurately. Work is continuing to elucidate how these performance advantages may have varied across the entire plesiosauria clade, taking into account factors such as flipper aspect ratio, and front to back flipper size ratio.

Enigmatic ichthyosaurs of the ‘lost’ Bennett Collection

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Walter Bennett (1892-1971) was a mining engineer and avid fossil collector, active throughout much of the 20th century (Sowan, 1971). The collection, around 175,000 fossils from across the world, was bequeathed to the Croydon Natural History and Scientific Society in the 1970s. A few choice pieces were put on display, whilst the rest remained stored in Bennett’s large wooden cabinets. In 1989, it came to the Horniman Museum and Gardens, where it fills a room in the off-site stores. Much of the material retains its original specimen labels assigned by Bennett, detailing locality, age and taxonomy, however, primarily due to the huge volume of material, until recently it was poorly documented digitally, and accessioned only in bulk.
A recent digitisation project, with the aim of documenting, researching, and preserving the Bennett Collection, has begun to uncover significant information about this hitherto poorly known material. Many of the vertebrate specimens were collected at quarries that are listed as Sites of Special Scientific Interest, as well as Geological Conservation Review sites (Benton and Spicer, 1995). Some of these sites are no longer accessible, making the necessity to bring the existence of this material to the attention of the academic community even more important. Particular discoveries that have come out of the recent research include significant cranial material from ichthyosaurs and a plesiosaur, what is thought to be the earliest known specimen of an ophthalmosaurid, and the first known ichthyosaur material from at least two British localities.
This paper will provide both an overview of the marine reptile material in the collection, and explore new insights into the significance of the most important specimens.

"*Scelidosaurus*" - a poorly known and misunderstood ornithischian

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Scelidosaurus harrisonii (Owen, 1861) is the first known, near-complete, ornithischian dinosaur; it is also Sinemurian (193 Ma) and therefore among the earliest members of the clade. It was described (confusingly) by Richard Owen and is, paradoxically, one of the least well-understood ornithischians. *Scelidosaurus* has now been described in detail. Contrary to previous understanding, the skull has a complete supraorbital series, two prominent occipital ‘horns’ and a large exostosis (but no osteoderm) on the mandible. The skull was also encased by a turtle-like casque of keratinous scutes. The interior of the skull reveals bones unique among ornithischians.

The postcranial skeleton is known in totality (including clavicles and the complete forelimb). The body surface was covered by a morphological variety of osteoderms. In the cervical region large osteoderms are underlain by base-plates that grew in the dermis and, during ontogeny, fused to form ‘tricorns’ and partial cervical collars. The torso bore three principal rows of ridged osteoderms and, between these, many subsidiary osteoderms and the skin generally was reinforced by a mosaic-like pattern of small osteoderms and overlying keratinous scutes. The osteoderms of the tail have a different arrangement to those seen on the rest of the body. Many aspects of the biology and inferred natural history of this animal can now be considered.

Since 1986 most systematic analyses position *Scelidosaurus* as the sister-taxon to Eurypoda (Ankylosauria + Stegosauria). Correcting many of the past as well as recently published character scores and re-running systematic analyses prompts a revision of this topology and a reconsideration of basal ornithischian systematics.

Validating an Echidna (Mammalia: Monotremata) Musculoskeletal Model to Inform Mammalian Forelimb Evolution

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The ecomorphological success of therian mammals has been linked to their unique and highly versatile forelimb morphology: fully mobile scapula, ventrally oriented ball−and−socket shoulder joint, and 'parasagittal' limb posture and movement. In contrast, the earliest synapsids ("pelycosaurs") had bulky and constrained 'sprawling' forelimbs and limited ecological scope. Although the morphological transformation of the forelimb is striking, the functional consequences of this profound reorganization is not well characterized. Here, we explore the ramifications of forelimb morphology on function by modeling the musculoskeletal anatomy of the monotreme echidna. Monotremes are sister to therians, but possess anatomical features reminiscent of earlier forms (e.g., numerous large interlocking pectoral bones anchoring the forelimb to the body, a saddle−shaped glenoid, and a sprawling gait dictated by apparently constrained forelimb mobility). As such, monotremes can be particularly useful in guiding and validating functional reconstructions of extinct taxa. Previously, we have estimated range of motion and muscle moment arms in a published model of an echidna forelimb. For refinement and validation, we have now added to this minimalist model: more accurate 3D−muscle paths using iodine−enhanced contrast staining, muscle architecture, and experimentally−obtained passive limb kinematics using XROMM. Overall, we found some types of mobility limited by the skeletal morphology of the forelimb, as well as by the soft tissues. Important aspects of the echidna's posture and gait (e.g., internal humeral rotation) were reflected in model estimates of moment arms and torques. Several muscles have different functional roles compared to therians, concomitant with their differing size and positions. Our model not only allows correlation of musculoskeletal anatomy and function in this unique animal, but also offers guidance in building and interpreting models of fossil taxa spanning mammalian evolution.

Probing melanosome chemistry using experiments and fossils

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Fossil melanosomes are a major focus of palaeobiological research as they can inform on pigmentary coloration in ancient animals. The chemistry of fossil melanin, however, is poorly understood. Our recent research shows that melanosomes in fossils can (but do not always) contain abundant Cu, which has been proposed as a biomarker for melanin, but that melanosomes in extant vertebrates commonly contain low amounts of Cu. The origins and nature of the Cu in fossils is unknown. Here, we apply an experimental approach to resolving this issue using controlled laboratory experiments. We matured melanin extracts from the skin and liver of the African clawed frog (*Xenopus laevis*) in distilled water and in a Cu-rich solution at 220 °C, 130 bar for 24h and analysed the residues using synchrotron X-ray fluorescence (XRF) and X-ray absorption near edge structure (XANES). Our experiments reveal that Cu concentrations are much higher in experimentally matured melanosomes from the skin than in the liver. Both samples are depleted in Fe following maturation. These results strongly suggest the presence of tissue-specific diagenetic pathways for melanin and the potential to reconstruct original tissue chemistry in fossils. Future experimental studies will provide a deeper understanding of the impact of diagenesis on melanin trace metal chemistry in order to better interpret preserved chemical signatures in fossils.

Investigating the biochemical fidelity of fossil feathers using sulfur speciation

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Fossil feathers provide key information regarding macroevolutionary events such as the dinosaur-bird transition and the origins of flight. Despite extensive research on the macro- and microstructure of fossil feathers, the chemical preservation of its primary biomolecular component, keratin, is poorly understood. Existing immunochemical evidence for fossil keratin is not widely accepted, in part because there is no adequate taphonomic model for keratin. Here we use sulfur X-ray absorption near-edge structure (XANES) spectroscopy to explore changes in keratin chemistry during controlled laboratory experiments simulating decay, burial, and sulfurization (a common diagenetic process involved in preservation of various soft tissues). Our taphonomic experiments used black feathers from the domestic chicken, *Gallus gallus*; samples were decayed for up to 12 months, matured at temperatures up to 250°C, and/or incubated in sulfide-rich media to promote sulfurization. Our results show that decay has minimal impact on sulfur chemistry and that progressive maturation is associated with progressive oxidation of sulfur: peaks for cysteine and cystine dominate spectra for untreated and decayed feathers, whereas cystine, sulfonate and especially organic sulfate dominate spectra for more matured samples. Sulfurization yields a complex suite of sulfur compounds, including sulfides. These data demonstrate that sulfur speciation can be used as an indicator of the taphonomic history of fossil feathers and provides a model for the degradation of keratin disulfide bonds under various taphonomic conditions. Broader applications of our analytical approach to fossil feathers will test the fidelity of preservation and will identify fossil targets for future biochemical studies.

How many spinosaur taxa are there in the Kem Kem beds of Morocco?

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The giant theropod dinosaur *Spinosaurus aegyptiacus* has gained iconic status in both the vertebrate palaeontological community and amongst the public at large. Perhaps the largest predatory dinosaur to have lived, this animal exhibits a bizarre range of features implying adaptations to a piscivorous diet and semiaquatic mode of life. Despite its popularity, the systematics of this taxon are still a matter of considerable debate. Spinosaur taxonomy is complex, with up to three separate taxa proposed for the Cretaceous Kem Kem beds of Morocco: *Spinosaurus aegyptiacus* Stromer, 1915, *Spinosaurus maroccanus* Russell, 1996 and *Sigilmassasaurus brevicollis* Russell, 1996.

Here, we examine the taxonomic status of spinosaurs in the Kem Kem beds, and re-evaluate the morphology of the cervical and dorsal vertebrae in the light of this taxonomic reappraisal.

The validity of *Spin. maroccanus* and *Sig. brevicollis* are not supported, as all proposed autapomorphies of these taxa are the result of intraspecific variation, or morphological changes through the axial column of a single taxon. Both taxa are synonymised under *Spin. aegyptiacus*.

Working with a single taxon, twelve distinct vertebral morphotypes are identified, representing cervicals 2-10 and dorsals 1-3, allowing for a reconstruction of the neck of *Spinosaurus*. Preliminary results indicate that the concavo-convex joints of the spinosaurid neck are significantly more resistant to joint failure than equivalent joints of other large theropods; the cervical vertebrae of *Spinosaurus* facilitate stable rotational movement whilst limiting translation, strengthening the neck against catastrophic joint failure.

No Small Feet: Heteropody & Mass Distribution in Tetrapods

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Why do some quadrupedal animals have different sized fore and hind feet? Could this be connected to the position of their centres of mass, as an attempt to equalise underfoot pressure? In the trace fossil record, where extreme heteropody is commonplace, could centre of mass position and pressure equalisation attempts account

for phenomena such as manus-only sauropod trackways? Using digitised skeletons, previously published data, and pressure mat readings, centres of mass for extant animals were analysed against differential manus and pes foot contact area, force, and pressure, with the aim to establish the presence or absence of a link between mass distribution and heteropody. A universal relationship between centre of mass position and heteropody appeared absent, with cursorial mammals clustering around an even distributiton and manus/pes ratio. However, semi-aquatic animals demonstrated a strong correlation between centre of mass position and heteropody, and other, non-cursorial animals and other groups of non-cursorial animals did not cluster in an even distribution. Pressure equalisation with heteropody appears to be a mechanism present in certain groups of tetrapods, lending tentative support to the idea that it was employed by dinosaurs with extreme heteropody.

The past, present and future of Jensen's Big Three sauropods

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In the 1970s, Jim Jensen excavated multiple gigantic sauropod dinosaurs from Dry Mesa Quarry (DMQ), Colorado. In 1985, he formally named *Supersaurus*, *Ultrasaurus* (later *Ultrasauros*), and *Dystylosaurus* based on these specimens. Later, Brian Curtice and coauthors referred the holotype vertebrae of *Ultrasauros* and *Dystylosaurus* to *Supersaurus*, and the referred scapulocoracoid of *Ultrasauros* to *Brachiosaurus*.

In 2016, we determined that a large cervical vertebra referred to *Supersaurus* in fact belongs to *Barosaurus*. Either *Supersaurus* is synonymous with *Barosaurus*, or it is distinct but some *Barosaurus* material has been incorrectly referred. The holotype of *Dystylosaurus*, an anterior dorsal vertebra, cannot belong to *Barosaurus* due to its unsplit neural spine, but no shared apomorphies support its referral to *Supersaurus* and the convenient referral of all large diplodocid material from DMQ to *Supersaurus* is no longer supportable in light of the *Barosaurus* cervical.

Nomenclatural issues pertaining to *Supersaurus* must be resolved by reference to its holotype scapulocoracoid. Jensen assigned two scapulocoracoids to *Supersaurus*, but his vague descriptions, and pervasive confusion around published specimen numbers, make it uncertain which of the two is the type. The two elements have subtle differences and may not belong to the same animal. This is unfortunate, since *Supersaurus* is the most complete, phylogenetically informative, and nomenclaturally stable of the "Big Three" Dry Mesa sauropods — or at least it was until now.

Finally, while the scapulocoracoid referred to *Ultrasauros* is probably from a titanosauriform, its coracoid does not closely resemble that of the holotype of *Brachiosaurus*, nor its scapulae those of *Giraffatitan*. In summary, the DMQ material includes at least three giant sauropods: a titanosauriform that may not be *Brachiosaurus*, and two diplodocids: *Barosaurus* and *Supersaurus* – but the diagnosis of the latter is muddied both by possible confusion with *Barosaurus*, and by definite confusion regarding the holotype.

Body size change in Chalk Sea sharks

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The iconic Chalk Group of southern England ranges in age from Cenomanian to Campanian and yields diverse fossil assemblages that have been collected for over 200 years. These fossils provide direct evidence of the impacts of the Cenomanian-Turonian extinction event; a major crisis in marine ecosystems associated with an interval of global warming, peak sealevel, and widespread oceanic anoxia (OAE2). This study utilized specimens from museum collections to determine how the body sizes of Chalk Sea sharks changed through this event, and in particular to test the hypothesis that marine animals become smaller with global warming. The dataset comprises 14 genera of lamniform sharks, plus the enigmatic durophagous genus *Ptychodus*. Tooth-size was used as a proxy for body size, with most specimens comprising disarticulated teeth. In all cases, the best-preserved available specimens were measured. The studied shark taxa record different size trends, which appear to correlate with feeding ecology. Turonian Lamniform shark teeth are much rarer than Cenomanian ones, which means that in most cases it is not possible to determine whether recorded size differences are significant. *Scapanorhynchus*, a Mesozoic relative of goblin sharks, is the most abundant genus during OAE2 and records significant, temporary, size reduction. Most lamniforms record larger sizes in the Coniacian to Campanian, when temperatures became cooler. In contrast, the durophagous *Ptychodus* remained abundant and common

throughout the Turonian, and did not decrease in size during peak warming. It too became significantly larger as oceans cooled in the later Cretaceous. Although museum collections suffer from various well-known biases, it seems unlikely that the different responses of body-size recorded in this study are solely driven by taxon-specific collection biases. Given their key ecological importance, changes in the size and abundance of Chalk Sea sharks have implications for how marine ecosystems functioned in response to past environmental change.

When the Mesozoic got ugly – naked, hairless, (and featherless) pterosaurs

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With key roles in flight, thermoregulation and protection of the body, the integument was of fundamental importance to pterosaurs. Determination of the basic anatomy of this structure could provide a range of new insights into the palaeobiology of these enigmatic volant reptiles. Presently, however, there are several conflicting hypotheses regarding the construction of the integument, all founded on limited numbers of specimens, and not one of which is fully consistent with the available fossil evidence. We have developed a new model based on investigations of more than 100 specimens all of which show some form of exceptional preservation. This data set spans the entire temporal and systematic ranges of pterosaurs and a wide variety of preservational modes. The model has three principal components: (1) A thin epidermal layer. The external surface of the integument was glabrous with a smooth, slightly granular, or polygonal texture. Attenuate 'bristles' fringed the jaws in two anurognathids and small tracts of filaments may have adorned the posterior cranium in some pterosaurs. (2) A layer of reticular and filamentous collagen and of variable thickness and complexity, formed much of the dermis. Helically wound bundles of collagen fibres (aktinofibrils), were present throughout all flight patagia. Variation of aktinofibrils in terms of their dimensions, packing, orientation and stiffness permitted localized variation in the mechanical properties and behaviour of the flight patagia which varied from relatively stiff distally to more extensible and flexible proximally. 'Feather-like' structures reported in Jeholopterus appear to be partially unraveled or decayed aktinofibrils. Collagen fibre bundles were also present in footwebs, and in the integument of the neck and body. These structures have often been mis-identified as 'hair' (pycnofibres). (3) A deep dermal layer with muscles fibres, blood vessels and nerves. The pterosaur integument was profoundly different from that of birds and bats, further emphasizing the sharp disparity between these volant tetrapods.

How to Make New Discoveries in (Human) Anatomy

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Despite the perception that human anatomy is a completed science, new discoveries continue to be reported. Some merely expand the previously known range of human variation, but others are gross structures present in most people, which simply escaped detection until recently. An analysis of recent discoveries suggests several avenues along which new discoveries might be sought:

1. Anatomically complex regions with multiple potential distractors: the anterolateral ligament of the knee escaped widespread appreciation until 2013, probably because the human knee is a forbiddingly complex structure that is rarely dissected completely, and several superficially similar structures are present in the same area.
2. Common characters of other taxa expressed as rare variants in humans: vagus nerve fibers to the trachea and esophagus are typically incorporated into the recurrent laryngeal nerve in humans, but form a separate recurrent pharyngeal nerve (RPN) in some other mammals, and rarely in humans.
3. Replaced peripheral nerves: nerve fibers from the 4th lumbar spinal level to the leg are usually incorporated into the femoral nerve, but in rare cases become part of the obturator nerve. In such cases, the posterior branch of the saphenous nerve appears to have been replaced by the obturator nerve. Similar replacements in other regions of the body are underexplored.

Most recent discoveries fall into a perceptual blind spot: medical students dissecting human cadavers have the opportunity to find these structures, but usually lack the expertise to recognize or preserve them. In contract, surgeons have the necessary expertise, but rarely have the opportunity to open people up sufficiently to identify or trace these structures.

If new discoveries remain to be made even in the well-trod ground of human anatomy, then many more surely await discovery in extant and extinct non-humans, and these guidelines may prove useful in other taxa as well.

Validating the Use of Dental Cementum Increment Analysis to Determine Season-at-Death in Humans and Other Mammals

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Dental cementum increment analysis (DCIA) was developed by zooarchaeologists to infer hunting strategies and seasonal timing from skeletal assemblages. DCIA is now used by paleodemographers, paleohistologists, bioarchaeologists and forensic anthropologists as the most accurate method by which to determine the age-at-death, and the only method for determining season-at-death in skeletal remains. DCIA has been successfully used in more than 50 species of mammal spanning many millennia. Of the several types of dental cementum, acellular external fiber cementum (AEFC) forms the outermost layer of mammalian tooth roots and binds to the periodontal ligament. In mammals, AEFC is laid down in pairs of bands that look like tree rings under transmitted polarized light. One light or translucent band is laid down in the spring/summer and one dark or opaque band in the winter/fall. AEFC is not remodeled or lost over time, which makes it a very good biomarker of life history. The number of pairs of AEFC bands can be added to the age at which the tooth erupts to derive an estimate of age-at-death. The color of the outermost band of AEFC can be used to determine season at death in mammals. The goal of this study is two-fold: to develop DCIA to the point where its results are deemed admissible as evidence in a court of law, and to put a powerful forensic tool in the hands of indigenous anthropologists of Central America who are currently trying to identify the victims of the genocides perpetrated in the 1980s-1990s. The scope of this research includes applying DCIA to all types of human teeth (e.g., incisors, canines, etc.), from individuals ranging in age from 18 years to 93 years, and from several latitudes and microenvironments. Thanks to conserved dental biology, these results should be applicable to most other mammals, extinct and extant.

POSTERS

A new notosuchian crocodylomorph from the Cenomanian Kem Kem beds of southeastern Morocco

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Notosuchians were an extinct clade of terrestrial crocodylomorphs that were abundant and diverse during the middle to Late Cretaceous of Gondwana. Unusually for crocodylomorphs, notosuchians exhibit considerable morphological and ecological diversity. Most of this diversity is found in South America, where over 70% of known notosuchian taxa have been discovered. However, the Cretaceous crocodylomorph record of Africa is still poorly sampled, hampering our understanding of large scale biogeographic patterns, especially pertaining to Gondwanan fragmentation, vicariance, and dispersal. Here, we describe two new notosuchian specimens, NHMUK PV R36829 and NHMUK PV R36874, from the early Late Cretaceous (~100–94 Ma) Kem Kem beds of Morocco. NHMUK PV R36829 is generally well preserved and comprises the whole dentary, left splenial and left angular. NHMUK PV R36874 consists of only the partial right dentary ramus and anterior surangular ramus. The possession of heterodont teeth with procumbent incisiviforms on the anterior region of the mandible, and broader molar teeth at the posterior end of the mandible, supports the position of both specimens within Notosuchia. Detailed comparisons and phylogenetic analysis, based on a data matrix comprising 110 taxa scored for 412 characters, indicates that these specimens represent a distinct notosuchian taxon. This new taxon demonstrates a greater diversity in the mid-Cretaceous of Africa than previously realised, adding an important new data point to our understanding of Mesozoic crocodylomorph evolution and Gondwanan palaeobiogeography.

Modularity in the skull of the dinosaur *Protoceratops andrewsi* and geometric morphometric evidence of a socio-sexually selected origin for the frill.

ANDREW KNAPP *, ROB KNELL & DAVID HONE

The purpose of the unique parietal-squamosal frill of ceratopsian dinosaurs has long been a source of debate. Recent studies have supported the hypothesis that the frill is a socio-sexually selected structure, but these findings have been based on limited linear measurements. Here, for the first time, we use three-dimensional geometric morphometrics to examine the morphology of an unprecedented 43 specimens of *Protoceratops andrewsi,* using a maximum likelihood approach to evaluate phenotypic modularity of the skull and to enable the assessment of relative growth patterns of different skull modules. We find that the frill formed a distinct phenotypic module, suggesting its evolution and development could proceed independently from the rest of the skull. The frill was found to have a significantly higher rate of both size and shape change through ontogeny than any other module, and the highest morphological variance. Together, these findings provide the strongest support yet for a socio-sexual role for the frill of *Protoceratops*.

A complete record of Early Cretaceous (late Barremian – early Aptian) Rebbachisaur (Sauropoda, Rebbachisauridae) remains found on the Isle of Wight, UK, including unpublished material

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The Rebbachisauridae is a widespread family of Cretaceous (Hauterivian-Coniacian) sauropods known from South America, Africa and Europe but their remains are rare. In the UK, only three specimens have formally been described, recorded from the Early Cretaceous (late Barremian – early Aptian) Wessex Formation on the Isle of Wight. However, many additional Rebbachisaur specimens have been found in these same deposits by collectors over a thirty year period including cervical, dorsal and caudal vertebrae, pectoral or pelvic material, and ribs. Some of the bones show signs tooth damage and most exhibit traces of invertebrate burrowing. Here these additional bones and the sites where they were found are described for the first time. In addition, all of the Rebbachisaur specimens found on the island, including the previously described elements, are in the process of being 3D scanned to create an accessible virtual collection to facilitate access to the material and aid the identification and description of the bones.

Metacarpus Morphospace Occupation in Non-Avian Dinosaurs

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The hand (manus) is one of the most important and adaptable skeletal structures in terrestrial tetrapods, not only for locomotion but also for its overall interactions with the environment, suggesting that complex selective pressures would have acted upon its morphology. Non-avian dinosaurs provide an excellent opportunity to study manus shape evolution due to their wide range of body sizes, ecological niches, and behaviours. Their ancestral bipedal bauplan allowed diverse morphologies and inferred hand functions to evolve, but multiple independent reversions to quadrupedality imposed some shared mechanical constraints.

In this study, we present the first assessment of metacarpus morphospace occupation and disparity in non-avian dinosaurs using two-dimensional geometric morphometrics. First-hand photographs and published figures of metacarpals in dorsal view were obtained for 70 taxa, representing all major non-avian dinosaur lineages including early diverging and deeply nested examples from Sauropodomorpha, Theropoda, and Ornithischia. Shape variation of each five individual metacarpals was quantified using a combination of four landmarks and 200 sliding semilandmarks (four curves of 50 semilandmarks, along the medial, lateral, proximal and distal surfaces). Landmarking was performed in tpsDig, while the R package geomorph was used to conduct Generalised Procrustes Analysis and Principal Component Analysis (PCA).

The first axis of the PCA explained over 74% of the variation, separating taxa with longer and more slender metacarpals (e.g., titanosaurids) from taxa with shorter shafts and proportionally wider proximal and distal ends to the other side (e.g., thyreophorans). PC2 (8%) appears related to the degree of shaft curvature. PCA indicates some clustering between clades, as well as identifying some extreme morphologies, such as *Camptosaurus* (ornithopod) and *Carnotaurus* (theropod), which both have a proximodistally shortened metacarpal I. Each major clade occupies distinct areas of morphospace, with some overlap between basal sauropodomorphs, thyreophorans and ceratopsians. In sauropodomorphs, the major axis of variation shows a clear shift from shorter metacarpals in basal taxa, to progressively longer, more slender elements in sauropods, all the way through to later titanosaurs. Finally, our results suggest broad convergence in the long and slender metacarpus of sauropods and hadrosaurs, associated with a more ‘columnar’ manus structure.

The Palaeontological Contributions of Nick Chase: A 20th Century Fox.

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Nick Chase was awarded the Palaeontological Association's prestigious Mary Anning award in 2018. This marked a lifelong career dedicated to collecting specimens from the Early Cretaceous Wealden exposures on the Isle of Wight's south coast. On the second day of Nick's first trip to the island in 1982 he discovered and excavated a beautifully preserved juvenile *Mantellisaurus atherfieldensis*, which is now housed in the Natural History Museum (NHMUK R 11521). This fortuitous event focussed his interests on dinosaurs and in 1989 he

moved to Freshwater to be close to the bone-beds. Collecting became an all-consuming vocation and he spent the next thirty years combing the beaches once or twice a day in all weathers, often hauling great weights up the cliffs. The spectacular results include some of the country's most complete dinosaur skeletons (*Mantellisaurus atherfieldensis, Valdosaurus canaliculatus, Hypsilophodon foxii*), a vast amount of as yet undescribed sauropod material, crocodiles, fish and even a new species of spider (*Cretamygale chasei*) found in the Cretaceous amber of the Wessex Formation. There are many parallels with the Reverend William Fox, the Island's famous 19th century collector. Both extremely knowledgeable men although not formally trained, both obsessed with collecting over any other occupation and both sharing the same sentiment expressed by Fox in a letter to Richard Owen, 'I cannot leave this place while I have any money left to live on'. Nick's legacy is twofold. Through his commitment to donating specimens to accredited museums (most notably Dinosaur Isle Museum) he has ensured that his finds have stayed on the Isle of Wight and supplied material for generations of researchers. He has also been generous with his hard-earned local knowledge, encouraging and helping anyone who shows an interest. An extraordinary man whose devotion has made a remarkable contribution to the field of British palaeontology.

Bennett's archosaurs from sites of recognised importance

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In the mid-1980s, the Horniman Museum acquired the 175,000 specimen strong Bennett Collection of fossil material from the Croydon Natural History and Scientific Society. Walter Bennett (1892-1971) was a mining geology engineer who travelled extensively, across the world, collecting fossils of all ages and taxonomic groups. Despite his collection being primarily amassed in the early-middle 19th century, the history of the Collection since his passing has been somewhat of a puzzle, due to the lack of (known) documentation. On the surface it is simple. The collection was bequeathed to the CNHSS following his death in 1971. A few choice specimens were put on display, whilst the rest remained stored in Bennett's large wooden cabinets. In 1989, it came to the Horniman Museum and Gardens, where it fills a room in the off-site stores.

Bennett collected much of the material from fossil reptile sites in Britain that are of recognised importance such as Black Horse Quarry in Telham, and Smokejacks Quarry in Surrey- made famous after Bennett's time by the discovery in the early 1980s of the theropod *Baryonyx walkeri* (Charig and Milner, 1986). Both of these quarries are categorised as Sites of Special Scientific Interest and listed as Geological Conservation Review sites (Benton and Spicer, 1995). The Black Horse Quarry in Telham is also the type locality of the Telham Bone Bed. The archosaur material collected from these sites in the middle of the 20th century includes a vertebra with clear skin impressions, and gastroliths, which were assigned to *Iguanodon* by Bennett.

This paper will detail the significant archosaur material held within the collection, and explore the importance of vertebrate material collected from these particular localities.

The cranial endocast of a new ankylosaur skull from the Lower Cretaceous of the Wessex Formation, Isle of Wight, UK.

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Ankylosaurs have been known from the Isle of Wight's Wessex Formation for over 170 years, yet cranial material assigned to them is rare. Here we study the cranial endocast of IWCMS:2012:1134, a partial skull which has previously been assigned to *Polacanthus foxii*, the only named ankylosaur taxa from the Wessex Formation. We compare it with the endocast of CAMSM X.26242 a previously described cranial endocast and partial braincase assigned cf. *Polacanthus*.

CT scans of IWCMS:2012:1134 were used to reconstruct the cranial endocast. A high-quality cast of CAMSM X.26242 (IWMCS 1158) has been recorded using photogrammetry and a digital reconstruction of the endocast created.

Comparison of the endocasts reveals similarities in morphology and the location of several of the major nerve foramen and vascular channels. Comparison of the skulls shows IWCMS: 2012:1134 differs from CAMSM X. 26242 in being smaller and less robust with a flatter dorsal skull surface, although this specimen is heavily beach-rolled making comparison challenging. Differences in endocast and skull morphology could be due to various factors including intraspecific variation or the specimens representing different ontogenetic stages.

IWCMS:2012:1134 and CAMSM X.26242 likely represent two specimens from the same taxon on the basis of similarities of their cranial endocasts and skulls but these specimens cannot but assigned to any taxa with

certainty and are here considered ankylosaur indet,. This conclusion that has implications for our understanding of Wealden ankylosaur diversity as previously it had been suggested these specimens might represent different taxa. This study also highlights the importance of digital techniques when comparing specimens and allows the manipulation of 3D data not possible using the actual specimens.

A revision of British Wealden Group ankylosaurs (Dinosauria: Ornithischia)

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Originating in the Middle Jurassic, the ankylosaurs achieved high diversity and a global distribution during the Cretaceous, although the early evolution of the group is poorly understood. The Early Cretaceous is therefore an important period for the group, with increased diversity, disparity and geographic distribution, and the Lower Cretaceous Wealden Group of southern England represents an important geographic and stratigraphic region, with three named taxa and dozens of specimens known. *Hylaeosaurus*, one of the three taxa used to define Dinosauria in 1842, was described by Mantell in 1833 based on a fragmentary specimen from the Valanginian of Sussex. *Polacanthus* is known from multiple specimens representing the majority of the skeleton and has been predominantly found on the Isle of Wight, although new specimens mean there is a possible geographical and stratigraphical overlap with *Hylaeosaurus*. *Horshamosaurus*, originally a second species of *Polacanthus*, is from the Barremian of Sussex and is a highly fragmentary, single specimen. Given the paucity of material in the holotypes of each species, and the high number of specimens that are assigned to each genus based on stratigraphy, a taxonomic revision of the Wealden Group ankylosaurs is presented here. The majority of British Early Cretaceous ankylosaur specimens were examined first-hand. *Hylaeosaurus* and *Polacanthus* are valid taxa, although *Hylaeosaurus* is restricted to the type specimen, and they are geographically and stratigraphically distinct. *'Horshamosaurus'* is an indeterminate ankylosaur and a *nomen dubium*. A new, undescribed specimen of ankylosaur from the Isle of Wight is distinct from *Polacanthus*.

A revision of *Temnodontosaurus crassimanus* (Reptilia: Ichthyosauria) from the Lower Jurassic (Toarcian) of Whitby, Yorkshire, UK

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Temnodontosaurus is known from the Lower Jurassic (Hettangian – Toarcian) of England, Germany, France and Belgium and is the largest Jurassic ichthyosaur known from complete remains. At least five different species are presently identified. In the UK, Lower Jurassic ichthyosaurs have been collected extensively from many localities, primarily Lyme Regis and Charmouth, Dorset, Street and Strawberry Bank, Somerset and Whitby, North Yorkshire. During the 19th century, the Yorkshire coast was extensively quarried for the manufacture of alum, which yielded many specimens during its operation, including a large, near-complete, three-dimensionally preserved specimen – the holotype of *Temnodontosaurus crassimanus* Blake (1876). While the holotype specimen of *T. crassimanus* still remains on display at the Yorkshire Museum, it has remained largely understudied and the species has been questioned. As part of this work, in order to determine the validity of this species, we present a detailed redescription of the holotype. Furthermore, additional specimens that have previously been tentatively assigned to *T. crassimanus* were located and examined as part of this research, and comparisons were made between several contemporaneous specimens of *Temnodontosaurus* from both Yorkshire, and several specimens of *T. trigonodon* from Germany. Although the redescription is currently ongoing, we recognise a combination of new morphological characters that distinguish the species from *T. trigonodon.* Although a thorough revision of *Temnodontosaurus* is beyond the scope of this study, our research will help to lay the foundations for a long overdue assessment of the genus.

The method of estimating bipedally dinosaur's posture from the ground based on walking bird's tarsometatarsus

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Birds are digitigrade animals, walking on a functionally tridactyl foot. The three toes are connected to the limb via the tarsometatarsus (TMT). Theropod dinosaurs, the ancestors of modern birds, possessed separate metatarsal bones, but as modern birds evolved and limb proportions changed, the metatarsals fused into a single

bone. Because all of the toes articulate with the TMT, their range of motion is determined by the morphology of this bone. Given that modern birds use their feet for a range of locomotor and other tasks such as walking, swimming, and grasping, the morphology of the articular condyles of the TMT may be a highly informative aspect of their functional morphology. This is of particular use in the fossil record, where the toes themselves are infrequently preserved compared with the more common long bones such as the TMT.

We quantified morphology of the distal TMT in 29 taxa, particularly the angle formed by the surfaces of the distal condyles. Ten species were recorded during locomotion in lateral view.

We found that the horizontal angle formed between the distal condyles of the TMT, i.e. a proxy of interdigital angle, varies depending on the angle at which the TMT is held relative to the ground. The largest angle between distal condyles occurred at a TMT angle corresponding to the propulsive phase in walking birds. This may provide a future method for estimating the angle of the foot in theropod dinosaurs from fossilized footprints.

You're going to need a bigger plane: body mass and flight capabilities of the giant pterosaur *Hatzegopteryx*

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The gigantic size and robust build of the Maastrichtian pterosaur *Hatzegopteryx thambema* make it a strong candidate for the largest known flying animal. Despite general interest in the flight of giant pterosaurs and some authors claiming that *Hatzegopteryx* was too heavy to fly, the body mass and flight capabilities of this poorly known azhdarchid are yet to be studied. Here, efforts to investigate these attributes are presented based on a new reconstruction of *Hatzegopteryx* anatomy. The skeleton and musculature were restored by incorporating published *Hatzegopteryx* fossils (including portions of the skull and mandible, a cervical vertebra, and several limb elements) into a generalised azhdarchid bauplan. Graphic Double Integration was employed to estimate total body volume and, using body part densities from previous pterosaur mass estimates, total mass was predicted. The reconstruction corroborates an extreme body size for *Hatzegopteryx* with a predicted wingspan of 10.4 m and an estimated mass of 360 kg - a value considerably higher than the 200-260 kg generally assigned to 10 m wingspan azhdarchids. Incorporating this mass estimate into pterosaur flight analyses implies that *Hatzegopteryx* was still volant, despite its size. Relative to body weight, *Hatzegopteryx* humeral bending performance is above average for a pterosaur, suggesting sufficient structural rigour to instigate flight via quadrupedal launching. Principal Component Analysis of *Hatzegopteryx* wing ecomorphology consistently places it within the flight-capable ecomorphospace of living vertebrate fliers. Depending on assumptions of wing area, Hatzegopteryx compares most favourably to thermal soarers or heavyweight sustained flappers, such as geese and bustards. The latter proposal is novel for a giant pterosaur, but sufficient muscle power may have been available for sustained flapping if, like many large volant birds, *Hatzegopteryx* had elevated flight muscle fractions.

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