

Programme and Abstracts



60th ANNUAL SYMPOSIUM OF VERTEBRATE PALAEOLOGY
AND COMPARATIVE ANATOMY

21st SYMPOSIUM OF PALAEOLOGICAL PREPARATION
AND CONSERVATION



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Schedule

Time	Monday 10th	Tuesday 11 th	Wednesday 12th	Thursday 13th	Friday 14th					
09:00		Ch. - Donoghue	Opening remarks	Ch. - Johanson	Forrest	Ch. - Barrett	Falkingham	Ch. - Buffetaut	Hooker	
09:20		Purnell	Evans	Wedel	Schulz					
09:40		Sansom	Foffa	Taylor	Cox					
10:00		Smith	Neenan	Henderson	Joomun					
10:20		coffee/tea								
11:00		Ch. - Sansom	Darras	Ch. - Unwin	Butler	Ch. - Dyke	McNamara	Ch. - Liston	Kolb	
11:20		Richards	Young	Buffetaut	Thompson					
11:40		Turner	Sweetman	Edwards	Viscardi					
12:00		Bermudez-Rochas	Martin	Walsh	Conway					
12:20		lunch break								
02:00	Opening remarks	Ch. - Purnell	Coates	Ch. - Benton	Unwin	Ch. - McNamara	Asher	SVPCA posters & light refreshments		
02:20	Forrest		Lopez-Arbarello		Naish		Corfe			
02:40	Garwood		Liston		Barrett		Gill			
03:00			Lloyd		Maidment		Sharp			
03:20							O'Meara		Earth Sciences	
03:40	coffee/tea									
04:00	SPPC posters Earth Sciences	Ch. - Coates	Pierce	Ch. - Butler	Norman	Ch. - Asher	Benoit			
04:20			Smithson		Prieto-Marquez		Hautier			
04:40	Benton		Hone		Straehl					
05:00	Lomax		MacLaren		Lister					
05:20	Informal icebreaker St John's College Bar									
05:40		Evening reception		Evening reception		SVPCA auction				
06:00		Earth Sciences		OUMNH		OUMNH				
06:20										
06:40										
07:00										
07:20						SVPCA dinner				
07:40						St Cross College				

SPPC Papers

The Dorset Fossil Code database

Richard Forrest

plesiosaur.com

The Jurassic Coast Fossil Database is a resource open to anyone to use. Its primary purpose is to enable people to see what specimens are being discovered and to allow access to that information, particularly for the research community.

A Microsoft Access database was created under West Dorset Fossil Code recording scheme and located in the Charmouth Heritage Centre. This limited the usability of the database, in particular that access is only from one location. There is also the risk of data loss if the host computer is faulty or stolen. A decision was made to migrate to an on-line version so that the database can be accessed from anywhere, and that data is stored much more securely.

The existing flat-field database was converted into a relational database to give much increased flexibility in accessing data. Open-source software, mysql and php, were used to build the database and the web interface. There is a large community of developers familiar with these applications, and such databases are more or less infinitely scalable.

Data be added from any computer linked to the internet. Access is controlled by an hierarchical system of users, such that anyone can view limited information on the specimens, but only those with access rights can add or amend data. The system is being tested on-line now, and will be more formally launched when feedback from users and academic interests has been taken into account in further development.

Virtual palaeontology: an introduction

Russell Garwood^{1,2}

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Virtual Palaeontology is the application of 3D data acquisition and computer reconstruction techniques to palaeontological problems. While the majority of fossils are flattened, and splitting a rock open to investigate the revealed surface is highly successful, three-dimensionally preserved specimens present problems for these traditional techniques. Virtual palaeontology can reveal their morphology in full, aid research, and provide an avenue for the digital archiving and dissemination of fossils. This talk will provide an introduction to the field including its history and an overview of surface-based data acquisition techniques. It will detail tomographic (slice-based) methods, both destructive and non-destructive, and also introduce different aspects of data visualisation. The talk will emphasise the power of these techniques for curation and examine considerations for digitising collections through virtual fossils. It will conclude with a case study demonstrating the power of virtual palaeontology for research.

SPPC Posters

Bad influence - Acetic acid preparation of a pterosaur in metamorphosed limestone

Lu Allington-Jones

Natural History Museum

This project combined the challenge of extracting extremely fragile and fragmented pterosaur bones in a limestone too hard for percussive preparation tools. Acetic acid preparation was the obvious choice for this material, but further problems developed. The limestone had undergone contact metamorphism, leading to uneven hardness and acid resistance. It was found that 10% acetic acid was needed for 48 hour immersions before any effect was observed on the metamorphosed limestone. This high strength had undesirably severe effects on softer sections of the matrix, causing undercuts and pockets to develop. This was successfully combated using localised barriers made from microcrystalline wax and Synocryl 9123s.

Going to the other side – Acid preparation of dinosaur bones from Atherfield Bay

Lu Allington-Jones

Natural History Museum

This poster outlines the acid preparation of a block of the Shepherd's Chine Member of the Wealden Group from the Isle of Wight, England. The block was severely weathered on one side and preparation from the reverse was desirable. The preservation of the association of the bones was also requested. Unfortunately the block measured little more than 1cm in depth and a system of temporary and permanent supports were devised to overcome this. These comprised silicon rubber, Synocryl 9123s and HXTAL.

Mechanical Preparation of Oligocene Fishes

Mark.R Graham

Natural History Museum

The Conservation Centre at NHM London undertook fossil preparation upon three Oligocene fish specimens which were of historical significance, being part of the Enniskillen Collection, purchased by the museum in the late 1880s.

The poster details the methodology employed during preparation of the specimens and focuses on a novel approach taken to reveal details of a key morphological feature on one of the specimens, the remora *Uropteryx*. This specimen was initially visible laterally across one surface of the shale with a layer of matrix covering the surface detail of the bones. The bones were initially developed by air abrasion which suggested that a key morphological feature (the adapted dorsal fin forming the characteristic 'sucker') might be present and better exposed from the opposite (left lateral) side of the specimen.

Due to the fragile nature of the fossil and extremely small features requiring preparation, a combination of techniques was employed successfully and these are recorded in the poster.

SVPCA Papers

The interplay of environmental change, behaviour response and morphological evolution: dental adaptation and diet in African Neogene to Quaternary Proboscidea

Adrian Lister

Natural History Museum

The fossil record richly demonstrates evolutionary responses to environmental change. Several recent studies, however, have suggested an apparent lag between habitat change and the morphological response of species. Among other causes, this might be due to the so-called 'Baldwin Effect', whereby organisms first accommodate behaviourally to changed conditions, enabling them to persist in the new environment while selection adapts the animal's morphology. Observing this effect in the fossil record requires us to break the circle of deducing behaviour from morphology. One route is to use stable isotopes and dental microwear as more direct indicators of feeding behaviour, and to compare this signal to morphological signs of adaptation such as dental anatomy. Carbon-isotope data from African Neogene to Quaternary Proboscidea indicate a shift from C3 browsing to C4 grazing in several lineages around 8 Ma, roughly concordant with the first significant regional spread of C4 grasses, but preceding by several million years the increases in molar crown height (hypsodonty) seen in several elephantid lineages and considered an adaptation to grazing. Possible explanations include the Baldwin effect, grazing adaptations other than hypsodonty (such as multiplication of tooth cusps), and the importance of dust and grit, rather than grass-eating per se, in accelerating tooth-wear and the evolution of hypsodonty. The shortened lifespan implied by grazing with low-crowned teeth would have been a powerful proximal stimulus for natural selection, but hypsodonty could have taken some time to evolve because of the necessary associated cranial modifications.

Homology and mammalian ear ossicles without evolution: the case of Karl Reichert

Robert Asher

University of Cambridge

Karl Bogislaus Reichert (1811-1883) was a German embryologist whose lifespan overlapped almost entirely with that of Charles Darwin (1809-1882). In contrast to Darwin, Reichert is relatively unknown beyond developmental and palaeontological biologists. Nevertheless, Reichert was the first to make one of the most important empirical observations in developmental biology of the last 200 years: the homology of mammalian ear ossicles with jaw elements of other vertebrates. In a different time and place, Reichert's remarkable discovery might have led him to recognize the larger theoretical framework later articulated by Darwin and Wallace, and given him much more recognition, both during his lifetime and today. Instead, Reichert was reluctant to extrapolate theoretical generalities from biological data, consistent with the inductive climate of his time. Here, I describe how Karl Reichert comprises an example of how the inductivism of early 19th century science, combined with much more banal personality conflicts with younger German scientists, impeded his recognition of what is today recognized as the basis for evolutionary biology: Darwinian descent with modification.

The earliest-known dinosaur?

Paul Barrett¹, Sterling Nesbitt², Sarah Werning³, Christian Sidor² & Alan Charig¹

¹*Natural History Museum*

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³*Museum of Paleontology, University of California, Berkeley*

Recent discoveries of early dinosaurs and non-dinosaurian dinosauromorphs, such as silesaurids, have unravelled the sequence of character acquisitions leading up to dinosaur origin. However, the timing of this event remains poorly constrained: all major dinosaur clades appeared in the Late Triassic, whereas ghost lineages derived from recent phylogenetic analyses indicate that the group should have originated much earlier, during the Anisian. Here, we provide a detailed re-assessment of material from the late Anisian Lifu Member of the Manda beds, southwestern Tanzania. This material, a specimen comprising an almost complete humerus and associated sacral and dorsal vertebrae, was previously described in an unpublished PhD thesis and subsequently mentioned in several faunal lists as "*Nyasaosaurus*". Apomorphy-based re-analysis of the specimen suggests that this individual, and a referred specimen ("*Thecodontosaurus alophos*"), represent either the earliest-known true dinosaur, or a taxon that is more closely related to Dinosauria than any currently-known dinosauromorph. Dinosaur synapomorphies present include an elongate deltopectoral crest (at least 30% of shaft length) and a minimum of three sacral vertebrae. In addition,

humeral histological data indicate that this taxon had an elevated growth rate similar to that of early dinosaurs. The presence of a dinosaur or near-dinosaur in the late Anisian removes the ghost lineage that currently separates the earliest occurrences of dinosaurs and silesaurids and potentially indicates that the rise of dinosaurs took place more gradually than the sudden appearance of theropods, sauropodomorphs and ornithischians in the late Carnian has indicated thus far.

The deep evolutionary root of Sirenia (Mammalia, Afrotheria) in freshwaters of Africa

Julien Benoit¹, Mustapha Ben Haj Ali², Adnet Sylvain¹, El Mabrouk Essid², Hayet Khayati², Laurent Marivaux¹, Gilles Merzeraud³, Samuel Merigeaud⁴, Monique Vianey-Liaud¹ & Rodolphe Tabuce¹

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Afrotheria is an odd group of placental mammals which includes living species showing great diversity in size, morphology and ecological niches. These mammals possibly share an African common ancestor, hence the name Afrotheria which literally means “African beasts”. Sea-cows or Sirenia (dugongs and manatees) are the marine representatives of Afrotheria. As such, Africa, or at least the Tethyan shores of the Old World might be the place where they originated. However, to date, the fossil record of stem sea-cows has been restricted to the late-early to early middle Eocene of Jamaica, where they are represented by the paraphyletic family Prorastomidae. Since the description of *Prorastomus* by Owen in 1855, the apparent contradiction between the first occurrence of stem sirenians in the New World and their presumed Old World origin has been a biogeographical and phylogenetic paradox. Here we use X-ray microtomography to investigate a newly reported sirenian petrosal from the late early Eocene of Djebel Chambi, Tunisia. This fossil represents the oldest occurrence of sirenians in Africa. The morphology of this petrosal is more primitive than that of Jamaican prorastomids, which testifies to the great antiquity of Sirenia in Africa, and supports their African origin. While isotopic analyses previously suggested that sirenians were initially adapted to marine environments, new paleoenvironmental evidence suggests a more freshwater habitat for stem sirenians.

The Chinese pareiasaurs

Michael Benton

University of Bristol

Pareiasaurs were important medium- to large-sized herbivores in the Middle and Late Permian, some 268-252 million years (Myr) ago. They are best known from abundant remains of several taxa each in South Africa, Russia, and China, with isolated finds from other parts of the world. Six genera and species of pareiasaurs have been described from China, and yet they have not been reviewed. Of these six, two are based solely on nondescript pareiasaur teeth, and so are designated nomina nuda, while the other four, which were named for separate finds from the Sunjiagou Formation (Changhsingian, 254-252 Myr) show considerable similarities. Despite earlier suggestions of independence, there are no convincing anatomical characters to distinguish *Shibitienfenia*, *Sbansisaurus*, and *Huangbesaurus*, and these three genera are synonymised as *Shibitienfenia permica* Young & Yeh, 1963. The fourth taxon, *Sanchuansaurus pygmaeus* Gao, 1989, shows distinctly different teeth from those of *Huangbesaurus* (= *Shibitienfenia*), and was about half the size, so it is retained as a second valid pareiasaur from the Chinese latest Permian. The Chinese pareiasaurs resolve phylogenetically among those from other parts of the world, indicating no evidence for provinciality, but some evidence for correlation between phylogenetic position and stratigraphic age within the Middle and Late Permian.

An overview of the hybodont record of the Cameros Basin (northwest of Iberian Range, Spain)

David Didier Bermúdez-Rochas

Universidad de Cantabria

The Cameros Basin (northwest of the Iberian Range, Spain), with a sedimentary record that ranges from the Tithonian to the early Albian, has recently been shown to yield a large number and high diversity of hybodont shark remains. The previous fossil chondrichthyan record of this basin, consisting mainly of continental sediments, is poor, but recent studies have shown a high diversity of sharks that were abundant in freshwater environments during the Early Cretaceous. As in other parts of the world, hybodont sharks seem to have been a dominant group in the freshwater environments of the Cameros Basin.

Previously, the only fossil hybodont sharks identified in the Cameros Basin were referred to *Asteracanthus ornatissimus* (in the Jurassic marine substrate), *Hybodus polybrion* (sic) and *Hybodus* sp. (in the continental filling). After surface prospecting in part of the Eastern Cameros sub-basin, and bulk sampling of four different sites of the Enciso

Group (early Aptian), remains of at least six different genera have been recorded: *Lonchidion*, *Lissodus*, *Parvodus*, *Hybodius*, *Planohybodus* and *Egertonodus*. Among them, *Lonchidion* is represented by the highest number of elements.

These shark assemblages show both endemic species, currently under description, and taxa shared with other Spanish localities (Iberian Ranges and Basque-Cantabrian Basin), and with the classical British Wealden hybodont faunas.

Finite element validation of bird beaks and skulls

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Finite element models are rapidly becoming important tools in the field of comparative anatomy. However models, by definition, provide a simplified version of reality. It is therefore crucial that we understand how these simplifications affect the model results, and consequently our interpretations. In this study, a finite element model of the skull of a Common Buzzard (*Buteo buteo*) was validated by comparing model strains with strain data collected *ex vivo* using Digital Speckle Pattern Interferometry. Birds provide several unique modelling challenges that make them ideal for study: they have remarkably thin, lightweight bones, a keratinous rhamphotheca covering the beak, and a mobile craniofacial hinge between the beak and the rest of the skull. To our knowledge this represents the first whole-skull validation of a neognathous bird. Results show that a homogeneous, isotropic, model is able to replicate patterns of bone strain well, despite taking material properties from a different bird species. However, contrary to expectations, the rhamphotheca presented very low experimental strains which are not replicated in the model. This suggests that if one is only interested in bone strains, it may only be sufficient to correctly model the geometry of the keratinous layer. However if one is interested in the behaviour of the beak, a more complex model of the keratin or craniofacial hinge could be necessary.

The giant bird *Gastornis* in Asia and gastornithid biogeography

Eric Buffetaut

CNRS

The only gastornithid bird currently known from Asia is *Zhongyuanus xichuanensis*, described by Hou in 1980 on the basis of the distal end of a large tibiotarsus from the Yuhuangding Formation (Early Eocene, Bumbanian Asian Land Mammal Age) of Henan Province, in central China. A re-examination of the type specimen in Beijing shows that differences between this Chinese form and European and North American specimens of *Gastornis* are of a minor nature. The Chinese gastornithid can therefore be referred to as *Gastornis xichuanensis*. In the Early Eocene, the giant flightless bird *Gastornis* thus had a Holarctic distribution, encompassing Europe, Asia and North America and mirroring that of various mammal genera. The occurrence of *Gastornis* in the Paleocene of Europe, whereas it is unknown in Asia and North America before the Early Eocene, suggests that the genus appeared in Europe and later dispersed to other land masses. Dispersal to North America probably was via a North Atlantic route, as suggested by *Gastornis* remains from Ellesmere Island. How *Gastornis* reached Asia is more uncertain, as both dispersal from North America via the Bering land bridge and from Europe across the Turgai Strait during a low sea-level episode are possible.

The enigmatic archosaur *Parringtonia gracilis* from the Middle Triassic Manda Beds of Tanzania, and new insights into the early archosaur radiation

Richard Butler¹ & Sterling Nesbitt²

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²University of Washington, Seattle

The Triassic radiation of crown group archosaurs fundamentally changed the composition of vertebrate communities on land. The early Middle Triassic (Anisian) Manda beds of Tanzania have yielded a diverse and highly important, but historically neglected, early archosaur assemblage. Within this assemblage, the enigmatic *Parringtonia gracilis* has previously proposed to have affinities with the aberrant pseudosuchian *Erpetosuchus* from the Late Triassic of Scotland. Here, we provide new descriptive data for *Parringtonia*, and confirm the close affinities of *Parringtonia* and *Erpetosuchus* on the basis of multiple synapomorphies throughout the skeleton. A comprehensive phylogenetic analysis of early archosaurs indicates that the position of these species within Archosauria is poorly resolved. However, *Erpetosuchus* and *Parringtonia* do not appear to have been closely related to Crocodylomorpha, as previously hypothesized. Erpetosuchidae is recognized as a clade of small-bodied archosaurs from northern and southern Pangea and ranging from the early Middle to Late Triassic. The diversity of archosaurs present in the Anisian of

Tanzania supports a temporally deeper major radiation of archosaurs within the Early Triassic. Unambiguous evidence for this radiation is currently limited to the ctenosauriscid pseudosuchian *Ctenosauriscus* from the Olenekian of Germany, although trackway data hint at the existence of a diversity of groups currently unsampled in the body fossil record. Archosaurs may have originated in the immediate aftermath of the Permian/Triassic extinction but remained at low abundances in highly unstable post-extinction Early Triassic faunas. The later appearance of diverse archosaur assemblages would then reflect an increase in abundance as faunas stabilized.

Vertebral architecture in the earliest stem tetrapods

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The construction of the vertebral column has been used as a key anatomical character in defining and diagnosing early tetrapod groups. Rhachitinous vertebrae - in which there is a dorsally placed neural arch and spine, an anteroventrally placed intercentrum and paired posterodorsally placed pleurocentra - have long been considered the plesiomorphic tetrapod condition. Nonetheless, very little is known about vertebral anatomy in the earliest stem tetrapods, as most specimens remain trapped in surrounding matrix, obscuring important anatomical features. Here we describe the three-dimensional vertebral architecture of the early stem tetrapod *Ichthyostega* using phase contrast x-ray synchrotron microtomography. The data reveal an array of new morphological and associated developmental and functional characteristics, including a possible posterior-to-anterior vertebral ossification sequence and the first evolutionary appearance of ossified sternal elements. However, one of the most intriguing features relates to the positional relationships between the vertebral elements, with the pleurocentra being unexpectedly sutured/fused to the intercentra that directly succeed them to form a horse-shoe shaped compound centrum and implying a 'reverse' rhachitinous condition. Comparison of *Ichthyostega* with two other stem tetrapods, *Acanthostega* and *Pederpes*, shows that 'reverse' rhachitinous vertebrae may in fact be the plesiomorphic tetrapod condition. This study rewrites our textbook understanding of vertebral column evolution in the earliest limbed vertebrates and makes us question the proposed vertebral architecture of tetrapodomorph fish and later, more crownward, tetrapods.

From Wood to trees: building a new character set for holocephalan phylogeny

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In the 1980s the noted fossil collector S. P. Wood discovered a pair of exceptionally intact specimens of the Lower Carboniferous holocephalan *Deltoptychius*, while excavating the fossil fish site at Bearsden, Scotland (Serpukhovian: ~326-318 Ma). We obtained a CT-scan of the most complete *Deltoptychius* specimen, identifying and digitally isolating individual parts of the skull, mandible, and pectoral girdle. *Deltoptychius* has been diagnosed by several features including a head shield composed of dermal plates and scales, and presence of mandibular spines. Our digital reconstruction of *Deltoptychius* reveals numerous characters that were previously unknown in this taxon, including details of jaw and braincase anatomy. These data provide a necessary check on existing interpretations of less well-preserved holocephalan taxa, several of which appear to possess very similar cranial morphologies. In particular, we draw comparisons with our own reassessment of the Viséan (~345-326 Ma) genus *Chondrenchelys*, perhaps the earliest holocephalan known from material other than isolated, fossil toothplates. We have exceptional fossil material, also collected by S. P. Wood, from the Mumbie Quarry locality in Scotland. Our as yet incomplete understanding of early holocephalan phylogeny and evolutionary history is being significantly enhanced by the addition of these and other emerging, character-rich descriptions of the Palaeozoic relatives of the modern chimaeroids. Holocephalans represent an important component of the post-Devonian evolutionary radiation of modern vertebrate clades, and will allow us to explore broader questions about the occupation of vertebrate ecomorphospace in the period following biotic turnover at the Devonian-Carboniferous transition.

All Todays: what would contemporary animals look like if we reconstructed them from fossils?

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Reconstructing animals from fossil remains is fraught with uncertainty. Many aspects of appearance and behaviour have to be guessed at, and often these involve the most visible characteristics. In order to help us gauge the accuracy of our reconstructions of prehistoric animals, we present a series of pictures of modern animals as if they had been reconstructed from fossils. Are they still recognisable?

The developmental basis of 200 million year old mammal teeth

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Applying insights from developmental genetics to extinct animals is made difficult by the limited number of ontogenies and other records of development preserved in the fossil record. Fossils do, however, provide information about variation, which can be examined from a developmental perspective. To examine the developmental potential of teeth at the base of mammalian evolution, we analysed morphological variation in the 200Ma old early mammal *Morganucodon*. We compared results with the dentally morphologically similar extant ringed seal (*Phoca hispida*), virtual *Morganucodon* teeth generated by a gene-network computer model of tooth development, and morphologically similar teeth of other extant carnivorans including lynx, marten, and raccoon dog. Using geometric morphometrics, results show variation in *Phoca* and *Morganucodon* dentitions are more similar than to other carnivorans. In particular, *Morganucodon* and *Phoca* teeth show linkage of variation in the anterior and posterior parts of the tooth; all other carnivorans show decoupling of variation. This decoupling may be related to the evolution of mammalian tribosphenic lower molar tooth morphology, with the anterior trigonid separate from the posterior talonid basin. The dental developmental model identifies only two genetic parameters able to produce this decoupling of anterior/posterior variation, suggesting avenues for future developmental investigations. An explanation for the lack of decoupling in *Phoca* may be the loss of well-defined occlusion of the molar teeth with the shift to a piscivorous diet. *Morganucodon* has only loose occlusion, suggesting that it lacked the developmental decoupling that may have been a prerequisite for the evolution of tribospheny.

Functional evolution of the feeding system in rodents

Philip Cox

Hull York Medical School

The masticatory musculature of rodents has evolved to enable both gnawing at the incisors and chewing at the molars. In particular, the masseter muscle is highly specialised, having extended anteriorly to originate from the rostrum. All living rodents have achieved this masseteric expansion in one of three ways, known as the sciurormorph, hystricomorph and myomorph conditions. Here, finite element analysis (FEA) was used to investigate the biomechanical implications of these three morphologies, in a squirrel, guinea pig and rat. In particular, I wished to determine whether each of the three morphologies is better adapted for either gnawing or chewing. Results show that squirrels are more efficient at muscle-bite force transmission during incisor gnawing than guinea pigs, and that guinea pigs are more efficient at molar chewing than squirrels. This matches the known diet of nuts and seeds that squirrels gnaw, and of grasses that guinea pigs grind down with their molars. Surprisingly, results also indicate that rats are more efficient as well as more versatile feeders than both the squirrel and guinea pig. There seems to be no compromise in biting efficiency to accommodate the wider dietary range and the more general feeding behaviour adopted by rats. The results show that the morphology of the skull and masticatory muscles have allowed squirrels to specialise as gnawers and guinea pigs as chewers, but that rats are high-performance generalists, which helps explain their overwhelming success as a group.

3D textural analysis of microwear and trophic ecology of placoderms

Laurent Darras & Mark Purnell

University of Leicester

Recent morphospace analyses of jaws in Palaeozoic aquatic gnathostomes have revealed a pattern of major structural diversification and trophic innovation in the late Silurian and early Devonian followed by a period where functional/trophic morphospace occupation remained stable. Evidence from extant aquatic gnathostomes introduces an important caveat into such analyses: morphology of the trophic apparatus and diet might not be closely correlated, so interpreting morphological patterns in terms of dietary ecology can be complicated. Preferably, functional hypotheses should be supported by independent evidence of diet: robust analysis of tooth microwear has the potential to provide such evidence.

Placoderms were a major component of Devonian aquatic ecosystems. We applied quantitative statistical analysis of microtextures to the wear on placoderm jaws, and assessed the power of this method to address questions of ecomorphology, ontogenetic shift in diet and predation-driven macroevolutionary events. Taking into account the

histological differences between placoderm jaws and those of most extant gnathostomes, our results suggest that analysis of microtexture on feeding elements can be used to test and constrain specific hypotheses of diet and trophic diversity in the earliest gnathostomes.

Variability in tooth wear indicates attritional wear: implications from feeding experiments with lagomorphs

Ellen Schulz

Biocentre Grindel and Zoological Museum

Dental microwear and 3D surface texture analysis are useful for inferring herbivore diets, with scratches usually interpreted as indicators of grass dominated diets and pits as indicators of browsing. We conducted feeding experiments on a captive population of 32 rabbits (*Oryctolagus cuniculus*) over a period of 25 weeks using four different pelleted diets: lucerne, lucerne & oats, grass & oats, grass. Lucerne is the perennial forage legume *Medicago sativa*. The lowest silica content was measured in the lucerne and the highest in the grass diet. After extended exposure to each diet dental castings were made of the rabbit's lower molars. Occlusal surfaces were then investigated using dental microwear and 3D areal surface texture analysis. In terms of classical microwear, we found our hypothesis supported, as the grass group showed a high proportion of (long) "scratches" ($p = 0.011$) and the lucerne group a high proportion of "pits" ($p = 0.004$). Regardless the uniform diets, variability of microwear and surface textures increased with lower silica content. A high variability in microwear and texture analysis thus need not represent dietary diversity, but can also be related to a uniform, low-abrasion diet. Thus, the uniformity or variability of microwear/texture analysis results may be associated to the degree of abrasion and attrition.

Mine's bigger than yours: the most comprehensive phylogeny of the Plesiosauria and the position of the leptocleidians

Mark Evans^{1,2}

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Twenty years on from the first cladistic analysis of the Plesiosauria (Sauropterygia, Reptilia) there is still a lack of consensus on the status, position and membership of some major postulated clades (e.g. Polycotylidae, Leptocleidia, Rhomaleosauridae). Previous attempts at resolving global plesiosaur phylogeny have identified the influence of taxon sample on the topology recovered. Here I present the largest phylogeny of the Plesiosauria attempted to date both in number of OTUs (Operational Taxonomic Units: 106) and characters (339).

The analysis found support for the Neoplesiosauria, comprising Plesiosauroidea and Pliosauroida, with non-plesiosaurian plesiosaurians and basal plesiosaurians forming a paraphyletic assemblage. The Plesiosauroidea included a series of basal taxa, including *Plesiosaurus dolichodeirus*, the Microcleididae, and a clade of cryptocleidids and elasmosaurs. Two clades of derived cryptocleidids were recovered, one including *Cryptocleidus eurymerus* and *Kimmerosaurus langhami*, and the other including species of *Muraenosaurus* and *Vinialesaurus caroli*. *Muraenosaurus leedsii* as traditionally understood was found to be paraphyletic.

The Pliosauroida included the Rhomaleosauridae and a clade including the Pliosauridae and Leptocleidia (leptocleidids and polycotylids). A paraphyletic assemblage was recovered outside of the latter, node-based, taxon. This includes newly recognised British Pliensbachian taxa as well as *Nichollsaura borealis* of the Albian of Canada. *Stratesaurus taylori* from the bottom-most Hettangian was also found to be a basal member of the clade encompassing the pliosaurids and leptocleidids, but its exact position was unclear. However, this indicates that the leptocleidians were pliosauroids, and that their lineage had been distinct from other plesiosaurians since the very earliest Jurassic.

Using penetrative tracks to reconstruct limb kinematics of bipedal dinosaurs traversing semi-fluid substrates

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The fossil tracks described by Edward Hitchcock and housed at the Beneski Museum of Natural History, USA, include a variety of track morphologies. Among them are tracks which show considerable variation over multiple surfaces. These successive impressions are subsequent exposures of penetrative tracks, where the trackmaker's foot has directly interacted with, and passed through, each layer. Track morphology on uppermost surfaces displays extremely narrow slit-like digit impressions, often with a long posterior impression behind the apex of the digits. At the lowest levels, track morphology is reduced to drag marks, formed from a sweeping motion of the foot. Intermediate surfaces show transitional morphologies. Most surfaces within a volume show an exit trace, formed as the foot is withdrawn. This exit trace occurs in a spatially consistent location throughout the track volume,

indicating a vertical foot withdrawal, rather than a forwards removal of the foot as in other deep dinosaur tracks (e.g. from Greenland)

The substantial deformation and considerable depth that some track volumes display implies that the substrate was so soft as to behave in a semi-fluid manner. In order to reconstruct the limb kinematics, including where, when, and how the substrate provided resistance and supported the foot during the step cycle, we used computer simulation and animation. Digitised fossil tracks were used to three dimensionally reconstruct the path of the foot. This foot motion was then used to generate virtual tracks that show similar track morphologies to those seen amongst the Amherst collection.

Skull anatomy and feeding biomechanics in pliosaurs

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Pliosaurs were large marine predators that topped the Mesozoic marine trophic web. Despite much being known about their ecology and behaviours, the biomechanics of their feeding has only been investigated in a limited way. An exceptionally well-preserved pliosaur from the Kimmeridgian of Weymouth Bay (UK) provides the ideal material for investigating the cranial optimizations associated with predation.

Computed tomography (CT) scans offered the chance to describe inaccessible internal anatomical structures and to create digital models of the rostrum and mandibles. These models revealed an unexpected, extensive broad neurovascular system through the snout to both teeth and foramina on the surface of the premaxillae. Digital modelling was used to reconstruct missing parts, combined with retro-deformation of the postorbital region to repair some deformation of the skull, and to enable the reconstruction of the adductor musculature.

Results from beam theory demonstrate that the structure of the rostral part of the snout is not specifically reinforced for dealing with any particular kind of stress. This, and comparisons with morphologically convergent taxa, show that the pliosaur rostrum is not optimized for shaking or twisting feeding, unlike many modern crocodylians. On the whole, this suggests a generalized feeding strategy. The lower jaws were loaded with forces from the reconstructed muscles to calculate maximum bite force. This was used in finite element analysis to study the stress pattern on both the rostrum and lower jaws. These studies provide the first set of tests of postulated feeding modes in pliosaurs.

The Weymouth Bay Pliosaur - What's happened since last year's meeting?

Richard Forrest

plesiosaur.com

The Weymouth Bay pliosaur is the most spectacular fossil to have been found in the UK for many decades. The stories of its discovery, its acquisition by the Heritage Lottery fund, and its progress towards becoming the key attraction in Dorchester Museum and have attracted great media and public interest. Having such an exceptional specimen helps us in our role as scientists to explain to the general public the nature of our work.

A danger with such specimens is that scientific work can be delayed or even forgotten, and it has been a major concern for the Heritage Coast team and Dorchester Museum that this is undertaken. Several lines of investigation are under way. A team from the University of Portsmouth is investigating of the epifauna trying to unravel a complex taphonomic history. CT scans by the Engineering Department of the University of Southampton provide the basis for work at Bristol University, using FEA to analyse mechanical performance, and have given unique insights into the internal architecture of parts of the skull.

The basic palaeontology - the anatomical description - is fundamental to providing the context for other investigations. To avoid the risk of a single researcher claiming the right to carry out such work, a "dream team" of pliosaur researchers was invited to collaborate on this aspect of the research.

Initial findings suggest that this is a new taxon, though there is a debate over whether or not it is a new species of *Pliosaurus*, or a new genus, complicated by uncertainty over the nature of *Pliosaurus*. Other huge pliosaurs from Mexico and Svalbard have reached the news recently, but have generated very little in the way of scientific description. The Weymouth Bay specimen will contribute to an interesting debate with wider relevance to our understanding of macroevolutionary patterns.

If it looks like a duckbill... The first (almost) complete tooththrow of *Teinolophos*

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Monotremes have a very sparse fossil record, and the Early Cretaceous basal platypus *Teinolophos*, from Australia's Flat Rocks locality, is critical to our understanding of their evolution. Tom Rich and co-workers have described partial dentary specimens, but a new specimen (NMV P229408) is the only one preserving the jaw anterior to the molars, and the most complete molar row, with four in situ molars. Most notable is the surprising elongation of the jaw, and comparison will be made with *Obdurodon*, a Miocene monotreme.

NMV P229408 is tiny and fragile, so only the buccal side and alveolar surface have been prepared out from the matrix block. The solution was high-resolution imaging using synchrotron XR-CT to produce a 3D digital reconstruction, and SEM imaging to establish the dental formula and look for evidence of premature shedding of the premolars. As with other Flat Rocks mammal fossils, the bones and teeth were initially finely preserved, showing detailed internal structure, but then suffered later crushing. *Teinolophos trusleri* has nine postcanines, a canine and at least one incisor, with a most interesting pattern of spacing of the premolars and molars.

Teinolophos has a hypertrophied mandibular canal; this latter linked to innervation of a sensory bill in modern *Ornithorhynchus*. The presence of teeth along the mandible of *Teinolophos*, suggests that a bill had not yet developed, but this basal platypus yields vital clues about the prior stages of its evolution.

Exploration in the Paleogene of Senegal and the end of the sirenian paradox

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The emerging consensus from molecular studies suggests that Afrotheria (elephants, sea cows, hyraxes, golden moles, tenrecs, sengis, aardvarks) from Africa and Xenarthra (sloths, armadillos, and anteaters) from South America represent deep branches of the placental mammal tree. This relationship implies that a major morphological dichotomy in mammal evolution has hitherto been overlooked. The anatomy of afrotherian stem groups remains central to understanding this evolutionary bifurcation. Although Africa seems to have played a pivotal role in the evolution of early mammals, little palaeontological work has been carried out in the sub-Saharan Africa. Unlike neighbouring Morocco, which has been intensely mined yielding one of the richest known Paleogene vertebrate faunas, the phosphates of Senegal have remained largely unexplored for decades. The primary aim of the PaleoSen research project (www.paleosen.com) is to document the exceptional Paleogene vertebrate faunas of Senegal by prospecting previously unexplored sedimentary basins. Since 2010, our team organized several palaeontological field expeditions to Eocene deposits in Senegal that revealed an untapped fossil resource. These pilot expeditions discovered numerous Eocene vertebrate fossils, including unique sirenian remains. The continued exploration of fossil-bearing horizons in Senegal has the potential to greatly improve our knowledge of the origin and evolution of African mammals, as well as the potential to fill a major gap in our understanding of sirenian evolution. It will also provide pivotal data to examine the potential connections between African and New World faunas, as well as the role continental drift played in driving their evolution.

Body and tooth mass estimates for the earliest bird, *Archaeopteryx lithographica* (Late Jurassic), and the insignificance of tooth mass in bird evolution

Donald Henderson

Royal Tyrrell Museum of Palaeontology

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

A mass mortality of juvenile Protoceratops

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Numerous monospecific aggregations of dinosaur fossils suggest that individuals of at least some species lived (and died) together. Notably, many of these groups comprise juveniles or subadults, suggesting they may have been more prone to group living than adults. A new site from the aeolian deposits of Tugrikin Shire, Late Cretaceous of Mongolia, preserves four juvenile individuals of *Protoceratops andrewsi* in extremely close proximity (within an area <1 m²). Although one individual has suffered erosion and some disarticulation, the specimens as a whole are well preserved, nearly complete and articulated. The individuals have different orientations in the horizontal plane but are all positioned with the head facing upwards. The positions of the animals relative to one another suggest that these animals died in the open and were not buried in a burrow. Previous aggregations of *Protoceratops* provided evidence that both adults and very young animals spent time together. Individuals from the new site are intermediate in size (skull length=140 mm) between those found in previous aggregations, suggesting that some level of sociality occurred throughout life. Caution must be taken however when inferring social living or activity in dinosaurs – extant amniotes exhibit a wide range of behaviours which may fall under the umbrella term ‘sociality’ and such behaviour can be plastic. Individuals or populations of a species may be solitary, or aggregate into social groups, or switch between the two, and groups may be formed of single or mixed age classes, or can be single sexed or mixed.

The evolution of the Pseudorhyncocyonidae, a European Paleogene family of insectivorous placental mammals

Jerry Hooker

Natural History Museum

Members of the family Pseudorhyncocyonidae occur in faunas ranging from the middle of the early Eocene to nearly the end of the epoch in France and Germany, but are always rare. With few exceptions, preservation types are polarized between assemblages with only one or two isolated teeth and that from Messel, with complete flattened skeletons, but whose teeth are difficult to observe. Although pseudorhyncocyonids have been considered to be sister group to the extinct insectivorous family Leptictidae, primitive members are almost unknown and consequently details of their relationships have been difficult to establish. Two new species represented by teeth from numerous loci, from the earliest Eocene of the UK, allow a better understanding of pseudorhyncocyonid dentitions. This facilitates the recognition of two further new species from the middle Eocene of Germany and the late Eocene of France. Study of occlusal relationships also helps to fill gaps in our knowledge of missing tooth loci. Cladistic analysis of pseudorhyncocyonids with their previously judged closest relatives, the Leptictidae, Pantolestia and Palaeonodonta, shows that two European species, *Diaphyodectes prolatus* and *Palaeictops? levei*, formerly thought to be leptictids, are instead primitive pseudorhyncocyonids, extending the range of the family further back in time to the middle Paleocene. The analysis also shows that the Pseudorhyncocyonidae are sister group to the other three groups combined and that family-level differentiation in this probable clade took place as early as the earliest Paleocene.

Evolution of bone repair via invasive growth of dentine in a 380 million year old fish

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The skeleton of early vertebrates such as heterostracans is dominated by dermal bone (aspidin) with dentine restricted to surface tubercles. In these early skeletons, in genera such as *Psammolepis* (Heterostraci; Psammosteida), invasive dentine grows to consolidate the bone. This pleromic dentine forms from primary tubercle pulp cavities and also from the dentine secondarily formed in the surface pore spaces between the tubercles. Both sources provide dentine that fills vascular spaces in spongy bone, consolidating dermal bone either in response to, or in advance of, surface attrition. However, *Psammolepis* specimens (Middle Devonian, Estonia) with deep injury to the bony shield show that subsequent repair occurred by massive, invasive, chaotic growth of dentine into the wound and onto the remaining bony scaffold. Dentine, rather than new bone, is involved in bone repair, derived from migratory odontoblasts, both from tubercle pulp cavities and from surrounding, flask-shaped crypts. We suggest that these crypts, associated with surface pores, are a stem cell niche capable of producing odontoblasts for secondary dentine and invasive repair, within the complex canal system of the bone. A comparable function was proposed for the pore canal system within dermal bone linked to dentine tubercles in the fossil osteichthyan

Meemannia, i.e., vascular transport of odontoblasts for dentine production at the bone surface, rather than a sensory function. Our observations suggest that this system was activated for wound repair and already present in taxa such as *Psammolepis*, a process retained in reparative dentine more commonly associated today with dentitions than skeletal dermal bone.

Dietary change and diversity in Palaeotheriidae (Mammalia, Perissodactyla) across the Eocene-Oligocene transition

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The mammalian fossil record shows evidence of a number of faunal turnover events that have alternately been explained by changes in climate or competition by invading species.

One such event, the Grande Coupure, occurred in the earliest Oligocene of Europe, coinciding with the final step in the transition from greenhouse to icehouse conditions, the first Oligocene Antarctic glaciation (Oi-1), and with the extinction of much of the endemic European mammal fauna and the migration into Europe of taxa from Asia. Among the larger mammals that were most affected, the Palaeotheriidae (Perissodactyla) showed a pronounced fall in species diversity with *Plagiolophus minor* being one of the few species to persist into the Oligocene.

The diversity and biogeography of European Eocene-Oligocene transition perissodactyls and artiodactyls is presented here with refined correlations based on a study of the Solent Group of the Hampshire Basin. Previous diversity studies have concentrated on patterns of change in the general dental pattern of the tooth; however this study includes dental microwear, a source of evidence for diet, which is independent of tooth structure.

An integrated dental mesowear and microwear study of four species of palaeotheres is compared with new data from artiodactyls. Each palaeothere species displayed significantly different diets within localities. Major dietary change took place before the incoming taxa arrived from Asia at the Grande Coupure and coincided with global cooling events. The first ~0.5 Ma after the Grande Coupure, however, was a time of no climate or dietary change.

Bone and tooth histological growth patterns in fossil and recent deer and their implications for island evolution

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Candiacervus from the Mediterranean island of Crete is an outstanding example of Late Pleistocene insular dwarfism. In contrast to this dwarf form stands *Megaloceros*, the giant Irish deer, known throughout the Pleistocene of Eurasia. *Megaloceros* and the fallow deer *Dama dama* are among the continental relatives of *Candiacervus*. Placing palaeohistological data of *Candiacervus* and *Megaloceros* in phylogenetic context reveals common patterns of growth and life history changes in fossil island forms.

For the first time bone histological examinations of different ontogenetic stages of *Candiacervus* and *Dama* are conducted. Most long bones of newborn *Candiacervus* already start with fibrolamellar bone as primary bone tissue and show a mainly plexiform arrangement of vascular canals as found in adult specimens. Similarity of bone tissue types in *Candiacervus*, *Megaloceros*, and *Dama* show a comparable mode of growth. Higher counts of lines of arrested growth and thicker growth zones indicate higher longevity and growth rates in *Megaloceros*. Those observations suggest a heterochronic process in *Candiacervus* to attain smaller size, probably one of shorter lifespan in combination with lower growth rates than the ancestor.

Ongoing tooth histological studies of *Megaloceros* and *Candiacervus* provide reliable estimates of individual ages (e.g. 8 years for an adult *Candiacervus*) and longevity in order to decipher the life history of *Megaloceros* and dwarfed island mammals such as *Candiacervus*. After comparisons with other investigations, this deer study demonstrates how different growth patterns have evolved on different islands and supports the potential of palaeohistology in studies of mammalian life history evolution.

Beating the bends: The spare ribs of Big Meg

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Historically, a large number of skeletal elements of the pachycormid suspension-feeder *Leedsichthys* have been uncertainly identified as ‘rib-shaped bones’. In an attempt to resolve this, the basic principle that the shape and architecture of a bone reflects the stresses that it operates and grows within (and the mechanical environment around it) was used, in an attempt to ‘reverse engineer’ a likely location for these unlocated elements. The ‘Big Meg’ specimen of *Leedsichthys* (GLAHM V3363) was selected for this analysis, as it has a particularly wide range of elongate bone morphologies referred to as ‘rib-shaped’. A series of thirty elements from the ‘Big Meg’ specimen were examined for their curvature, and the normalised results plotted, using the following equation:

$$\text{normalised bone curvature } (\xi) = X/2L \times 100$$

where the orthogonal distance (X , the moment arm of the axial component of force acting on a bone) was measured from the chord ($2L$) between the proximal and distal ends. For comparison, two partial articulated pachycormid specimens (MOZ-Pv 1160, MOZ-Pv 0281) from the Upper Jurassic Neuquén Basin of Argentina were used. In these closely related taxa the bone positions were accurately known. In MOZ-Pv 1160 the pleural ribs were measured, and in MOZ-Pv 0281 the neural and haemal spines. The plotted normalised curvatures of the three specimens were then compared.

Leedsichthys elements plotted into three discrete clusters, representing grades of curvature. The Argentinian pachycormids demonstrated a growth in curvature from the tail forward, only achieving mid-grade curvature as a maximum, for mid-body pleural ribs.

Affects of ancestral character estimation on methods for estimating rates of evolution in discrete morphological characters

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With its ability to sample from multiple different time periods palaeontology is able to make a unique contribution to studies of evolutionary rates. So far such work has concentrated on rates of diversification or change in continuous characters such as body size. However, considerable information is also present in cladistic character-taxon matrices. In a previous contribution we developed four methods for rate estimation in discrete characters and applied them to lungfish, a group previously identified as showing a major post-Devonian slow-down in rates leading to their description by Darwin as “living fossils”. Those results are revisited here using a novel likelihood approach for estimating ancestral character states that better accounts for uncertainty. We show that the nuanced nature of some of our earlier results, including a peak in rates around the Permian-Triassic boundary, tend to be smoothed away. This was likely the result of characters previously being artificially “clumped” by the use of ACCTRAN and DELTRAN optimisations. However, the overall pattern of a significant difference between high Devonian and low post-Devonian rates is reconfirmed. In addition we show major differences in rate estimation between internal and terminal branches that is ultimately an artefact of how palaeontological trees are dated.

An *Ichthyosaurus breviceps* specimen collected by Mary Anning: new information on the species

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An ichthyosaur (CAMS MX.50187) in the collections of the Sedgwick Museum was collected by the renowned early fossil collector Mary Anning, but has never been adequately described in the literature. As an Anning specimen, it is certainly from the Lower Jurassic of Lyme Regis, west Dorset. The near complete, articulated presacral skeleton is lying on its left side and includes a complete skull, one complete and one partial forefin, pectoral bones, both pelves, and both hindfins. Most of the caudal centra are from another individual and probably replaced the original ones. The specimen is identified as *Ichthyosaurus* based on the morphology of the humerus and forefin, and presence of a tripartite pelvis. It is assigned to *I. breviceps* on the basis of the relatively short snout, large eye, and tall neural spines on the dorsal vertebrae. This is the only *I. breviceps* to preserve a complete pelvis, which may prove to be diagnostic of the species. This individual is the largest *I. breviceps* known, with jaw length of 33.5 cm and estimated length from snout to tail bend of 1.6 m.

The controversial phylogenetic relationships of the basal actinopterygian lineages

Adriana López-Arbarelo

Living actinopterygians represent more than 50% of all living vertebrates and include more than 27000 species of teleosts, 1 bowfin, 7 species of gars, 27 species of acipenseriforms and 12 species of bichirs. The latter four groups represent basal lineages that were very diverse during the early Mesozoic and the origin of which can be traced back to the Early Triassic or Palaeozoic. Therefore, even considering the possibility of a rather conservative genotypic and/or phenotypic morphology, the living members of these groups are just the tip of an iceberg of more than 240 Ma of evolution. Except for the bowfin and the gars, almost all of the species of acipenseriforms (25 of 27) and bichirs (11 of 12) are endangered and included in the IUCN Red List of Threatened Species. Attending to this critical situation, these fishes have been the focus of intensive research during the last few decades. However, after two centuries of systematic research, the phylogenetic relationships among these fishes are still unclear. We know that bowfins, gars and teleosts are neopterygians, but we still don't know how these three lineages are related to each other. Similarly, the relationships of acipenseriforms and bichirs outside and in respect to the Neopterygii are controversial. Although fossils always provide incomplete information, I present examples that strongly indicate that the phylogenetic relationships among these basal lineages can only be solved including the high diversity of the fossil taxa in cladistic analyses of the living forms.

Jaw Disparity in Herbivorous Dinosaurs: Trends in Morphology and Function

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The diversity of herbivorous taxa in palaeoenvironments can provide key insights into prehistoric communities and population ecology. We quantify morphological and functional disparity using landmark and biomechanical traits analysis respectively within herbivorous dinosaur mandibles (Sauropodomorpha and Ornithischia) to test patterns and convergences in jaw mechanics through time and across palaeolatitudinal space. We also compare the biomechanical profiles of various sub-clades and vertical partitioning of ecospace. Sauropodomorphs and ornithischians are shown to occupy significantly discrete regions of morphospace and function-space, with ornithischians occupying larger regions and stegosaurs and heterodontosaurs accounting for the majority of overlap. Evidence suggests that basal-most ornithischian mandibles are morphologically and functionally similar to those of sauropodomorphs, however there is very little clade overlap in mandibular function-space before the Upper Cretaceous. Disparity calculations show a gradual increase in morphological jaw disparity through the Mesozoic, peaking in the Cretaceous, whilst functional disparity plateaus by the Early Cretaceous and does not increase further. Greatest morphological disparity is observed in northern-temperate palaeolatitudes, whereas functional disparity remains relatively stable across palaeolatitude. Significant variation in ceratopsian mandibular morphology accounts for increased morphological disparity in the Cretaceous and northern palaeolatitudes. Disparity in high-browsing sauropodomorphs is found to be comparable to that of low-browsing taxa. Patterns of morphological and functional variation between Sauropodomorpha and Ornithischia offer new insights into the relationship between form and function, potential inter-specific competition, niche occupation and dinosaurian feeding habits.

The evolution of quadrupedalism in ornithischian dinosaurs

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The most primitive ornithischian dinosaurs were bipedal, but they radiated into a diversity of quadrupedal and bipedal forms. Quadrupedalism evolved in the three major ornithischian lineages independently. Outside of Ornithischia, the reversion to quadrupedalism from bipedal ancestors has only occurred on two other occasions in the whole of tetrapod evolution (in the silesaurid dinosauriforms and the sauropodomorph saurischian dinosaurs); thus examination of the convergent acquisition of this stance in ornithischians is warranted. We use a diversity of techniques to investigate how and why multiple clades of ornithischian dinosaurs evolved quadrupedal locomotion. Muscle reconstruction suggests that quadrupedal ornithischians adopted a variety of different stances. Disparity in limb scaling between clades could be due to clade-specific behaviours. Anatomical features related to the evolution of quadrupedalism do not appear to have been acquired in the same order in all lineages, and mosaic character evolution in ornithopods suggests multiple independent acquisitions of quadrupedalism in the clade. Moment arm modelling suggests a more columnar hind limb in stance phase and loss of femoral rotation as a form of lateral limb support in quadrupedal ornithischians, and a wide-gauged stance in thyreophorans and ceratopsids. Centre of mass modelling indicates that ceratopsids may have evolved quadrupedalism due to the development of large heads, frills and horns as display structures. However, thyreophorans did not become quadrupedal as a result of development of hypertrophied dermal armour. Overall, quadrupedal ornithischians display a previously unrealised diversity in stance and locomotor mode, and do not appear to have been significantly constrained in their style of locomotion by their bipedal ancestry.

A novel approach to estimating pterosaur bone mass using CT scans

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Body mass estimation in extinct animals can provide information about ecology and biomechanics of the animal and is vital for flying animals as it determines its ability to take off, land, and indeed, fly. However, existing mass estimation methods for pterosaurs produce a wide range of values, especially in the larger animals. This hinders our understanding of their flight capabilities and indicates a need for a more accurate method for estimating body mass. A novel approach has been developed that uses CT scans of pterosaur wing bones to determine the volume of bone material and thus the bone mass. Results show much larger masses for some bones than previous methods, which indicates that a reassessment of methods for estimating total mass in pterosaurs is required.

Experimental maturation of feathers: implications for reconstructions of fossil feather colour

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Fossil feathers often preserve evidence of melanosomes – micron-scale melanin-bearing organelles that have been used to infer original colour patterning in the plumage of dinosaurs. Such reconstructions of original coloration do not incorporate contributions from all colour-producing mechanisms and assume that melanosome geometry is not altered during fossilisation. Here, we use high pressure-high temperature autoclave experiments on modern feathers to simulate the effects of burial on feather colour. Our experiments show that melanosomes are retained despite complete degradation of other colour-producing nanostructures (e.g. quasi-ordered arrays in barbs and the keratin cortex in barbules) and loss of visual evidence of non-melanin pigments. Significantly, however, melanosome geometry is altered by the effects of pressure and temperature. These results demonstrate that reconstructions of original plumage coloration in fossil theropods based largely on preserved features of melanosomes should be treated with caution. Reconstructions of original plumage coloration in fossils require original melanosome geometries to be elucidated and, ideally, incorporation of chemical and anatomical data on the preservation of other feather pigments and colour-producing structures.

A small-bodied azhdarchoid pterosaur from the Isle of Wight (UK): its implications for pterosaur phylogeny, anatomy, diversity and distribution

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We report a new, three-dimensional pterodactyloid pelvis (total length 40 mm) from the Aptian Atherfield Clay Formation of the Isle of Wight (UK). Fusion of pelvic, intervertebral and neural sutures suggests skeletal maturity for this individual; it is significant in providing new information on the small-bodied pterodactyloids present in Europe during Aptian times. The presence of a postacetabular process with a distinctly waisted shaft and an expanded, dorsoposteriorly convex apex indicate azhdarchoid affinities. Diagnostic characters on the ilium allow the specimen to be recognised as a new taxon.

A substantial variation present in the pterosaur pelvis has long been noted. Despite this, published phylogenetic analyses have utilised none, one or three pelvic characters. We identified 23 characters in the pterosaur prepubis, pelvis and sacral vertebrae that could be coded for analysis. We analysed a pelvis-only data set to see whether pelvic characters alone carried a phylogenetic signal similar to that recovered from analysis of the whole skeleton. A majority rule consensus tree recovered non-pterodactyloids and ctenochasmatooids as a series of outgroups to a clade including ornithocheiroids, dsungaripterids and azhdarchoids in most fundamental trees. The Atherfield Clay taxon grouped consistently with tapejarid and neoazhdarchian azhdarchoids. Inclusion of the Atherfield Clay taxon in a dataset of characters from across the skeleton resulted in its consistent grouping with azhdarchoids, though its affinities within this clade could not be resolved. Poorly formulated phylogenetic definitions mean that the nomenclature of pterosaur clades is in need of revision.

The cranial morphology of the Chinese placodont *Psephochelys polyosteoderma* (Sauropterygia, Placodontia), a reconstruction based on μ CT data

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Placodontia are an unusual group of durophagous and often heavily armoured marine reptiles that inhabited shallow marine environments of the Tethys Ocean from the early Middle to the Late Triassic (Anisian–Rhaetian). They are

well known from Europe, especially Germany, Switzerland and Italy, and have recently been discovered in southern China, with four new taxa being described in the last twelve years. However, detailed phylogenetic and palaeoecologic analyses that go beyond the primary osteological descriptions have not yet been conducted for all of these new taxa. As part of an on-going project to create a comprehensive phylogeny of the Placodontia, and by extension Sauropterygia, the exceptionally preserved holotype skull of *Psephochebys* (IVPP V 12442) was scanned using micro-computed tomography (μ CT). This included many important details that were obscured or unclear during the initial description of the taxon, such as the general pattern of dermatocranial elements (e.g., the exact position of the squamosal and nasal bones) and the morphology of the chondrocranium and mandible, both of which have not yet been described. Furthermore, the correct tooth formula could be reconstructed as having 2 maxillary, 2 palatine and 2 dentary teeth on each side (the premaxilla is edentulous).

These results are not only significant for the understanding of placodont relationships and dispersal but, due to the plesiomorphic position of Placodontia within Sauropterygia, also have implications for our understanding of sauropterygian palaeobiogeography in general.

Iguanodontian systematics and the origin of hadrosaurs: A case of not being able to see the roots for the trees?

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The problem. Hadrosaurian iguanodontians are abundant and speciose herbivores within communities of dinosaurs of Campanian-Maastrichtian age. However the details governing their evolutionary transition from the derived iguanodontian to that of the definitive hadrosaurian state, although perhaps understood in general terms, has proved illusory.

Confounding factors. Lack of resolution is compounded by an Albian-Coniacian 'gap'. Several newly described iguanodontians have begun to bridge the gap.

Analytic approach. The derived euiguanodont-euhadrosaur transition will be analysed by reference to three independent, yet correlated, lines of investigation: chronostratigraphy, comparative morphology and the comparative topology of trees. These approaches explore when, where and how the hadrosaur bauplan was assembled in the lineage that led to the first diagnosable members of the clade Euhadrosauria.

Resolution. Basal iguanodontians ('clypeodonts') exhibit shield-shaped and differentiated 'off-set' teeth; derived dryomorphans show modified jaw, pelvic and hindlimb anatomy. Euiguanodontians develop jaw-dominated skulls and tooth magazines, as well as a diversity of 'muzzle' morphologies. Hadrosauromorphs are morphologically conservative serially derived euiguanodonts basal to the clade Euhadrosauria, with modified postcranial morphology that anticipates the configuration seen in 'true' hadrosaurs (Euhadrosauria).

Pattern indicative of process? Hadrosauromorphs are rare and first appear in the Cenomanian of Europe. During the Cenomanian-Santonian interval sporadic discoveries of hadrosauromorphs at various locations in the northern Hemisphere indicates a geographically diffuse 'lag-phase' in their diversification prior to a 'log-phase' in the Campanian. This pattern may indicate 'bottle-necking' linked to the assembly of euhadrosaurian anatomy.

Evidence for determinate skull growth and rapid juvenile growth in *Morganucodon watsoni*

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Determinate growth is an important mammaliaform apomorphy whose origin is strongly interlinked with the evolution of diphyodont dental replacement. Correlation of these characters, supported by their co-occurrence in *Morganucodon*, has led to the hypothesis that they are associated with the origin of lactation. Evidence for determinate growth in *Morganucodon* has previously been inferred from a relatively small sample of *M. oehleri*. To evaluate determinate skull growth across *Morganucodon* species, we investigated 531 specimens of *M. watsoni* from Rhaeto-Liassic fissure deposits of South Wales. Mandibular measurements were also taken from small extant mammals known to show determinate growth (*Erinaceus europaeus*, *Mustela erminea*), and from animals lacking mammal-like growth patterns: the sea turtle (*Chelonia mydas*) and a lepidosaur from the same fissure deposits as *M. watsoni*. The distribution of mandibular data for extant mammals was found to be platykurtic (*E. europaeus*: $g_2 = -0.98$, $p < 0.05$; *M. erminea*: $g_2 = -0.89$, $p < 0.05$); no significant kurtosis was found in those animals without mammal-like growth (*C. mydas*: $g_2 = -0.57$, $p > 0.3$; lepidosaur: $g_2 = 0.11$, $p > 0.5$). In the platykurtic data distributions of extant mammals, both left and right tails are truncated relative to the normal distribution. Cessation of growth at a maximum size accounts for right-tail truncation, while rapid juvenile growth, resulting in fewer animals of small size being sampled, could explain left-tail truncation. The data distribution for *M. watsoni* was also found to be platykurtic ($g_2 = -0.54$, $p < 0.02$), supporting hypotheses of determinate growth, of rapid juvenile growth, and hence also of possible maternal provisioning by lactation, in *Morganucodon*.

A reappraisal of the hollow-crested hadrosaurid (Dinosauria, Iguanodontia) *Magnapaulia laticaudus* (new combination) from the Late Cretaceous of Baja California, Mexico

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The anatomy, phylogenetic systematics, and historical biogeography of the lambeosaurine hadrosaurid *Magnapaulia laticaudus* are revised. It is rediagnosed based on the possession of two autapomorphies (i.e., longest haemal arches of proximal caudal vertebrae being at least four times longer than the height of their respective centra; base of prezygapophyses in caudal vertebrae merging to form a bowl-shaped surface) and a unique combination of characters (i.e., downturned cranioventral process of the maxilla; tear-shaped external naris with length/width ratio between 1.85 and 2.85; neural spines of dorsal, sacral, and proximal caudal vertebrae being at least four times the height of their respective centra). Maximum parsimony analysis showed that *M. laticaudus* and *Velafrons coahuilensis* (upper Campanian of northern Mexico) constitute a clade of southern Laramidian lambeosaurines, which forms a sister relationship with the clade of helmet-crested lambeosaurines, including *Corythosaurus* and *Hypacrosaurus*, from the northern regions of the continent. The existence of taxonomically and phylogenetically informative differences between *M. laticaudus* and *V. coahuilensis*, and the lack of shared diagnostic characters among the known overlapping elements, warrants their taxonomic separation. The results of Dispersal-Vicariance analysis indicate that southern Laramidian lambeosaurines split from the northern forms via vicariance from a widespread ancestor no later than the late Campanian. At over 12 m in body length, *Magnapaulia* is the largest recorded lambeosaurine and one of the largest known hadrosaurid species worldwide. In North America, *M. Laticaudus* may have been rivaled in size by the largest individuals of saurolophines *Edmontosaurus annectens*, *Kritosaurus navajovius*, and *Anasazisaurus borneri*.

Compositional evidence for homology of exceptionally preserved non-skeletal body-parts in early vertebrates

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Like many basal members of extant phyla, chordates and vertebrates dating from around the origins of the clade were entirely soft-bodied. It follows from this that some of the most important fossil vertebrates, in terms of their broader evolutionary and phylogenetic significance, are specimens that preserve the remains of non-biomineralized tissues; examples of exceptional preservation. Unfortunately, many of these fossils are also among the most controversial, with considerable disagreement concerning the homologies of the anatomical characters preserved, leading to equal uncertainty and debate over their correct phylogenetic placement. Much of this disagreement is unnecessary and emerges from failure to articulate or consider fully all the basic elements of fossil interpretation. Topological relationships – similarities in the spatial juxtaposition of body parts - are crucial in establishing structural correspondence and putative homology between body parts in two or more organisms, but in fossils lacking well-preserved skeletal landmarks (i.e. non-biomineralized taxa) topological data are sometimes equivocal or unobtainable. In such cases other criteria, normally subordinate to topology, assume greater importance. These include the intrinsic properties of body parts, such as compositional or microstructural evidence. Understanding how the processes of decay and preservation influence compositional and microstructural evidence is obviously critical in this context. We show how experimental decay combined with high magnification imaging (optical and SEM) of fossil and extant remains provide important constraints on the homology of non-skeletal characters in early vertebrates.

New specimens of Symmoriidae sharks from the Carboniferous limestone of the Derbyshire Peak District

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The history of dental and fin-spine based taxonomy has left fossil shark systematics rife with synonymies, inadequate diagnostic descriptions, incertae sedis and 'bucket' taxa. In few families is this more obvious than the Symmoriidae, a family of small Palaeozoic sharks found across the Northern Hemisphere (US, UK). Here we describe new material from two horizons in one Derbyshire locality; absolute ages of the dark grey limestone horizons are unknown but borehole data indicates a separation of 26 metres of limestone. This implies a substantial temporal separation of the two horizons. *Stethacanthus altonensis* has previously only been recorded from the Bear Gulch locality in Montana and is represented in the upper horizon of the Derbyshire locality by cranial and dental material including a neurocranium and associated palatoquadrate and teeth, an indistinctly preserved jaw with teeth, distal pectoral fin radials and, probably, proximal pelvic fin elements. *Akmonistion zangerli*, known previously from the Bearsden deposits of Scotland, is now represented in the Derbyshire lower horizon by a scapulacoracoid and

Meckelian cartilage. The restricted and unique nature of skeletal material described here offer a palaeobiological snapshot of Symmoriidae evolution; however, further research is needed in order to determine whether the faunal composition of the two horizons indicates competitive exclusion or taxonomic turnover.

Can we reconstruct phylogenetic relationships using the vertebrate fossil record? Differences between hard and soft data

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Fossils play a pivotal and unique role for the reconstruction of historic evolutionary events and their timing. Their utility in this context is entirely dependent on our ability to accurately place extinct taxa in phylogenetic frameworks. Fossils are, however, notoriously incomplete and the information they contain has been subject to fundamental taphonomic filters, largely leaving only hard anatomy like bones and teeth. Do the filtered data that the fossil record provides allow us to accurately reconstruct phylogenetic relationships, and subsequently test evolutionary hypotheses? To investigate this issue, 75 published cladistic data matrices for a diverse range of extant vertebrate clades were subjected to partition tests based on tree length and tree topology. Significant differences were found between the hard, biomineralized characters and soft, less-fossilizable characters in several datasets. These differences potentially undermine our confidence in fossil phylogenies. Furthermore, significant results are often clustered in particular clades (e.g., acanthopterygian fish, frogs) indicating that poor palaeontological fidelity seems to be an inherent property of certain clades. Only by applying these tests and making this distinction is it possible to identify which areas of the fossil record we can have confidence in and which must be interpreted with greater caution.

Cranial form and function in the largest ever marsupial, *Diprotodon optatum*: A comparative finite element analysis

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The extinct *Diprotodon optatum* was the largest ever marsupial. Despite its large size, the skull of *Diprotodon* is remarkably fragile, composed of thin cranial bone and extensive endocranial sinuses that encase a small brain. The frontal sinuses in *Diprotodon* are especially large and divided into a series of chambers by delicate bony struts. This cranial structure is unlike any seen in other extinct or extant species, and therefore the function of such a structure is not obvious. In this study a functional analysis of the skull was undertaken to assess its mechanical performance during biting. To identify areas of high and low stress, a finite element analysis (FEA) was performed on a three-dimensional model of the skull. In addition, comparisons were undertaken with other marsupials, including the common wombat (*Vombatus ursinus*) and koala (*Phascolarctos cinereus*), which do not have extensive endocranial sinuses. The results indicate that those species without extensive sinuses were less able to dissipate stress over the cranium. However, *V. ursinus* could withstand higher stress than both *P. cinereus* and *Diprotodon*. Further examination of the cranial structure and manipulations to the 3D model will likely provide additional insights concerning distribution and tolerance of stress, efficiency of skull structure, function of extensive frontal sinuses and the behaviour and ecology of *Diprotodon*.

The End-Devonian Mass Extinction, Romer's Gap, and the Lilliput Effect

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A mass extinction event at the end of the Devonian has been associated with a faunal turnover affecting most vertebrate groups. However, the succeeding 20 million years are marked by a dearth of fossils – not only of vertebrates, but of invertebrates. This fossil-poor interval has been named Romer's Gap and several ideas have been put forward to explain it. One possibility, the Lilliput Effect, has been observed for both vertebrates and invertebrates following mass extinctions, such as that at the Permo-Triassic boundary. The effect shows that many larger forms were wiped out, and that for the succeeding several million years, the remaining fauna was composed of smaller individuals and species than before the extinction event. A similar phenomenon may account for the lack of finds from Romer's Gap. Our recent discovery of Tournaisian vertebrates in the Ballagan Formation of the Scottish Borders corroborates the Lilliput Effect. Tetrapod, rhizodont, lungfish and Gyraacanthus elements from the lowest parts of the sequence so far, are all of small size for their groups. Tetrapod specimens recovered most recently include an array of tiny phalanges, ribs, gastralia and skull bones from the lowest sampled horizon (VI palynozone) at Burnmouth, and a small lower jaw showing primitive characters from a new site in Northumberland. At about 300 m above the lowest Burnmouth sample (mid-upper CM palynozone) large tetrapods, rhizodonts, lungfish and Gyraacanthus had already appeared. We anticipate further finds that will provide a time scale for their re-radiation.

Comparative cranial osteology and feeding mechanics of two Late Jurassic macrophagous metriorhynchids from Europe

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Metriorhynchidae was a peculiar and long-lived group of marine Mesozoic crocodylomorphs. We have reassessed the systematics of two contemporaneous species from the Late Jurassic of Europe, *Dakosaurus maximus* and *Plesiosuchus manselii*. *Dakosaurus maximus* had macroziphodont dentition, tightly fitting tooth-to-tooth occlusion and extensive macrowear on the mesial and distal margins. Under SEM, the macrowear surfaces have parallel apicobasal striations, which in extant mammals reflect tooth-tooth contact. *Plesiosuchus manselii* is distinct in having: non-amblygnathous rostrum; long mandibular symphysis; microziphodont tooth serrations; tooth crown apices that lack spalled surfaces or breaks, and no evidence for occlusal wear facets. The sympatry of *Dakosaurus* and *Plesiosuchus* is similar to North Atlantic killer-whales, which have one larger 'type' that lacks tooth-crown breakage being sympatric with a smaller 'type' that has extensive crown breakage. Assuming this morphofunctional complex is indicative of diet, then *Plesiosuchus* would be a specialist feeding on other marine reptiles while *Dakosaurus* would be a generalist and possible suction-feeder. This hypothesis is supported by *Plesiosuchus* having a very large optimum gape (gape at which multiple teeth come into contact with a prey item), while *D. maximus* possesses craniomandibular characteristics observed in suction-feeding odontocetes (toothed whales): shortened tooth-row, amblygnathous rostrum and a very short mandibular symphysis. We hypothesise trophic specialisation enabled these two large-bodied species to coexist in the same ecosystem. Phylogenetic analysis finds *D. maximus* as the sister taxon to be the South American *D. andiniensis*, and *P. manselii* is in a polytomy at the base of the Geosaurini (the subclade of macrophagous metriorhynchids).

Bone histology and bone compactness of fossil and recent xenarthran long bones

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Xenarthrans include anteaters, sloths and armadillos, and also a wide array of fossil forms. Their ecomorphological diversity and physiological specializations such as low metabolic rate make the first broad-scale palaeohistological study of this group worthwhile. Previously, osteoderm histology was shown to provide some phylogenetic and functional signal in xenarthrans. In this study, we focus on the histology of fossil and recent long bones. Thin sections were analyzed qualitatively and quantitatively by means of bone compactness profiles.

Dense Haversian tissue made up of several generations of secondary osteons was detected. In some samples, only up to three potential growth marks were identified. A similar structure of highly remodeled bone tissue was identified in long bones of extant sloths. Extant armadillos and anteaters, on the other hand, showed a lower degree of organization. Primary reticular bone tissue was very common, but some areas with only longitudinal vessels occurred.

Bone compactness of humeri and femora were correlated, with generally higher values for humeri. Within-group variation in bone compactness was high and no clear pattern coupled with locomotion could be detected. In general, values were highest in anteaters for both humeral and femoral bone compactness. Additionally, femoral bone compactness was higher in anteaters and sloths than in cingulates. Thus, compactness of xenarthran long bones could potentially provide some phylogenetic signal.

A new bernissartid crocodyliform from the Barremian Wessex Formation (Wealden Group) of the Isle of Wight, southern England

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A substantially complete and well preserved skull of a small crocodyliform was recently found on the foreshore near the village of Yaverland on the south-east coast of the Isle of Wight, southern England. The specimen comprises two parts found by different collectors and in a remarkable stroke of serendipity the gracile rostral section, which has suffered little post-exhumation abrasion, was recovered some three months after the posterior part. Both are now in the collections of the Isle of Wight County Museum Service. The locality, mode of preservation and associated matrix confirm that the skull is derived from one of the plant debris beds of the Lower Cretaceous Wessex Formation (Barremian, Wealden Group) exposed in low cliffs and occasionally on the foreshore in the immediate vicinity. The dentition, unique among crocodyliforms, serves to confirm that the specimen is referable to the, until now, monotypic family Bernissartidae Dollo, 1883. Autapomorphies, including the disposition of cranial sutures demonstrate that the Isle of Wight skull cannot be referred to *Bernissartia fagesii* Dollo, 1883, known from contemporaneous strata at the type locality, Bernissart, Belgium, and possibly Galve, Spain. Furthermore, placement of the secondary choana suggests that the specimen should be referred to a new genus and species rather than a new species of *Bernissartia*. Uniquely among neosuchian crocodyliforms, the secondary choana is bounded entirely by the pterygoids, although occupying an extreme anterior position within them.

Re-evaluating “*Apatosaurus*” *minimus*, a bizarre Morrison Formation sauropod with diplodocoid and macronarian features

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American Museum of Natural History 675 is a sauropod specimen consisting of a sacrum with fused ilia, two ischia and a partial pubis. It was initially described as belonging to *Apatosaurus*, and subsequently given its own species, *Apatosaurus minimus*. However, it is universally recognised that this assignment was incorrect: the specimen differs from *Apatosaurus* in many respects including proportional width of the sacrum, relative lowness of the neural spines, apparent absence of pneumatic foramina in the sacral centra, low and broadly flared ilia, and less expanded distal ends of ischium and pubis. Numerous other details preclude referral to other well-known Morrison sauropods.

The specimen shows a strange mix of diplodocoid characters (the tall and elaborately laminated neural spines), macronarian characters (the breadth of sacrum and flaring ilia), and characters unique to it (e.g. the ilium remains vertical as it projects laterally, and has a distinctive horizontal ridge above the pubic articulation).

We attempted to determine its affinities by phylogenetic analysis. In a diplodocoid-focussed analysis, “*Apatosaurus*” *minimus* was scored for 22 of 189 characters (12%), yielding 3 most parsimonious trees differing only in the arrangement of diplodocines. In all trees, “*Apatosaurus*” *minimus* was the most basal diplodocoid. However, in a more general sauropod analysis, scoring for 37 of 331 characters (11%) yielded 86 most parsimonious trees, of which 74 placed “*Apatosaurus*” *minimus* as a very derived titanosaur, sister to *Saltasaurus*. These conflicting results underline the paradoxical nature of the specimen. Whether it belongs to Diplodocoidea or Macronaria, it has features convergent with the other clade.

Justifications for combining data partitions in phylogenetics

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In phylogenetics, researchers aim to reconstruct evolutionary trees using all relevant forms of data. This may simply involve the combination of cranial and postcranial characters in a purely palaeontological analysis or, as is becoming increasingly common, the combination of large numbers of genetic loci with a morphological dataset. This data combination is often performed despite apparent disagreement between the topologies produced by each data partition in isolation. In such analyses the underlying assumption is that signal common to the majority of partitions should dominate the combined topology at the expense of any signal idiosyncratic to an isolated partition, theoretically resulting in a topology that more closely reflects the true course of evolution. A number of metrics, including hidden branch support (HBS), have been used to demonstrate unexpectedly high levels of support for such combined topologies. Here, we use artificial and real datasets to assess when HBS reflects synergy across data partitions, as opposed to data set conflict. We have found that high levels of hidden support do not necessarily justify data combination, but they do provide a valuable tool for exploring the interactions of such disparate datasets. Through careful application and interpretation of such metrics, morphologists can gain a better insight into the contribution of their characters to a phylogenetic hypothesis based on as large a dataset as possible. Ultimately

such an understanding should serve to promote the inclusion of morphological data in the ever expanding molecular datasets, ensuring that the fossil record informs the systematic hypotheses of the future.

Lazarus shark taxa in the Triassic of Australia

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Early Triassic (~250–235 Mya) xenacanthiform sharks first described in 1908 by Arthur Smith Woodward from the Wianamatta Group of the Sydney Basin, New South Wales, are being restudied based on new specimens including from older records in the Narrabeen Group and elsewhere in eastern Australia. Type and new material are known from complete specimens and isolated teeth and dorsal spines. Although earlier xenacanthids are known from the Lower Carboniferous in Queensland, there are no known Australian taxa in the later Palaeozoic but clearly they survived the P/T extinction somewhere. Hints exist in the earliest Triassic in the Arcadia Formation, central Queensland and the Knocklofty Formation of Tasmania. This part of Pangaea might have been a refugia. The younger "*Xenacanthus*" *parvidens* is known from large, ca 2-m specimens. This taxon was reassigned to a new genus, *Mooreodontus* based on similarity of teeth to those from the Late Triassic of Britain, Germany and western USA. This study looks at teeth from Australia in more detail and makes comparison with material from elsewhere in Gondwana. Some 5 new sites around Sydney have yielded specimens, which are not easily extracted from the fresh dark grey to black iron-rich shale. Apart from xenacanthids, there are rare hybodont sharks not yet studied, amphibians, several bony fish taxa, with insects and bivalves indicative of a lacustrine environment. The fish apparently died in drying-up ponds and/or because of fish-kill events; there is new evidence of predation by xenacanthids ingesting other fish. The type material from St Peters brick pit (some of it in the Natural History Museum, London), and that found from Somersby clay pit in 1987 exhibit sexual dimorphism; details of claspers suggest that there is more than one taxon. Only one (lost) shark egg case specimen recorded in 1912 is known.

A short tale: Darwinopterus, ontogeny and pterosaur evolution

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The discovery of *Darwinopterus*, a 'long-tailed' basal monofenestratan pterosaur from the Middle-Upper Jurassic of northeast China, provided the first detailed insights into a major evolutionary event: the origin of 'short-tailed' pterodactyloid pterosaurs. Other intermediate forms that might throw further light on the transition from basal pterosaurs to pterodactyloids have yet to be found but, thanks to new specimens of *Darwinopterus*, ontogenetic patterns can now be used to tackle this problem. We have compiled a near complete growth series for *Darwinopterus*, ranging from an extremely young individual, through juveniles, to osteologically and sexually mature adults. This series yields new insights into the origin of key pterodactyloid characters such as the short tail. In the youngest known individual of *Darwinopterus* the tail consists of just 15 caudals and is shorter than the dorsal+sacral vertebral series (DSV). Older juveniles have the full complement of 30 vertebrae and the tail reaches maximum length (>3 x DSV) and complexity in adults. The short, simple tail present in the youngest individual of *Darwinopterus* is identical to that found in pterodactyloids. We postulate that the condition in pterodactyloids was achieved through paedomorphosis, a heterochronic process involving a relatively sharp deceleration in the rate of growth and development of the tail compared to the rest of the skeleton. If true, then the way in which this complex, multi-component anatomical module was modified identifies heterochrony as part of the suite of mechanisms that generated the seemingly modular pattern of evolution that led to the Pterodactyloidea.

How long is a piece of Strix? Methods in measuring and measuring the measurers

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Measuring features of preserved specimens provides a simple method of making quantitative morphological comparisons. Such measurements are the mainstay of traditional morphometric techniques and form the basis of a great deal of research. With advances in information technology, analyses have become capable of dealing with large quantities of data, enabling the investigation of composite datasets compiled from literature and collaborating researchers. However, these meta-analyses are often conducted without acknowledgement of caveats pertaining to data consistency, in particular the amount of error due to variation associated with data contributed from multiple sources.

Here we present the results of an experiment to quantify intra- and interobserver variation in anatomical measurements that was conducted using a sample of 51 anatomists at the 56th Symposium of Vertebrate Palaeontology and Comparative Anatomy, Dublin, 2008. Surprisingly, significant interobserver variation was identified, with a difference of as much as 14% of the mean specimen length being reported. Illustrated instructions were not found to reduce the amount of variation reported, but the scale and complexity of the elements being measured was found to influence variation, with both larger and more complex structures increasing the variation. A bootstrap analysis indicated that disparity in measurement increases logarithmically with the number of observers. Our findings raise concerns about the introduction of noise and potential bias that should be taken into account when analysing composite datasets for meta-analyses.

The size of the avian cerebellar flocculus fossa cannot be used to predict flying ability in extinct birds

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The Principle of Proper Mass predicts that the relative importance of sensory modalities in a particular taxon will be reflected by the size of brain regions engaged in processing those stimuli. Extinct animal behaviour has long been inferred on this basis from qualitative assessments of brain region size in endocasts. For instance, flight capability in pterosaurs and early birds has been inferred from the relative size of the cerebellar flocculus, which in life protrudes from the lateral surface of the cerebellum. The flocculus integrates sensory information about head rotation and translation in order to stabilise visual gaze via the vestibulo-ocular reflex (VOR). The VOR is more important for highly manoeuvrable flying species, so the flocculus should be relatively larger in those than in less manoeuvrable fliers and flightless birds. However, this assumption has never been tested empirically. Here, we used micro-CT analysis of the skulls of 60 extant bird species to reconstruct 'virtual' endocasts. The volumes of the flocculus fossa and brain cavity as a whole were measured and these values correlated with indices of flying behaviour. No significant relationship was found between flocculus fossa size and flight behaviour, a result likely to be due to variable development of vascular structures within the floccular fossa. Our findings demonstrate THAT the relative size of the flocculus on endocasts is unreliable for use in inferring locomotor behaviour in extinct birds. Furthermore, the large flocculae of bird-like theropods cannot be used as evidence FOR THE derivation of these taxa from an avialan ancestor.

The evolution and development of skeletal pneumaticity: Exceptions to the epithelial hypothesis suggest other levels of control

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According to Witmer's epithelial hypothesis (EH), pneumatic diverticula resorb bone wherever they can, bone grows in response to biomechanical stress, and the morphology of a pneumatic bone represents an optimisation between these opposing forces. EH predicts that bone cannot persist adjacent to a diverticulum unless it is maintained by loading. However, examples of incomplete pneumatization suggest three categories of exceptions to EH:

Evolutionary—In basal sauropodomorphs postcranial pneumaticity is limited to scattered vertebral fossae. Fossae are evolutionarily antecedent to more invasive forms of pneumaticity, so EH may describe the behaviour of derived pneumatic systems but not the early evolutionary stages in which the morphogenetic "rules" are still being worked out.

Anatomical—Scattered fossae in the tails of *Apatosaurus* and *Giraffatitan* are puzzling, because the presacral vertebrae are highly pneumatic, without obvious reservoirs of unresorbed bone. It is as if, upon expanding into a new body region, the diverticula had to re-evolve the ability to pneumatize bone. Furthermore, in basal saurischians postcranial pneumaticity is less invasive than cranial pneumaticity. So diverticula may behave differently in different body regions of the same animal.

Ontogenetic—Finally, even in derived pneumatic systems such as mammalian cranial sinuses and bird vertebrae, large volumes of unpneumatized bone may persist next to otherwise invasive diverticula. Some ornithologists have suggested an ontogenetic window for pneumatization, an idea in need of testing.

Numerous observations from medicine, comparative anatomy, and palaeontology are consistent with EH, so it remains a useful model for pneumatization apart from these confounding factors.

SVPCA Posters

A reappraisal of the aberrant pterodactyloid *Istiodactylus latidens* from the Wessex Formation, Isle of Wight, Southern England

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University of Portsmouth

Istiodactylus latidens (sail finger - broad tooth) is an aberrant ornithocheiroid pterosaur from the Wealden Group (Barremian-Aptian, Lower Cretaceous) of the Isle of Wight, southern England. Formerly known as *Ornithodesmus latidens*, it was placed in a new genus, *Istiodactylus* when the type specimen of *Ornithodesmus* was shown to be dinosaurian.

The holotype of *Istiodactylus latidens* (NHMUK PV R.176) was discovered by amateur palaeontologist, Reverend William D. Fox, sometime in the 1800s, but certainly before his death in 1881, and was sold to the NHM in 1882. Although named by Seeley, the holotype was not described in any detail until Reginald Walter Hooley's publication of 1913 where, along with an additional two topotypes, it was covered in some considerable detail. Since then, istiodactylid-like pterosaurs have been discovered in China and possibly the Lebanon. (An istiodactylid from Canada is most likely non-pterosaurian). More recently, it has been recognised that *Istiodactylus* and allies are an unusual group of pterosaurs in that the rostrum and lingually compressed, triangular teeth differ significantly from all other ornithocheiroid pterosaurs. Thus, the family *Istiodactylidae* has been erected for their reception.

It is the aim of this project to re-evaluate and describe the osteology of *Istiodactylus* and attempt to determine aspects of the animal's palaeoautecology and evolutionary relationships using modern palaeontological techniques. All specimens referred to *I. latidens* are preserved in 3D, with much of the skull known and some of the bone surfaces bearing well-defined muscle scars, all of which provide an opportunity to investigate the biomechanics of this taxon.

Although *Istiodactylus* has been included in a number of important cladistic studies of the Pterosauria as a whole, all of these analyses appear to be based largely on data derived from older studies. Recently Witton performed a cladistic analysis of putative istiodactylids, finding many to lie outside the clade. A new, more inclusive specimen based analysis is required to determine the integrity and scope of *Istiodactylidae*.

Fossil mammals, phylogenies and climate: the effects of phylogenetic relatedness on range sizes and replacement patterns in changing environments

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Recent studies have indicated that relatedness, speciation rates, and dietary specialisation have differing influences on evolutionary dynamics within different Cenozoic mammal orders and families. Additionally, the finding that Cenozoic mammals have predictable (directional) range sizes has been called into question recently. The NOW (New and Old Worlds) database of fossil mammals contains extensive information on Cenozoic (65 Ma–recent) land mammal taxa and localities. A key strength of the NOW database is that, in addition to the locality-taxon data, the taxa are recorded with their eco-morphological properties. However, the lack of a comprehensive, large-scale phylogenetic framework has prevented quantifying the importance of relatedness of taxa in the observed evolutionary patterns in past NOW related studies. To address this problem, we are constructing supertrees, using both extinct and extant taxa, for a number of major mammalian clades, starting with the orders Carnivora and Proboscidea. These novel supertree phylogenies, NOW data, Cenozoic climate/environmental proxies, existing and new phylogenetic comparative and range-overlap methods, are used to explore several macro-evolutionary questions relating to range sizes, occupancy, replacement and co-occurrence patterns of mammals. Initial results with Eurasian localities and taxa indicate that while body size is heritable, range size is neither heritable nor does it correlate with bodysize. However, there is, as expected, a correlation between taxon duration and range size, but whether this is due to sampling effects has not yet been determined. The importance of relatedness in taxon replacement varies among clades and between time intervals.

New chondrichthyan-like scales from the Lower Silurian of Mongolia

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A new chondrichthyan-like scale based genus is identified on the basis of micro-remains from the shallow marine Llandovery-Wenlock Chargat Formation of NW Mongolia. This new taxon adds to the diverse gnathostome fauna already known from the Chargat, including acanthodians, mongolepids, and two yet to be described *Elegestolepis* species.

The morphology of the new scale taxon varies between ovate, lanceolate and extremely elongate, with recorded antero-posterior size range of 0.4-1.4 mm. The polyodontode crowns are composed of three strongly ornamented principle odontodes sutured posteriorly to gracile, cylindrical secondary odontodes. Hard tissue preservation of sectioned specimens has proven sufficient to detect odontocyte cell lacunae with polarized tubules ramifying inside distal portions of odontodes, while the thin scale bases do not exhibit significant histological detail.

A notable characteristic of the studied material is the extremely complex nature of the internal canal system revealed by volume renderings of micro-CT data. The primary odontodes possess dendritic pulp cavities formed from horizontal and vertical canals that give rise to numerous shorter branches along their course. Secondary odontodes contain pulps of simpler architecture connected to neck-type canals exposed at the posterior surface of the base.

The data presented suggest greater variation in scale morphogenesis, histology, and vascularization than previously understood in gnathostome groups close to the chondrichthyan stem, warranting a more integrated approach to studying these skeletal elements for systematic purposes.

A 3D reconstruction of the skull of the sauropod dinosaur *Camarasaurus lentus*

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The sauropods constituted one of the most important groups of megaherbivores during the Mesozoic, and have a rich and diverse fossil record. Despite this, the small and fragile nature of the sauropod skull means that cranial material is rare and often fragmentary. In consequence the functional morphology and trends in evolution of the skull of sauropods are poorly known. An exception to this general paucity of cranial material is the genus *Camarasaurus* from the late Jurassic Morrison Formation of North America, which is known from multiple specimens including skulls. CT scanning of a skull of a juvenile *C. lentus* allowed the production of a 3D model of the skull, with reconstruction of missing and deformed features. This permits inspection of anatomical information that is difficult to observe in specimen owing to preparatory difficulties, notably the dorsal and lateral aspects of the palate, and also of internal features such as the replacement teeth. This skull is to be subjected to finite-element modelling, along with those of other exemplar taxa as part of a comparative study to address functional hypotheses associated with skull performance. These results will form the core of a larger study into the mechanics and evolution of the sauropod skull.

New details about the Ordovician jawless fish *Sacabambaspis jannvieri*

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Sacabambaspis jannvieri is the oldest known articulated vertebrate possessing an extensive biomineralized dermal skeleton. This taxon has been collected from the Middle-Upper Ordovician deposits from Bolivia, Australia, Argentina and Oman. Its morphology is very peculiar, with a mix of both primitive and derived characters. For that reason, its phylogenetic position still remains debated. Recently, new studies have revealed or reviewed some details of the anatomy of *Sacabambaspis*. Here, we present some of these new findings, and we provide an up to date reconstruction of the anatomy of *Sacabambaspis*. Previous interpretations suggested that the anterior end of the ventral shield is formed by two oral plates, which are composed of several series of small dermal units. However, we have observed in a newly studied specimen that the series are arranged differently. This suggests that the series may have been flexible, at least in their anterior end, and may actually represent kind of rays somewhat similar (not homologous) to lepidotrichia. The position of gill openings, still debated, seems to be located between the branchial plates and the supramarginal plates rather than between each branchial plates.

We also show that the paired dorsal foramina, previously interpreted as pineal and parapineal foramen, may be paired endolymphatic foramina. An independent pineal plate, as in osteostracans, may have occupied the rostral groove, which separates the dorsal shield and the rostral plate. In this case, the depression located in the midline of the rostral groove may have been a pineal foramen.

The palaeontology and sedimentology of the Downton Bone Bed

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As a component of this current research a section from the upper Silurian (Ludlow series) of the Welsh borderland is being documented. The locality contains a previously, very poorly documented bone bed. Previous studies of analogous bone beds have yielded fossil remains of jawless fish and early jawed vertebrates in addition to early plants and some of the first land animals (Arthropoda).

This research is part of IGCP 591 entitled early to middle Palaeozoic revolution.

In order to process large amounts of the bone bed to extract the fossil content a sample was sent to a Swiss organization (SEFRAG) to see if a new technique using high voltage electric pulses could fragment the rock so that the microfossils can be extracted quickly and easily as an alternative to the time-consuming methods that will be used otherwise. Once processed, scanning electron and light microscopy will be used to identify the fossils. The sedimentology will be studied by using hand specimens and thin sections.

The residue that has been picked so far contains a good volume of the thelodont *Paralagonia ludlowiensis* as well as the remains of other early fish although their affinities are yet to be confirmed. Conodonts have been recovered but they are rare in this deposit, more common is the remains of the brachiopod *Tunisiglossa?* cornea.

Progress so far has involved curating the lithological specimens, a lithostratigraphical review, initial processing, lithological descriptions of the bone bed and its component horizons, and fieldwork to collect more samples, place the Downton Bone Bed in a stratigraphical context and determine and its lateral extent.

Evolution and development of a morphological innovation: The pufferfish beak (Tetraodontiformes; Teleostei)

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The Gymnodontes (Tetraodontidae, Diodontidae, Triodontidae, Molidae) are unusual among Tetraodontiformes (pufferfish relatives) in having their jaw dentition modified into a beak-like structure. Other Tetraodontiformes (Triacanthodidae, Triacanthidae, Ostraciidae, Balistidae, Monacanthidae) have separate teeth along the jaw margins. Despite these divergent dentitions, the Gymnodontes illustrate the developmental transition from separate teeth along the jaw to continuous growth dentine bands within the jaw. In *Monotretes* (Tetraodontidae), the beak develops from an initial dentition of several individual teeth. These are lost except for four teeth, one in each jaw quadrant, at the symphysis (parasymphysis). These produce continuously growing dentine tissue, forming successive jaw-length bands in the bone below, each longer than the previous as the jaw grows. Beak development involves loss of the initial teeth via wear, loss of tooth resorption and suppression of successor teeth, continuous dentine growth from the four remaining tooth sites, and a topographical shift of dental structures from the jaw surface into cavities deep within the jaw. Nomarsky optics, Micro-CT and OPT (Optical Projection Tomography) provide developmental details of evolutionary changes in the dentition of other families in the gymnodont clade. This includes separate tooth-like structures of *Triodon* (Triodontidae, including fossil taxa), to the more block-like dentine structures in *Diodon* (Diodontidae), to continuous dentine bands in *Monotretes*. Although this beak-like dentition of pufferfishes appears to be an innovative structure, it is derived, not from a new genetic blueprint, but by tinkering with a developmental plan of a generalized osteichthyan dentition itself retained over 400 million years.

The turtle genus *Hylaeochelys* from the Portland Stone Formation of Dorset

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A new specimen of the pancryptodire turtle genus *Hylaeochelys* has been collected from the Portland Stone Formation at Fancy Beach Quarry, Portland. It comprises an incomplete carapace, together with a mandible, a hyoplastron and a limb bone. The specimen will be described as a new species, based on character-states of the anterior carapace. A second specifically indeterminate specimen of *Hylaeochelys* was collected at Portland in the 19th century but not described and probably belongs to the same taxon. These finds represent the first Jurassic record, and hence the earliest occurrence, of the genus *Hylaeochelys*. The mandible is the first cranial material to be securely

associated with a *Hylaeobelys* carapace. It is clearly distinct from the mandible of *Portlandemys mcdowelli*, one of the skull-taxa from Portland, but resembles the mandible of *Plesiochelys (Stegochelys) planiceps*, the other skull taxon from Portland. This raises the possibility that *Hylaeobelys* is an immediate relative of *Plesiochelys*, and not just a gradistically similar pancryptodire.

A reappraisal of the taxonomic diversity of British Jurassic pterosaurs

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University of Portsmouth

Pterosaurs were one of the dominant tetrapod groups during the Mesozoic. They first appeared in the Late Triassic, and persisted for more than 145 million years. Initial diversity was thought to be low before rising in the Late Jurassic and peaking in the Early Cretaceous. Pterosaurs remained speciose until the Late Cretaceous. This view has been challenged by recent discoveries in China which suggest a higher Middle Jurassic diversity than previously realised. This and the demonstration that in the Jurassic diversity seems directly proportional to the number of sites calls for a reappraisal of Middle Jurassic pterosaur diversity. Numerically speaking, UK collections contain the largest number of pterosaur fossils of this age outside of China. This study reanalyses material stemming from the Middle Jurassic of the UK to establish what taxa are present, how the diversity compares to Chinese deposits and what can be established regarding pterosaur evolution at this time. A major focus of this work is the pterosaur assemblage from the Taynton Limestone Formation, previously thought to have been monogeneric. Preliminary analysis of the holotype of *Rhamphocephalus prestwichi* suggests it may not be pterosaurian. This combined with the absence of associated material makes re-identifying the material all the more significant. Work so far suggests possibly 5 families are present. Among these are some of the largest basal pterosaurs known, with wingspans estimated at up to 2m or more.

Preparation of the holotype of *Pliosaurus*

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The fossilized bones of pliosaurs (Reptilia: Sauropterygia) were first recovered from the Late Jurassic sediments of southern England in the 1820s, and the genus *Pliosaurus* was named by Sir Richard Owen in 1841. Despite the increasing wealth of material, the phylogenetic relationships within Pliosauroida remain unclear. All attempts to disentangle pliosaur phylogeny have been hampered by the lack of a modern description of *Pliosaurus brachydeirus* Owen 1841, the type species and the nominotypical genus of the family Pliosauridae and superfamily Pliosauroida. The holotype of *Pliosaurus* has never been fully described or figured, and this is a major obstacle for both the classification of pliosaurs and to understanding the relationships between plesiosaurians in general. Preparation work has begun on the skull of the historic holotype of *Pliosaurus brachydeirus* housed in the Oxford University Museum OUMNH J.9245A, B, J.9247-J.9301 and J.10453/1-7 (usually referenced as OUM J.9245B i.e. the lower jaw used by Owen to erect the taxon). The holotype consists of an incomplete cranium, mandible and post-cranial material, including ten cervical vertebrae, thirteen dorsal vertebrae, a caudal vertebra, a coracoid, the right femur, possibly a humerus and numerous fragments from neural arches, ribs and limb girdles. The specimen was partially prepared back in the 1830s and it is now hoped modern preparation techniques will clarify details of the skull and postcranial anatomy that are still obscured by sediment. This invaluable work will enable the first full description and interpretation of the *Pliosaurus* holotype, since its original and incomplete study by Owen in 1841.

Modelling the impact of phylogeny on interpretations of extinction in deep time

Laura Soul

University of Oxford

Palaeontologists and biologists have previously used different methods when analysing comparative datasets. This is problematic because it has meant that results from the two communities are not directly comparable. To achieve synthesis of results, palaeontological data must be analysed within a comparative framework that corrects for species non-independence. However, there are important differences between fossil phylogenies and phylogenies of extant taxa that must be considered before results are interpreted. Through simulating fossil phylogenies, I am investigating what these differences are, which ones are important, and whether we can correct for any biases that arise. Further to this, I have used simulation modelling to investigate whether taxonomy can be used as a reasonable substitute for the most recently available phylogenetic reconstructions when performing comparative analyses. Implementing results from these simulations, I am exploring patterns of phylogenetic clustering of extinction through time. Initial results suggest that misplacement of ancestral taxa as sister groups to their descendants in palaeontological trees impedes accurate recovery of phylogenetic signal in extinction.

Unravelling the dynamics behind the ecological radiations of Mesozoic crocodiles and their ancestors

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Following a major evolutionary bottleneck at the end-Triassic, crurotarsan archosaurs were reduced to a single lineage, the crocodylomorphs. Living crocodylians are morphologically and ecologically conservative but Mesozoic crocodylomorphs exhibited diverse morphologies, possibly representing considerable ecological diversity. However, no study has investigated major macroevolutionary trends within crurotarsans following the end-Triassic extinction and it is presumed they became negligible components of Jurassic and Cretaceous ecosystems. We explore the ecological diversity and trophic radiations of Mesozoic crurotarsans through a quantitative analysis of morphological and functional disparity in lower jaw elements. Results show morphological and functional disparity peaked during the Late Triassic followed by a congruent decline in the Early Jurassic. After this morphological disparity steadily increased and recovered by the Late Cretaceous but functional disparity plateaued, remaining remarkably stable through the Jurassic and Cretaceous. Underlying these patterns were contrasting dynamics of morphological and functional evolution during the trophic radiations of marine piscivorous thalattosuchians in the Jurassic and trophically diverse neosuchians and notosuchians in the Cretaceous. Crocodylomorphs were not stagnant components of Jurassic and Cretaceous ecosystems, they evolved an exceptional range of morphologies and functional profiles, recovering ecological roles occupied by Late Triassic crurotarsans. This study provides the first insights into patterns and processes associated with the radiation of this exceptional clade, while reiterating complex dynamics between form and function in the evolution of morphological systems.

Pterosaur tooth anatomy

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Pterosaur dentitions are highly diverse. Some basal forms possess distinctive heterodont dentitions, whereas the derived pterodactyloids have specialized homodont dentitions as a trend, but in a few cases heterodonty is observed (e.g. *Pterodaustro*). Despite this diversity, little interest has been taken in their teeth. With the exception of a brief study to determine the histological nature of the teeth of *Pterodaustro*, there are currently no publications reviewing the internal structure and composition of pterosaur teeth. In reaction to this gap in our understanding of pterosaur biology, several ornithomimid teeth from the Kem Kem beds (Morocco), Santana Formation (Brazil) and Crato Formation (Brazil) were sectioned and subjected to S.E.M analysis. During these studies the DDL (durable dental layer), a layer of apatite which spanned between the gingivium and enamelled crown was discovered. Subsequently, a *Rhamphorhynchus* tooth was studied in the same way as the aforementioned, after a *Campylognathoides* tooth which was sectioned in the late 19th Century yielded no results. The collective results of these studies include information on the enamel (its type, thickness and distribution), DDL, dentine and pulp cavity and provide a phylogenetic bracket.

A fresh look at azhdarchoid pterosaur interrelationships

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University of Portsmouth

The azhdarchoid pterosaurs are an important group of Cretaceous pterodactyloids comprised of the short-faced tapejarids, slender-jawed chaoyangopterids, sail-crested thalassodromids and (often) gigantic azhdarchids. Although the content of this clade remains relatively uncontroversial, a long-running disagreement exists over whether thalassodromids and chaoyangopterids are more closely related to tapejarids or azhdarchids. A reappraisal of azhdarchoid taxonomy suggests that some reported synapomorphies of azhdarchoid clades are deeply rooted within Pterodactyloidea (e.g. slender, vertical lacrimal process) or may oversimplify complex anatomies (e.g. cranial crest morphology). Moreover, existing schemes may be overlooking useful apomorphies of the skull and forelimbs (e.g. the morphology of the posterodorsal premaxillary bar). A cladistic analysis of pterodactyloids comprising 40 taxa (3 outgroup taxa, 14 purported azhdarchoid species) and 118 characters (8 new, 14 modified) was developed from existing analyses of pterosaur relationships and analysed in TNT to test these assertions. The resultant 6 MPTs support the formation of a clade comprising Chaoyangopteridae, Thalassodromidae and Azhdarchidae defined by elongate jaws and expanded frontoparietal regions with significantly depressed orbits. Neoazhdarchia, a previously identified clade comprising Azhdarchidae and Thalassodromidae, is united by the development of notaria and unique wing finger phalange proportions. Two newly described azhdarchoid taxa used in this study had not been subjected to cladistic analysis before. The purported early azhdarchoid *Auroazhdarcho primordius* is found to be a ctenochasmatid closely related to *Pterodactylus longicollum* and *Gnathosaurus*, while *Microtuban altivolans* is recovered as a sister taxon to all other azhdarchoid clades.

Delegates

Lu Allington-Jones Natural History Museum (*Conservation*)
Plamen Andreev University of Birmingham (*Earth Sciences*)
Robert Asher University of Cambridge (*Zoology*)
Paul Barrett Natural History Museum (*Palaeontology*)
Julien Benoit ISEM-UM2 (*Paleontology*)
Michael Benton University of Bristol (*School of Earth Sciences*)
David Didier Bermúdez-Rochas Universidad de Cantabria (*Didáctica de las Ciencias Experimentales*)
Martin Brazeau NCB Naturalis
Jen Bright University of Bristol (*Earth Sciences*)
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Richard Butler Ludwig Maximilian University of Munich (*GeoBio-Center*)
David Button University of Bristol (*Earth Sciences*)
Marco Castiello University of Milan
Robert Christian
Jennifer Clack University of Cambridge (*Zoology*)
John Clarke University of Oxford (*Earth Sciences*)
William Clemens University of California Berkeley (*Museum of Paleontology*)
Dorothy Clemens University of California Berkeley (*Museum of Paleontology*)
Michael Coates University of Chicago (*Organismal Biology & Anatomy*)
John Conway Ontograph Studios
Ian Corfe University of Helsinki (*Institute of Biotechnology*)
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