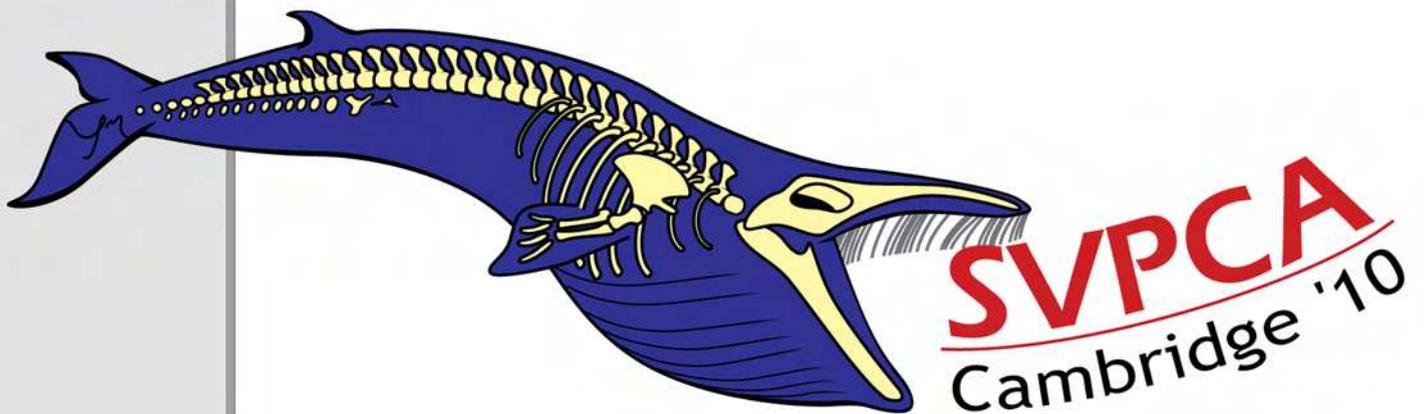


Symposium of Vertebrate Palaeontology and Comparative Anatomy

AND

Symposium of Palaeontological Preparation and Conservation

2010, University of Cambridge



Department of
Zoology



SVPCA 58, Cambridge 2010, Preface

Welcome to the 58th Symposium of Vertebrate Palaeontology and Comparative Anatomy, hosted by the University Museum of Zoology, Cambridge. We very much hope you find the meeting rewarding, and that you have time to enjoy the other attractions of the university, colleges, and city centre.

The meeting logo was designed by Julia Molnar¹ and depicts the finback whale (*Balaenoptera physalus*) on display above the Museum of Zoology.

Enjoy your time in Cambridge!

¹ Julia Molnar, Royal Veterinary College, jmolnar-at-rvc.ac.uk

SPPC/SVPCA 2010 Programme Overview

Tuesday 14th September: SPPC

Session 1, Chair: Matt Lowe

- 15.30-15.50** **Christian Baars**
Infacol – if it's good enough for babies, it's good enough for ammonites.
- 15.50-15.10** **Nigel R Larkin**
The joy of steel: How to master your awkward fossil in the field.
- 16.10-16.30** **Frank Osbaeck**
Mechanical and chemical preparation methods used on the lower Eocene cementstone concretions from the Mo-Clay of northern Denmark
- 19.00 onwards** **EVENING RECEPTION, ZOOLOGY MUSEUM**

Wednesday 15th September

- 9.10-9.20** **Welcome, notices for the day**

Session 1, Chair: Paul Barret

- 9.20-9.40** **Eric Buffetaut *et al.***
The Early Cretaceous vertebrate assemblage from the Napai Formation of Guangxi, southern China: a comparison with Thai assemblages
- 9.40-10.00** **Michael J Benton *et al.***
Recovery and expansion of marine vertebrate faunas in the Triassic of South China
- 10.00-10.20** **Susan E Evans and Magdalend Borsuk-Bialynicka**
The Early Triassic faunal assemblage of Czatkowice, Poland
- 10.20-10.40** **Sweetman, Steven C**
The first records of amphibians, lizards and maniraptoran dinosaurs from the Lower Cretaceous Hastings Group of south-east England
- 10.40-11.10** **COFFEE BREAK**

Session 2, Chair: Jenny Clack

- 11.10-11.30** **Tim Smithson and Stan Wood**
Eliminating Romer's Gap: new tetrapods from the basal Carboniferous of the Scottish Borders

- 11.30-11.50** **Per E Ahlberg *et al.***
A primitive Devonian tetrapod from the lower Famennian of south Timan, Russia
- 11.50-12.10** **Shin-ichi Fujiwara and John R Hutchinson**
Moment arm analysis of elbow flexor/extensor muscles in sprawling tetrapods
- 12.10-13.30** **LUNCH BREAK**

Session 3, Chair: Matt Friedman

- 13.30-13.50** **Philip S. L. Anderson and Emily J. Rayfield**
Functional morphology and disparity of the early gnathostome radiation
- 13.50-14.10** **Ben Davies *et al.***
An experimental investigation into the hydrodynamics and locomotion of the Palaeozoic jawless vertebrates *Poraspis*, *Errivaspis* and *Ateleaspis*
- 14.10-14.30** **Emma-Louise Nicholls**
Patterns in the palaeoecology of Cretaceous chondrichthyan faunas
- 14.30-14.50** **Stefanie Klug**
Dental morphologies and sexual dimorphism in stem-group neoselachians (Synchodontiformes): implications for taxonomic diversity
- 14.50-15.10** **AFTERNOON BREAK**

Session 4, Chair: Susan Evans

- 15.10-15.30** **Matt Friedman *et al.***
The evolution of giant suspension feeders: toward a comparative approach
- 15.30-15.50** **Neil Curtis *et al.***
Functional analysis of skull shape
- 15.50-16.10** **Marc E H Jones *et al.***
Cranial joints in *Sphenodon* and other Rhynchocephalia with implications for lepidosaur skull mechanics
- 16.10-16.30** **Andrew R Milner and Angela C Milner**
Ontogeny and phylogeny in procolophonids - Evidence from a new *Leptopleuronine* from the Middle Triassic Otter Sandstone of Sidmouth, Devon
- 16.30-16.50** **Yasuhisa Nakajima**
Evaluating the utility of limb bone internal structure as an indicator for aquatic adaptation of Testudines
- 19.00 Onwards** **RECEPTION, SEDGWICK MUSEUM**

Thursday 16th September

Session 1, Chair: Phil Cox

- 9.00-9.20** **Robert Asher and Richard Thompson**
Morphology and molecules in insectivoran-grade mammal phylogeny
- 9.20-9.40** **Katrina E Jones and David Weishampel**
Understanding conflicting topologies: The role of character complexes in tree incongruency
- 9.40-10.00** **Shoji Hayashi *et al.***
Bone histological variations of desmostylians (Mammalia, Tethytheria)
- 10.00-10.20** **Mette Elstrup Steeman**
Evolution of gulp-feeding in baleen whales
- 10.20-10.40** **Manja Voss**
New insights into the interrelationships of the *Halitherium*-species-complex
- 10.40-11.10** **COFFEE BREAK**

Session 2 ,Chair: Marc Jones

- 11.10-11.30** **Pam G Gill *et al.***
A functional investigation into the jaw joints of two of the earliest stem mammals; *Morganucodon watsoni* and *Kuehneotherium praecursoris*
- 11.30-11.50** **Andrew J Smith**
The taxonomic diversity of the stem mammal *Morganucodon* (Morganucodonta: Morganocodontidae) from late Triassic-Early Jurassic fissure deposits of Glamorganshire, Wales, UK
- 11.50-12.10** **Vera Weisbecker and Anjali Goswami**
Mammalian brain evolution: Marsupials vs. placentals
- 12.10-12.30** **Laura Soul *et al.***
A taxon-free model for brain size determination in Mammalia
- 12.30-13.30 LUNCH BREAK**

Session 3, Chair: Pam Gill

- 13.30-13.50** **Eva Bärmann and Marcelo R Sánchez-Villagra**
Suture closure as a paradigm to study late growth in Recent and fossil mammals: A case study with ectocranial patterns in Cetartiodactyla
- 13.50-14.10** **Jen Bright *et al.***
Mammalian skull construction and the importance of cranial sutures in biomechanical finite element analysis: a validation using the modern domestic pig
- 14.10-14.30** **Philip Cox *et al.***
Morphology of the jaw-closing muscles and the biomechanics of feeding in sciuriform, hystricomorph and myomorph rodents
- 14.30-14.50** **Lionel Hautier *et al.***
Changes in the direction of mastication and the remodeling of the masticatory apparatus during mammalian evolution: the case of the Issiadoromyinae (Rodentia).
- 14.50-15.10** **AFTERNOON BREAK**

Session 4 ,Chair: Vera Weisbecker

- 15.10-15.30** **Peter L Falkingham *et al.***
Difficulties in inferring limb kinematics from fossil tracks – internal track morphology as a function of substrate mechanics.
- 15.30-15.50** **Hutchinson, J R *et al.***
Three-dimensional whole-bone scaling in the limbs of terrestrial vertebrates
- 15.50-16.10** **Mark Evans and Roger B J Benson**
New plesiosaurs from the basal Lias Group of South West England
- 16.10-16.30** **Mark Purnell and Nia Roderick**
Tooth microtextural analysis and diet in pliosaurs
- 16:30-18:00 **POSTER SESSION.** All authors are asked to be available adjacent to their posters in the Zoology Elementary Lab (across from the Main Lecture Theatre). Please remove your posters by Friday 4pm!
- 19.00 Onwards** **RECEPTION, ZOOLOGY MUSEUM FOLLOWED BY AUCTION, ZOOLOGY MAIN LECTURE THEATRE**

Friday 17th September

9.10-9.20 **Announcements**

Session 1, Chair: Paul Upchurch

9.20-9.40 **Michael Pittman *et al.***
The evolution of the stiff theropod tail into a flexible aerodynamic surface.

9.40-10.00 **John Martin *et al.***
Neck posture in extant and extinct vertebrates I: Osteology and behavior

10.00-10.20 **Kent A Stevens and John Martin**
Neck posture in extant and extinct vertebrates II: Computational modeling of range of motion

10.20-10.40 **Koen Stein and Martin Sander**
Sauropodomorph long bone histology through time and ontogeny

10.40-11.10 **COFFEE BREAK**

Session 2, Chair John Hutchinson

11.10-11.30 **Michael P Taylor and Mathew J Wedel**
Why giraffes have such short necks

11.30-11.50 **Matthew J Wedel and Michael P Taylor**
Caudal pneumaticity and pneumatic hiatuses in the sauropod dinosaurs *Giraffatitan* and *Apatosaurus*

11.50-12.10 **Andreas Christian and Gordon Dzemski**
Evidence for high browsing in the sauropods *Brachiosaurus brancai* and *Euhelopus zdanskyi*

12.10-12.30 **Philip D Mannion and Paul Upchurch**
Where have all the sauropods gone? The mid-Cretaceous 'sauropod hiatus' and the impact of uneven sampling of the fossil record

12.30-13.30 **LUNCH BREAK**

Session 3, Chair: Angela Milner

13.30-13.50 **Susannah C R Maidment and Paul M Barrett**
Evolution of locomotor musculature in ornithischian dinosaurs

13.50-14.10 **David Norman**

- 14.10-14.30** Wealden Group iguanodontians: their history and taxonomy
Roger Benson *et al.*
Pneumaticity in theropods
- 14.30-14.50** **Stig Walsh**
Quantitative characterisation of avian brain morphology using X-ray
CT approaches
- 14.50-15.10** **AFTERNOON BREAK**

Session 4, Chair: Dave Norman

- 15.10-15.30** **Paul M Barrett *et al.***
The first spinosaurid (Dinosauria, Theropoda) from the Lower
Cretaceous of Australia: implications for Gondwanan
palaeobiogeography
- 15.30-15.50** **Colin Palmer**
Using engineering analysis to bracket the morphological
possibilities for pterosaur wing shape
- 15.50-16.10** **David M Unwin *et al.***
An adult–egg association and its implications for pterosaur
reproductive biology
- 16.10-16.30** **Donald M Henderson**
Quetzalcoatlus northropi as a secondarily flightless pterosaur
- 16.30** **Announcements/Closing Remarks**
- 19.00** **CONFERENCE ANNUAL DINNER**

Saturday 18th September

FIELD TRIPS

SPPC Talks

Infacol – if it's good enough for babies, it's good enough for ammonites.

Christian Baars

National Museum Wales, Department of Geology

A project to conserve, cast and repackage a collection of over 160 Jurassic ammonites from Dorset is currently being undertaken. The specimens are all cited and figured and include holotypes and paratypes. They had been previously consolidated with the acrylic resin Bedacryl, and some are embedded in plaster. The Bedacryl has become tacky with age and attracted dirt and dust. Pyrite is present in the rock and some ammonites are affected by pyrite decay. The specimens were cleaned, treated for pyrite decay if required, re-consolidated with Paraloid B72 and re-packaged. Due to the scientific importance of the collection, casts were made to ensure a record of the morphology should any further deterioration occur. Following re-consolidation, silicone moulds were made of the specimens. The intricate nature of the moulds made casting more difficult than originally anticipated. Jesmonite was used for the casts but it was difficult to avoid the formation of bubbles. After some experimentation it was found that adding some Infacol ("formulated to relieve wind, infant colic and griping pain") significantly reduced the number of bubbles in the casts.

The joy of steel: How to master your awkward fossil in the field.

Nigel R. Larkin

Natural History Conservation

Occasionally, fossils can be extremely big, very heavy, or horribly fragile. Sometimes they may present all three problems at once – the most problematic of which is fragile - and getting them from the field to the lab can be a challenging process. Polyurethane foam jackets are a quick but messy solution and should no longer be used on health and safety grounds. Plaster jacketing is a well known and very useful technique but on its own is not always up to the job. Splints are frequently added to plaster jackets, but often in an ad-hoc manner.

A very secure method is to bolt together a rigid cage of channelled galvanised steel around the specimen in the field and secure it sturdily to the plaster jacket. This gives rigidity in three dimensions, protects vulnerable elements and provides specific and secure places to attach cables or straps to a crane.

The channelled steel and appropriate nuts and bolts do not rust, can be cleaned and stored indefinitely and re-used almost endlessly. Most importantly, if assembled competently the structure will allow a very large, heavy and fragile specimen to be lifted and transported much more safely than would otherwise be the case.

Mechanical and chemical preparation methods used on the lower Eocene cementstone concretions from the Mo-Clay of northern Denmark

Frank Osbaeck

Museernes Bevaringscenter i Skive

For five years Museernes Bevaringscenter in Skive have worked on several rare specimens from the Mo-Clay Formation of Fur and Mors resembling the fauna of the London Clay Formation. Foremost an almost complete tarpon (115cm), one of the best preserved in the world, which was prepared combining acid and mechanical methods. To start with the specimen weighed a tonne. This specimen's matrix was in part extremely delicate, and would break down if water or acid was applied. The skull of the tarpon is 3D preserved and due to a fracture down the middle presents a fully prepared brain cavity. It went for the exhibit after 1 1/2 years of preparation. The new preparation of an old specimen of a two meter long leatherback turtle has yielded many new details as well as possible soft tissue structures. Lastly I will present two small turtles with exceptional preservation- the last one with ossified horn covering of the skeletal plates.

SPPC Poster

Preservation potential of elasmobranchs

Trine Sørensen

Department of Conservation, Museum of Southern Jutland, Fabriksvej 17-21, DK-6510 Gram, Denmark

Different parts of the elasmobranch skeleton are unevenly represented in the fossil record. Fossilization of different types of tissue depends on structure and chemistry of the tissue and of a number of taphonomic factors. A single vertebra and fragments of gill rakers of a shark, *Cetorhinus* sp., from the Late Miocene Gram Formation was examined for variations in mineral contents within the tissues and in the surrounding clay sediment. During preparation a systematic, visual description was performed and samples were taken for microscopy and XRD mineralogical analyses and for SEM/EDX and EMPA geochemical analyses. The vertebra and gill rakers are composed of apatite-minerals containing fluorine with resemblance to recent shark skeletons. Apatite in the sediment below the vertebra may in part be due to dissolution. Authigenic minerals such as siderite, calcite and Mg-calcite are present in both fossil and sediment in a pattern related to the vertebra. Pyrite is evenly distributed. Several parameters increase the preservation potential of the shark. These include the precipitation of carbonate-concretions around and within the vertebra, secondary calcification of the vertebra, the closely packed structure of the surface of the gill rakers, a calm sea, a high sedimentation rate and the right geochemical conditions.

SVPCA Talks

A primitive Devonian tetrapod from the lower Famennian of south Timan, Russia

Per E. Ahlberg¹, Pavel Beznosov², Ervins Luksevics³ and Jennifer A. Clack⁴

¹*Subdepartment of Evolution and Development, Department of Physiology and Developmental Biology, Uppsala University, Norbyvägen 18A, 752 36 Uppsala, Sweden*

²*Institute of Geology, Komi Scientific Centre, Ural Division of Russian Academy of Sciences, 54, Pervomayskaya St., 167982 Syktyvkar, Russia*

³*Department of Geology, University of Latvia, Rainis Boulevard 19, Riga LV-1586, Latvi*

⁴*University Museum of Zoology, Downing Street, Cambridge CB2 3EJ, UK*

The lower Famennian Sosnogorsk Formation outcropping along the Izhma River, Komi Republic, Russia, represents a coastal lagoon and contains a diverse vertebrate fauna including an undescribed tetrapod, first identified by A.O. Ivanov and now known from numerous bones collected during 2008 and 2009. In general it resembles previously known Famennian genera (excepting *Tulerpeton*). However, it has some surprisingly primitive features. Autapomorphies include a pterygoid dentition composed of two diverging rows of small teeth, and an angular orbit bounded anteriorly by a vertical buttress. Primitive features include a partly ornamented cleithrum and *Elginerpeton*-like (but less elongated) coronoids with an elaborate dentition. Most importantly, the skull table does not resemble those of known Devonian tetrapods but is remarkably similar to that of *Tiktaalik*; the braincase attachment suggests that a lateral commissure was present, implying that the hyomandibula had not yet been transformed into a stapes. No limb elements have been recovered, but the shoulder girdle is of tetrapod rather than elpistostegid type, suggesting that limbs were present. We tentatively place the new taxon on the internode between *Tiktaalik* and *Ventastega* as the most primitive tetrapod known from extensive remains.

Functional morphology and disparity of the early gnathostome radiation

Philip S. L. Anderson and Emily J. Rayfield

University of Bristol

Studies of ecological structure and diversity in extinct faunas have always been challenged by the inability to directly observe the functional interactions of fossil taxa. Superficial morphological analyses can give misleading results in terms of functional diversity patterns. An alternative approach is to use morphological metrics based on a paleobiomechanical paradigm. A series of biomechanically relevant metrics and discrete characters were collected from the lower jaws of Devonian gnathostome groups, including placoderms, acanthodians, and osteichthyans. This data set was analyzed using multivariate statistical methods to create a functionally-informed morphospace of early

gnathostome jaws. Disparity metrics were compared between major groups and across large-scale time slices, including across the Frasnian-Famennian boundary.

Functional morphological disparity reached a significant peak in the Early Devonian followed by stable disparity levels through the Middle and Late Devonian. Comparisons with turnover rates show that although there were significant taxonomic changes, the level of functional diversity among gnathostomes was relatively constant. The morphospace also indicates that placoderms maintained a high level of functional disparity relative to other clades up to the Famennian, calling into question the hypothesis that they were out-competed by osteichthyan groups.

Morphology and molecules in insectivoran-grade mammal phylogeny

Robert Asher and Richard Thompson

University of Cambridge

Morphological data have resolved such deep vertebrate nodes as synapsids and diapsids, marsupials and placentals, and most mammalian orders. In contrast, confidence in our understanding of mammalian inter-ordinal interrelationships has required the addition of molecular data, leading some to question the capacity of paleontologists to understand the ordinal affinities of some fossil taxa which generally lack molecular data. Here, we analyze a combined morphological-molecular dataset for insectivoran-grade mammals. We find that morphology contributes positively to clade support in a combined analysis, whether or not that clade is present in a tree derived from morphological data alone (a concept known as "hidden support"). We investigated hidden support among African insectivorans, and found that the addition of a morphological partition improves branch support for most nodes present in both the optimal MP and Bayesian topologies of a DNA-indel dataset, even though many clades are not present in the morphology-only analysis. Hence, for this dataset, we may be reasonably confident about the placement of fossil taxa for which no molecular data are available. Generalizations on the inadequacy of "morphology" for ordinal-level phylogeny reconstruction are unwarranted but should be investigated on a case-by-case basis.

Suture closure as a paradigm to study late growth in Recent and fossil mammals: A case study with ectocranial patterns in Cetartiodactyla

Eva V. Bärmann¹ and Marcelo R. Sánchez-Villagra

¹*Museum of Zoology, University of Cambridge, Downing St. CB2 3EJ, UK*

²*Paläontologisches Institut und Museum, Karl Schmid-Strasse 4, CH-8006 Zürich, Switzerland*

Sutures are the joints at which bones articulate through intervening fibrous connective tissue, serving as sites of bone expansion during growth. They obliterate postnatally in a species-specific sequence. We examined ectocranial suture closure across terrestrial cetartiodactyls using event-pairing in a phylogenetic framework to analyze the effect of size changes, modularity and phylogenetic signal. We recorded 30 sutures in 50 species of all major living clades and several fossil ones. Although differences exist among species, the overall shared sequence is highly conservative for the beginning sutures to obliterate, which involve the interparietal, exoccipital, and basioccipital, followed by those related to the skull base. This overall pattern is similar in other mammalian clades. The basal living groups, including pigs, camels and hippos, obliterate most of their ectocranial sutures, whereas the ruminants obliterate only a small portion of them. The latter is especially marked in bovids and cervids, with exception of *Megaloceros*. The interfrontal and frontal-parietal sutures obliterate in basal forms, but only in a few specimens of cervids, moschids, and bovids. Small species tend to obliterate less sutures than larger species. Intermaxillary and interpalatine sutures never obliterate in ruminants, but do so in camels, suids and hippopotamids.

The first spinosaurid (Dinosauria, Theropoda) from the Lower Cretaceous of Australia: implications for Gondwanan palaeobiogeography

Paul M. Barrett¹, Roger B. J. Benson², Thomas H. Rich³ and Patricia Vickers-Rich⁴

¹*Natural History Museum, London, UK*

²*University of Cambridge, Cambridge, UK*

³*Museum Victoria, Melbourne, Australia*

⁴*Monash University, Melbourne, Australia.*

A cervical vertebra from the Lower Cretaceous (Aptian–Albian) Eumeralla Formation of Victoria, southeastern Australia is the first spinosaurid dinosaur from eastern Gondwana. A previously reported Australian spinosauroid (cf. *Megaraptor*) represents a neovenatorid allosauroid. Referral to Spinosauridae is supported by one synapomorphy, a

fine lamina that internally divides the pneumatic foramen of the centrum, and a unique character combination. Discovery of an Early Cretaceous Australian spinosaurid significantly extends the geographic range of the clade and increases the diversity of the Otway Group theropod fauna (comprising a tyrannosauroid, oviraptorosaur, neovenatorid and possible ornithomimosaurian). Representatives from the same groups are known from coeval Laurasian sites, suggesting a longer interval for faunal exchange between Gondwana and Laurasia, and across Gondwana, than appreciated previously. For example, the hitherto unexpected presence of tyrannosauroids and oviraptorosaurs in Australia demonstrates that 'Laurasian' taxa were present in Gondwana and suggests that such groups had potentially cosmopolitan distributions. Theropod phylogenies predict the origins of major coelurosaurian clades in the Middle Jurassic, an inference supported by new discoveries. This East Gondwanan Early Cretaceous material implies that many theropod lineages were present in areas that are currently poorly sampled (e.g., Africa, India, Madagascar, Antarctica).

Pneumaticity in theropods

Roger Benson¹, Richard Butler², Matthew Carrano³ and Patrick O'Connor⁴

¹*University of Cambridge*

²*Bayerische Staatssammlung für Paläontologie und Geologie*

³*Smithsonian Institution*

⁴*University of Ohio*

Postcranial bones pneumatized by air-filled diverticulae of the respiratory tract are a 'characteristically avian' feature that evolved in non-avian predecessors, the theropod dinosaurs. The detailed distribution and evolution of skeletal pneumaticity is documented for the first time and the relationship between body size and pneumaticity is examined statistically. A 'common pattern', in which the cervical and anterior dorsal vertebrae are pneumatic, evolved early in theropod history and is conserved on the line leading to birds. Twelve other theropod lineages independently acquired more extensive skeletal pneumatization. Among basal theropods these gains occur only at large body sizes, suggesting a role in mass reduction at large size. However, among derived, bird-like theropods, extensive pneumatization evolved even at small body size, similar to those represented by extant birds. Pneumatization replaces heavy, metabolically expensive bone and marrow with air. This results in energy savings that may have been crucial to highly active dinosaurs with an avian-like physiology. Thus, decoupling of the relationship between body size and skeletal pneumatization in bird-like dinosaurs may indicate homeothermic endothermy. This is consistent with an ever-growing list of bird-like features shared by theropod dinosaurs.

Recovery and expansion of marine vertebrate faunas in the Triassic of South China

Michael J. Benton¹, Quiyue Zhang², Shixue Hu², Zhong-Qiang Chen³, Wen Wen², Jun Liu² and Changyong Zhou²

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²*Chengdu Institute of Geology and Mineral Resources (CIGMR), 2 Beisanduan, Yihuanlu, Chengdu 610081, Sichuan Province, China*

³*School of Earth & Environment, University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia*

The Triassic was a time of turmoil, as life recovered from the most devastating of all mass extinctions, the end-Permian event 252 million years ago. The Triassic marine rock succession of southwest China provides unique documentation of the recovery of marine life through a series of well dated, exceptionally preserved fossil assemblages in the Daye, Guanling, and Falang Groups. Numerous individual marine reptiles, fishes, and invertebrates are currently under study, including the world's oldest turtle, and the exceptional preservation provides unique anatomical detail. The wider potential of this series of snapshots into marine life is to document in detail one of the times of greatest expansion of life and the construction of new kinds of ecosystems.

Mammalian skull construction and the importance of cranial sutures in biomechanical finite element analysis: a validation using the modern domestic pig

Bright, J.A.

Dept. Earth Sciences, University of Bristol

Mammalian cranial sutures have been proposed to act not only as regions of growth, but also as areas of flexibility mitigating high bone strains. As Finite Element Analysis (FEA) gains popularity with palaeontologists, an understanding of the effects of sutures is crucial in producing valid results. Digital Speckle Pattern Interferometry (DSPI) was used *in vitro* on the zygomatic arch of a modern domestic pig (*Sus scrofa*) to assess the nature of strain and displacement across a suture. Results show that the suture localises a high strain gradient, and whilst it does not greatly reduce the nearby bone strain, it does permit the independent movement of adjacent bones. The best way of modelling cranial sutures in FEA is demonstrated by introducing regions of more compliant 3D elements. Further sutures were then introduced to a whole-skull model, and the results compared with *in vitro* strain gauge data, and models without sutures. Thus, the cumulative effects on the overall distortion of the skull from multiple small displacements at the sutures were observed. With a better picture of sutural mechanical behaviour established, questions regarding the ontogenetic and evolutionary patterns of suture fusion may begin to be addressed using FEA.

Mammalian skull construction and the importance of cranial sutures in biomechanical finite element analysis: a validation using the modern domestic pig

Jen A Bright¹, Flora Gröning² and Emily J Rayfield¹

¹*Department of Earth Sciences, University of Bristol, UK*

²*Department of Archaeology and Hull York Medical School, University of York, UK*

Mammalian cranial sutures have been proposed to act not only as regions of growth, but also as areas of flexibility that mitigate high bone strains. As Finite Element Analysis (FEA) gains popularity with palaeontologists, an understanding of the effects of sutures is crucial in producing valid results. Digital Speckle Pattern Interferometry (DSPI) was used *in vitro* on the zygomatic arch of a modern domestic pig (*Sus scrofa*) to assess the nature of strain and displacement across a suture. Our results show that the suture localises a high strain gradient, and whilst it does not greatly reduce the nearby bone strain, it does permit the independent movement of adjacent bones. We show that the best way of modelling cranial sutures in FEA is to introduce regions of more compliant 3D elements. Further sutures were then introduced to a whole-skull model, and the results compared with *in vitro* strain gauge data, and models without sutures. Thus, the cumulative effects on the overall distortion of the skull from multiple small displacements at the sutures were observed. With a better picture of sutural mechanical behaviour established, questions regarding the ontogenetic and evolutionary patterns of suture fusion may begin to be addressed using FEA.

The Early Cretaceous vertebrate assemblage from the Napai Formation of Guangxi, southern China: a comparison with Thai assemblages

Eric Buffetaut¹, Jinyou Mo², Haiyan Tong¹ and Romain Amiot³

¹*CNRS, UMR 8538, Laboratoire de Géologie de l'École Normale Supérieure, Paris, France*

²*Natural History Museum of Guangxi Zhuang Autonomous Region, Nanning, China*

³*CNRS, UMR 5125, Université Claude Bernard Lyon 1, Villeurbanne, France*

Although abundant vertebrate remains are known from many Early Cretaceous localities in northeastern and northwestern China, relatively little is known about the Early Cretaceous assemblages of southern China. One of the few vertebrate-bearing Early Cretaceous formations in that part of China is the Napai Formation of Guangxi Zhuang Autonomous Region, from which dinosaur remains were first reported in 1975. In recent years, a number of new specimens have been collected from the red beds of the Napai Formation, providing a better image of its vertebrate assemblage, which includes semionotiform fishes, turtles (*Kizylkumemys*, *Shachemys*), crocodylians, theropods (including a Siamosaurus-like spinosaurid and a form with blade-like teeth), sauropods (*Fusuisaurus zhaoi* and another form) and iguanodontian ornithopods.

Geographically and stratigraphically, the Napai formation is close to the vertebrate-bearing Sao Khua and Khok Kruat Formations of the Khorat Group of northeastern Thailand. A detailed comparison shows strong similarities with the Khok Kruat Formation, especially among turtles and dinosaurs. Like the Napai Formation, the Khok Kruat Formation has yielded ornithischians, whereas they are not known from the Sao Khua Formation. The Khok Kruat Formation is fairly well dated as Aptian, and a similar age is likely for the Napai Formation.

Evidence for high browsing in the sauropods *Brachiosaurus brancai* and *Euhelopus zdanskyi*

Andreas Christian and Gordon Dzemski

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For the sauropods *Brachiosaurus brancai* and *Euhelopus zdanskyi* analyses of the stress pattern in the intervertebral cartilage along the neck indicate approximately straight habitual neck poses with angles between the neck and the horizontal of between 40 and 50 degrees. For both sauropods, the biomechanically reconstructed neck postures are in accordance with the concept of browsing at great or medium heights. For *Brachiosaurus*, this result is corroborated by a computer-based analysis of the flexibility of the foremost neck section. Energy expenditure owing to high browsing is compared with energy costs for walking a distance. Although energy costs for vertical neck movements and expenditures owing to an increased blood pressure during high browsing increase over-proportionally with body size, high browsing was worthwhile even for a large sauropod like *Brachiosaurus* if resources were far apart.

Morphology of the jaw-closing muscles and the biomechanics of feeding in sciuriform, hystricomorph and myomorph rodents

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The Rodentia is the largest mammalian order, containing over two thousand species. Yet, despite this huge biodiversity, they can all be assigned to one of three non-monophyletic groups based on the arrangement of the jaw-closing muscles: the sciuriforms, hystricomorphs and myomorphs. Conflict exists in the literature as to the precise architecture of the masseter in these groups, and so the morphology of the muscles was re-examined using contrast-enhanced microCT imaging in three rodents representing the three subgroups: squirrel, guinea pig and rat. Muscle layer attachments were determined from microCT scans and three-dimensional reconstructions. It was hypothesised that variation in muscle architecture would lead to different stress and strain patterns being generated across the skull during feeding in the three subgroups. To test this hypothesis, three digital models of rodent skulls were constructed from the microCT images. The models were loaded to simulate the two major feeding modes, gnawing and chewing, and were analysed using finite element analysis. Results indicate substantial differences in the strain patterns between the three subgroups and between the two feeding modes. These outcomes help to further our understanding of rodent evolution and shed light on the overwhelming success of the order.

Functional analysis of skull shape

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Understanding the underlying factors contributing to skull form is important in comparative anatomy. Historically, hypotheses frequently propose specific adaptations that relate to function and the way the skull resists loads. However, the direct correlation between skull loads and skull shape remains uncertain. Using the engineering techniques of multibody dynamics analysis (MDA) and finite element analysis (FEA) we study the skull of the reptile *Sphenodon* (Diapsida: Rhynchocephalia). Skull feeding forces derived from the MDA were applied to the FE model, where skull deformations were predicted to examine the relationship between skull load, skull strains, and ultimately skull form. We show that individual bites deform the skull in a different way, and that some areas of the skull experience relatively high strains while others experience low strains. This strain gradient hints that the skull is not optimally designed for mechanical function; however, assessing the combined peak strains over all bites does produce a relatively uniform strain distribution. This does therefore support hypotheses that the skull is designed to resist forces generated from feeding. We conclude that skulls are optimally adapted to everyday loads, and morphological differences in structural bone are likely due to differences in feeding behaviour in most animals.

An experimental investigation into the hydrodynamics and locomotion of the Palaeozoic jawless vertebrates *Poraspis*, *Errivaspis* and *Ateleaspis*

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Ostracoderms represent a crucial phase of vertebrate evolution during which many of the characters that are now taken as typical vertebrate features appeared for the first time. While recent work has gone a long way to clarifying relationships and patterns of character acquisition, understanding of the ecology and biomechanics of these early fishes has lagged behind. Very little is known, for example, about how they swam.

An experimental investigation was conducted into the hydrodynamic characteristics of three ostracoderm species, *Poraspis polaris*, *Errivaspis waynensis* and *Ateleaspis tessellata*, using models mounted in a wind tunnel. The experimental data suggested that *Ateleaspis* was more suited to a benthic lifestyle than *Poraspis* or *Errivaspis*, being able to utilize ground effect to swim very economically while close to the bottom and having a morphology that would permit it to turn rapidly in the horizontal plane. *Poraspis* was found to have a morphology suited to minimising drag for greater hydrodynamic efficiency and executing rapid manoeuvres in mid water column. *Errivaspis* was found to have a morphology with adaptations for both benthic and mid water swimming, suggesting that it was a generalist.

New plesiosaurs from the basal Lias Group of South West England

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The earliest articulated plesiosaur specimens are known from the Rhaetian of Street (Somerset, UK). The fauna at Street includes at least nineteen specimens representing small-bodied, relatively long-necked individuals, many of which were collected by the eccentric Thomas Hawkins in the first half of the nineteenth century. These include the holotypes of three nominal taxa: *Plesiosaurus etheridgei* Huxley, 1858; *P. eleutheraxon* Seeley, 1865; and *P. cliduchus* Seeley, 1865; as well as the lectotype of *P. hawkinsii* Owen, 1838. All these small-bodied specimens and nominal taxa were referred to *Thalassiodracon hawkinsi* (Owen, 1838) in the most recent review of this material.

Here we report that the Street fauna does indeed contain more than one taxon of small plesiosaur. A partial skeleton in the University of Oxford Museum of Natural History is distinct from *T. hawkinsi* in aspects of both its cranial and post cranial morphology and represents a new taxon. It shares some features with currently undescribed specimens from the Pliensbachian, as well as pliosaurid pliosauroids. In addition another two new taxa from Street have also been recognised. This contributes to our knowledge of early plesiosaurians, and sheds light on to diversification of the clade.

The Early Triassic faunal assemblage of Czatkowice, Poland

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The microvertebrate locality of Czatkowice in southern Poland is of earliest Late Olenekian age. The original Czatkowice material is karstic breccia from which bone was acid-prepared and then sorted. As a result, the material is disarticulated and dissociated, but shows exquisite three-dimensional preservation, permitting detailed description, reconstruction, and phylogenetic analysis. Czatkowice is exceptional in yielding a diverse herpetofauna including stem anurans, relictual non-lissamphibian temnospondyls, derived procolophonians, lepidosauromorphs and archosauromorphs, as well as fish. Almost all of the known taxa were of small body size, ranging from around 50 mm snout-vent length to 1 m, and most seem to have been insectivorous/ carnivorous. Czatkowice seems to represent an upland oasis within the xeric circumequatorial belt that existed at this latitude in Northern Pangaea, and preserves a community of small amphibians and reptiles living in and around a small pool (or series of pools). The assemblage is largely Pangean in character, but lacks any trace of the synapsids still found in many contemporaneous Gondwanan deposits.

Difficulties in inferring limb kinematics from fossil tracks – internal track morphology as a function of substrate mechanics.

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The fossilized tracks of vertebrates present the only direct evidence of locomotor mechanics and other aspects of the palaeobiology of extinct animals available from the fossil record. Track morphology, specifically variations in track depth and features associated with the base of the track, has traditionally been used to infer peak under-foot pressures or varying ground reaction force vectors associated with limb kinematics (e.g. touch down, weight bearing, and kick off phases). Virtual experiments carried out using finite element analysis have shown that features at the base of a track, superficially similar to those hypothesised to result from limb kinematics, can be formed through pure substrate mechanics irrespective of the limb motion or loading. Displacement of substrate beneath a vertically loaded indenter can create mediolateral ridges (typically thought to represent three-phase limb movement) in undertracks. Asymmetric indenters, such as those used here to represent theropod pedes, produce tracks deeper at the posterior when loaded vertically and uniformly. These experiments show the importance in fully characterising a substrate, and reproducing tracks in the lab experimentally, before interpreting limb motion from fossil tracks.

The evolution of giant suspension feeders: toward a comparative approach

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Modern large-bodied marine suspension feeders comprise mysticete whales and four chondrichthyan lineages. Comparisons drawn with living relatives of these planktivores reveal few clues about the sequence of changes associated with the evolution of suspension feeding. The fossil record is uninformative for chondrichthyan examples, but a wealth of stem mysticetes provide a picture of anatomical transformation and experimentation leading to the origin of baleen whales. Despite this detail, it is difficult to extract generalities associated with the evolution of suspension feeding in the absence of comparative cases. During the Mesozoic, large planktivores were represented by a subset of pachycormid fishes, including the Middle Jurassic *Leedsichthys*. The discovery of additional material belonging to members of this radiation has clarified many aspects of their morphology, and greatly expanded both their stratigraphic and palaeogeographic range. Inspired by these finds, we review our current understanding of suspension-feeding pachycormids, including new specimens from Europe and North America, and present a revised anatomical perspective on enigmatic Early Jurassic taxa that document the sequence of character changes preceding the presumptive origin of planktivory in this clade. The emerging picture for the evolution of suspension feeding in pachycormids reveals interesting parallels with those already documented for whales.

Moment arm analysis of elbow flexor/extensor muscles in sprawling tetrapods

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The many phylogenetic shifts within the continuum from sprawling to erect limb postures have been a major focus of biomechanical and evolutionary studies. Muscle moment arms (leverages) and their relationship to posture (limb joint angles) are important components of these shifts but have not yet been widely investigated. Here we focus particularly on the muscle moment arms about the elbow joint in more sprawling tetrapods including turtles, toads, crocodiles and other taxa. We compare them to those in more erect and inverted (upside-down) tetrapods which respectively rely on extensors and flexors for body support. We did this using three-dimensional musculoskeletal models based on computed tomographic images, in order to quantify the relationship between muscle moment arms and elbow joint angles. Both the extensors and flexors show significantly increased moment arms at particular angles in erect tetrapods. However in sprawling tetrapods the flexor moments are most effective at a flexed angle, whereas the extensors are much less effective at all angles, and the extensors' pattern of moment arm – joint angle relationships resembles those of inverted tetrapods. Therefore in terms of elbow muscle moment arms, sprawling tetrapods have more in common with inverted tetrapods than with erect tetrapods.

A functional investigation into the jaw joints of two of the earliest stem mammals; *Morganucodon watsoni* and *Kuehneotherium praecursoris*

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The evolution of the jaw joint is of pivotal importance in early mammal evolution, and here we investigate feeding-induced loads at the jaw joint in two important stem mammals. Previous research we conducted suggested that *Morganucodon* fed on 'hard-object' prey, whereas *Kuehneotherium* was specialized for rapid, snapping jaw closure and consuming more malleable foodstuffs, indicating early ecological diversity within basal mammals. We now test the hypothesis that the dentary-squamosal jaw joint was operational and functionally important in these taxa. Mandibles were CT scanned to generate a 3D virtual jaw and finite element (FE) model for each taxon. For similar muscle loadings, we compared the effects on the jaw joint of chewing with the teeth in close proximity to biting with a wider gape (45 degrees). We also manipulated the ratio of muscle loadings, to simulate the increasing development of the masseter musculature in mammalian evolution. Our results, coupled with the poorly developed dentary condyle in *Kuehneotherium*, suggests that a surangular-squamosal contact may have been present. In current phylogenetic analyses, *Kuehneotherium* is placed further up the stem than *Morganucodon* and this more plesiomorphic jaw articulation in *Kuehneotherium* illustrates the mosaic nature of early mammal evolution.

Changes in the direction of mastication and the remodeling of the masticatory apparatus during mammalian evolution: the case of the Issiadoromyinae (Rodentia).

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The direction of mastication revealed by dental microwear was studied in relation to changes in the structure of the masticatory apparatus in Issiadoromyinae (Rodentia, Mammalia). This extinct subfamily displays a wide range of orientation of chewing movements from oblique to nearly propalinal mastication. Our results offer a rare opportunity to assess the order of establishment of the morphological characters that are related to the acquisition of propalinal mastication in an extinct lineage. The acquisition of propalinal mastication during the evolution of Issiadoromyinae was associated with the transformation of the molar occlusal surface from cuspidate to flat but also to changes of the whole masticatory apparatus. *Elfomys* and *Pseudoltinomys* show cuspidate tooth crowns, a high mandibular condyle and an important latero-medial orientation of the masticatory muscles (superficial masseter and internal pterygoid) in association with oblique chewing movements. In contrast, *Issiadoromys* lineage is characterized by flat molar occlusal surface, a low mandibular condyle and posterior orientation of the masseter and pterygoid associated with slightly oblique to propalinal chewing. We showed that potential information can derive from microwear patterns insofar as detailed evolutionary interpretation of functional aspects of the cranial structure is conducted and compared with fossil evidence.

Bone histological variations of desmostylians (Mammalia, Tethytheria)

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Desmostylians are an enigmatic group of extinct mammals with unique osteological and dental morphologies. Desmostylians are presumed to be amphibious, but their paleoecology has been equivocal. Bone histology can be

used as a tool to infer habitats of extinct animals; however, histological studies of desmostylians are scarce. Therefore, we compared histology of *Behemotops*, *Paleoparadoxia*, *Ashroa*, and *Desmostylus* using thin-sections and CT scans of ribs and limbs, to better understand desmostylian habitat and evolutionary history. Cortical bone of desmostylians is composed of fibrolamellar bone with multiple growth marks, indicating similarity with sirenians. All desmostylians lack medullary cavities. In extant mammals, this has been demonstrated to be an aquatic adaptation. Bone histology of *Behemotops* and *Paleoparadoxia* shows osteosclerosis, while that of *Ashroa* shows pachy-osteosclerosis. *Desmostylus* bone histology is different from that of other desmostylians in that it shows osteoporosis. High bone density (osteosclerosis or pachy-osteosclerosis) is an aquatic specialization that provides static buoyancy control for animals living in shallow water, while low bone density (osteoporosis) is associated with dynamic buoyancy control for animals living in deep water. Our study thus suggests that all desmostylians evolved aquatic adaptations and changed their habitats and/or aquatic locomotion throughout their evolutionary history.

Quetzalcoatlus northropi as a secondarily flightless pterosaur

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New mass estimates for pterosaurs, using a method successfully tested on models of 6 extant birds ranging in size from a starling to an ostrich, predict a mass of 544 kg for *Q. northropi*. The mass gap between *Q. northropi* and the next heaviest pterosaur is parallel to that between extant flying and flightless birds. Could *Q. northropi* be a flightless pterosaur? Accepting this possibility frees us from the mental gymnastics required to generate an anatomy with sufficient muscle mass and power to be able to fly when possibly weighing more than thirty times that of the heaviest, living, volant birds such as the 16kg Kori Bustard. As a ground-dwelling pterosaur, a larger body size will have a lower cost of transport, and be better able to resist predation at all stages of its life by large and small predatory dinosaurs. Remains of *Q. northropi* have been recovered from rocks that record inland, terrestrial environments, very different from the marine and lacustrine environments that other large pterosaurs are typically associated with. This habitat difference immediately suggests a very different mode of life for this pterosaur.

Three-dimensional whole-bone scaling in the limbs of terrestrial vertebrates

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Scaling studies relate properties of animals, such as bone morphology to body mass, in order to infer basic size-related principles across wide ranges of organisms. Typically only the midshaft of bones is studied focusing on its external diameter or circumference in relation to bone length or body mass.

However bone shape varies widely across bone length (e.g. epiphyses v. diaphyses) and amongst different bones (e.g. humerus v. fibula), as well as among species. We have developed a new technique in open source ImageJ software that quantifies cross-sectional geometry throughout the entire bone using CT scan data. We have applied this technique to the limb bones of taxa ranging from felids to bird species as well as ontogenetically within elephants, and included phylogenetically independent contrasts analysis.

Although some clades have unique scaling trends that relate to locomotor specializations and limb posture, some trends hold for all species investigated. Metaphyses occupy a greater proportion of the total bone length in larger species and ontogenetic stages, indicating an increased requirement for even strain distribution. Calculating scaling exponents at multiple sites reveals local specialisations, such as at muscle attachments or around joints, missed by simple mid-shaft measurements.

Understanding conflicting topologies: The role of character complexes in tree incongruency

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Different kinds of phylogenetic data (morphological and molecular) may produce different topologies despite containing signal from the same ancestral pattern. Both datasets undoubtedly represent some combination of phylogenetic signal and noise; however the signal can become obscured if noise is non-random with respect to phylogeny. To distinguish signal from noise we must distinguish homology from homoplasy using independent lines of evidence. However, an abundance of character data makes this task daunting. To focus this effort, we propose a method to identify which nodes and characters contribute most to the incongruence between two trees. We map the morphological characters

onto the molecular topology, and then identify characters that have more steps than on the most parsimonious tree. We search for patterns of conflict on the molecular topology representing support for morphological relationships by finding complexes that changed together on the same branches of the tree. A bootstrapping method compares the observed character overlap with the distribution of overlaps produced by 1000 trees of the same length with randomised character placement. Morphological data from Chiroptera were used as a case study and character complexes associated with three monophyletic groups were identified. Possible functional linkage and impact on topology will be discussed.

Cranial joints in *Sphenodon* and other Rhynchocephalia with implications for lepidosaur skull mechanics

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Despite representation by a single living genus, *Sphenodon*, increasing fossil evidence shows that Rhynchocephalia were once a globally widespread and diverse group. In particular they demonstrate variation in terms of feeding apparatus and a possible evolutionary trend towards increased bite force because derived taxa tend to possess shorter out-levers, stouter teeth, and larger adductor chambers. An aspect of skull anatomy that remains largely overlooked in rhynchocephalians (and indeed most vertebrate clades) is variation in the structure of cranial joints. In life these are maintained by soft tissues that permit small movements that are suspected to reduce peak stresses in surrounding bone. A detailed survey of the cranial joints in several rhynchocephalians and stem lepidosaurs shows that in comparison to basal taxa (e.g., *Gephyrosaurus*) derived taxa (e.g. *Sphenodon*) have larger and more elaborate cranial joints. Therefore, derived taxa possess an increased surface area for soft tissue attachment and probably a greater capacity to deal with stress sustained during feeding. Differences in cranial joint shape are also found between derived taxa and how this relates to deformation under loading is investigated using a computer based finite element model of *Sphenodon*.

Dental morphologies and sexual dimorphism in stem-group neoselachians (Synchodontiformes): implications for taxonomic diversity

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Identifying the interrelationships of extinct neoselachians is one of the major challenges in reconstructing the evolutionary history of sharks in general. Although great progress has been accomplished resolving the systematic positions of their living relatives a comprehensive phylogeny, including fossil taxa, is still lacking. This discrepancy is related to the nature of preservation. Extinct forms are generally known from isolated teeth only, whereas skeletal remains are very scarce throughout their evolutionary history. Consequently, a tooth-based taxonomy was established largely excluding articulated material. Nevertheless, only little is known about the nature of odontological differences in closely related taxa. For instance, possible ontogenetic or sexual dimorphism are generally neglected although tooth differences related to these phenomena occurs in extant taxa. Dental sexual dimorphism in fossil neoselachians has not yet been scrutinized in detail and hence the origin of this feature is completely unknown. Recent analyses of the early Jurassic shark *Palidiplospinax*, a member of the neoselachian stem-lineage Synchodontiformes, provide the first direct evidence of dental sexual dimorphism in a basal shark. Comparison with other synchodontiforms supports the interpretation that this feature is commonly present in early neoselachians. Sexual tooth difference is plesiomorphic for neoselachians and probably also for elasmobranchs.

Evolution of locomotor musculature in ornithischian dinosaurs

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The earliest ornithischian dinosaurs were bipedal but they radiated into a diverse range of body shapes. Quadrupedalism developed in three ornithischian lineages, causing profound musculoskeletal transformations. We use the extant phylogenetic bracket to reconstruct locomotor musculature in ornithischians. A well-developed scapula

acromial process provides attachment for forelimb protractors, while the prominent deltopectoral crest of quadrupedal ornithischians is a correlate of the major humeral retractor. These features are well developed in thyreophorans and ceratopsians, but are less well-developed in hadrosaurs. The elongate iliac preacetabular process is broadened transversely, providing a large area for attachment of the predominant femoral protractor. The elongate prepubis and broad ilium provide attachment for lower limb extensors, suggesting protraction and antebrachial extension become more important in quadrupedal than in bipedal locomotion. The retroversion of the pubis in ornithischians would have resulted in the loss of the moment arm of the puboischiofemoralis externus for femoral protraction; the subsequent reduction of the postpubis in many ornithischians probably correlates with the loss of this muscle group entirely. This study is the first to reconstruct musculature in ornithischians from both a functional and phylogenetic perspective and is timely since biomechanical methods are being used increasingly to understand dinosaurian locomotion.

Where have all the sauropods gone? The mid-Cretaceous 'sauropod hiatus' and the impact of uneven sampling of the fossil record

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The absence of sauropod dinosaurs in the mid-Cretaceous of North America and Europe has led several authors to suggest this represents a sauropod extinction, followed by a latest Cretaceous austral reinvasion. However, several lines of evidence indicate this hiatus is a sampling artefact. New fossil discoveries have considerably shortened the hiatus, reducing it to the Turonian–early Campanian in North America, and to the late Cenomanian–early Turonian and late Coniacian–Santonian in Europe. Palaeoenvironmental analyses demonstrate inland preferences for titanosaurs; however, during the hiatus there was a decline in inland deposits in Europe and North America, which would have greatly reduced the probability of preserving titanosaurs. Statistical comparisons also demonstrate positive correlations between mid-Late Cretaceous inland deposits and sauropod occurrences. Lastly, cladistic and biogeographic analyses do not support placement of latest Cretaceous North American and European titanosaurs within austral clades. Thus, the hiatus is most plausibly interpreted as the product of a sampling bias pertaining to the rarity of inland sediments preserved in these two regions. The presence of titanosaurs in these areas during the latest Cretaceous can be explained by descent from Early Cretaceous incumbent faunas or dispersal from Asia, rather than invasion from southern continents.

Neck posture in extant and extinct vertebrates I: Osteology and behavior

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The reconstruction of sauropod neck posture is critical to the interpretation of their feeding behavior. While the undeflected or osteologically neutral pose (ONP) has been proposed as the characteristic pose (CP) for the sauropod neck, the suggestion that sauropods habitually held their necks in ONP has been questioned, since some extant vertebrates habitually hold the head higher than ONP. Behaving animals do not have but one CP; rather, there are characteristic poses for locomotion (CLP), feeding (CFP), vigilance (CVP), etc. Across a wide range of extant taxa (22 birds in 20 orders; 10 herbivorous mammals; two non-avian archosaurs; and three other reptiles), the head is generally lowered to feed, i.e., CFP < ONP, and when not feeding, ONP approximates CLP and CVP in most vertebrates. Exceptions include highly vigilant, extreme low browsers (such as ostrich and hare, where CFP << CVP) which spend little time in the intermediate ONP. For the great majority of vertebrates examined, however, ONP is close to both CVP and CLP. But as regards feeding, since CFP < ONP with few exceptions, we conclude that ONP has high value regarding sauropod feeding, despite their having no close analogue among extant tetrapods.

Ontogeny and phylogeny in procolophonids - Evidence from a new Leptopleuronine from the Middle Triassic Otter Sandstone of Sidmouth, Devon

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A new procolophonid specimen raises the possibility that some characters used in phylogenetic analyses of the group may change during ontogeny. It comprises an isolated small skull and attached mandibles from the Middle Triassic Otter Sandstone Formation near Sidmouth, Devon, England. The specimen was partly prepared and then studied using

X-ray microCT imaging. The skull appears generally similar to that of the later *Leptopleuron* from the Lossiemouth Sandstone Formation of Scotland. The presence of quadratojugal and supratemporal spikes, the massive first dentary incisor and the absence of maxillary depression, all suggest a derived leptopleuronine. However it appears more primitive than all other leptopleuronines in the possession of rows of vomerine teeth and the absence of the jugal spikes found in some derived taxa. The small size of the specimen, together with the open sutures and absence of jugal spikes suggest that it may be a juvenile, although the supratemporal and quadratojugal spike array is fully developed. The presence of vomerine teeth may thus also be a juvenile character. The absence of the back of the skull, combined with the mandibles clamped in place, suggests that it may have been bitten off and rejected during predation.

Evaluating the utility of limb bone internal structure as an indicator for aquatic adaptation of Testudines

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Alternation in bone compactness such as osteosclerosis and osteoporosis-like state occurred with frequency through the aquatic adaptation of vertebrates and has been emphasized as an indicator for secondary aquatic adaptation of fossil amniotes. In this study I conducted micro-CT analysis of humeri of modern turtles in order to examine the correlation between long bone microanatomy and mode of life within Testudines. Comparison of diaphyseal transections revealed that compactness profiles do not differ significantly among terrestrial, amphibious and aquatic groups, except for *Dermochelys* showing extreme osteoporosis-like state. Significantly, humeri of some terrestrial taxa have an entirely compact cross-section. Moreover, compactness changes in longitudinal profile do not show any characteristic tendency in each group. On the other hand, it was revealed that substantial sectional area near the humeral head is lower in highly aquatic turtles (*Chelonia*, trionychoids and chelonioids), and higher in terrestrial and amphibious taxa. These data indicate that osteosclerosis recognized from sectional compactness does not suggest aquatic adaptation in Testudines, and that transition of bone substantial cross-sectional area in longitudinal profile changes according to aquatic adaptation and might be useful for ecological reconstruction of fossil turtles.

Patterns in the palaeoecology of Cretaceous chondrichthyan faunas

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Top marine predators such as selachians regulate entire trophic structures by directly or indirectly controlling the total biomass of species populations in lower levels. Due to their fundamental role they are excellent indicators of many environmental, ecological and biological phenomena both in Recent and prehistoric times. Selachians exhibit polyphyodonty, a continual shedding of teeth. As a result, the selachian fossil record exhibits a high abundance of specimens relative to other organisms. The dentitions of apex predators in the fossil record facilitate the acquisition of general data regarding palaeoenvironment, nutrient levels, salinity and trophic structure. Information such as diversity, prey type, life habit and environmental preferences specific to the group can also be obtained. In order to make viable geographical, environmental and temporal comparisons of fossil selachian faunas, it was necessary to sample localities that cover both temporal and geographical distances. Four Maastrichtian sites in Morocco spanning from deepwater to nearshore environments, plus two Albian sites in Western Europe, the North Sea Basin and the Anglo-Paris Basin, were bulk sampled for selachian material. Faunal comparisons allowed eight specific hypotheses to be tested whilst providing data for site descriptions, enabling large scale patterns in selachian palaeoecology to be identified.

Wealden Group iguanodontians: their history and taxonomy

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The Lower Cretaceous continental deposits of NW Europe are synonymous with the dinosaur *Iguanodon*. This taxon has the historic burden of being one of the earliest dinosaurs described and named. One consequence of this history is that *Iguanodon* became an unavoidable repository for all fragmentary ornithomimid dinosaur remains collected from Wealden-aged deposits.

Spanning some 34Ma of geological time, the low generic and specific diversity among iguanodontian ornithomimids in NW Europe, contrasts markedly with higher levels of diversity that are being reported from a relatively newly

prospected contemporary interval in North America.

Fresh analysis of the Wealden Group iguanodontian material is producing results indicate that the discovery and disassociated nature of the original material attributed to the genus *Iguanodon* (as well as comparatively poor understanding of anatomy and geology) has had an unfortunately repressive influence on general understanding of Wealden-aged iguanodontians. New taxa, new material and new interpretations are presented and their overall implications are considered.

Using engineering analysis to bracket the morphological possibilities for pterosaur wing shape

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The majority of reconstructions of pterosaurs wing morphology are based upon anatomical analysis. While wing bones are generally well known, the extent of their articulation is open to interpretation and does not provide a firm constraint to morphological reconstruction. Engineering analysis can provide additional constraints to these anatomical reconstructions. The engineering constraints vary in tightness. One of the firmest is that the centres of mass and pressure (lift) are longitudinally coincident. Other, more flexible aerodynamic constraints include requirements for flight stability and minimising aerodynamic drag. Structurally, there are limits to wing bone deflection and tension requirements for membrane stability. The maximum bending deflection of the wing bones was estimated from consideration of surface strain and analogy with extant tension structures was used to define the shapes of the free margins of the wing membranes. A vortex lattice code was used to calculate the centres of lift, which were related to recent centre of mass estimates from the literature. The engineering considerations indicate that the wings must be swept more anteriorly than in most anatomical reconstructions, have greater posterior curvature in the wing bones, a significantly more concave posterior margin and possibly a lunate shape in the distal region.

The evolution of the stiff theropod tail into a flexible aerodynamic surface

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A quantitative analysis of theropod tails reveals dramatic differences in caudal flexibility along the theropod tree stem: along the non-avian stem flexibility was constant characterized by lower ventral flexibility and higher dorsal and mediolateral flexibility. But, along the avian stem there was a decrease in dorsal and mediolateral flexibility and perhaps an increase in ventral flexibility. Thus, a similar degree of tail stabilizing function operated along the non-avian stem whilst change along the avian stem led to the development of more precisely-controlled aerodynamic tail function. In all regions of the tail we observe neural spine heightening and lateral and ventral growth of the transverse processes along the avian stem. This decreased dorsal, ventral and mediolateral flexibility made the tail easier to lift and swing. But, chevrons were lost along the avian stem which increased intervertebral joint mobility and increased ventral flexibility. However, functional differences between chevron and transverse process modifications should have helped control lift forces. The stiffening effect of neural spine and transverse process changes were important for control of tail position after chevron loss. These changes in tail morphology along the avian stem produced a flexible, controllable aerodynamic surface that was presumably integral to improvements in flight ability.

Tooth microtextural analysis and diet in pliosaurs

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Recent work on pliosaurs from the Peterborough Member of the Oxford Clay Formation suggests that they differed in their preferred prey. According to this hypothesis *Liopleurodon* ate large, hard-boned prey, while *Simolestes* consumed mainly invertebrates, probably cephalopods (Noe, 2004, Abstracts of the Palaeontological Association Annual Conference, Palaeontology Newsletter 57). These interpretations are based on functional morphological analysis and comparisons with living analogues. Here we use microtextural analysis - quantitative measures of the surface texture of

worn tooth surfaces derived from high resolution 3D data - to test these hypotheses. Analysis of data from the teeth of *Liopleurodon*, *Simolestes* and *Physeter* (sperm whale) demonstrates that the technique is applicable to large aquatic predators. We were unable to reject the null hypothesis that microwear in *Liopleurodon* and *Simolestes* does not differ, but the hypothesis that microwear in either of these taxa is the same as that of *Physeter* could be rejected with a high level of significance. Our results do not support hypotheses that *Liopleurodon* and *Simolestes* had significantly different diets, and do not support the hypothesis that *Simolestes* was a cephalopod specialist.

The taxonomic diversity of the stem mammal *Morganucodon* (Morganucodonta: Morganucodontidae) from late Triassic-Early Jurassic fissure deposits of Glamorganshire, Wales, UK

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Triassic-Jurassic fissure fills from Glamorganshire, Wales, offer a unique window into the evolution of Mesozoic mammals. Among the many fissures of this region, diverse and depauperate assemblages have yielded a wealth of fossil vertebrate material, including two early mammals, *Morganucodon* and *Kuehneotherium*. At present, all *Morganucodon* specimens from these fissures are attributed to a single species *Morganucodon watsoni*. However, previous studies of the fissure material in this area have identified a taxonomically diverse population of *Kuehneotherium*, and I hypothesize that a similar diversity exists in *Morganucodon*. Disparity and morphometric data obtained from abundant *Morganucodon* dental material was analysed via Principle Component Analysis (PCA) and Principle Coordinate Analysis (PCoA). Upper and lower molars cluster in morphospace relative to locality, and this separation is statistically supported by Discriminant Analysis of Euclidian values from PCoA ($P < 0.001$). These results identified size, buccal cingulum morphology, cusp proportions, and inter-cusp distances as significant components driving taxonomic diversity. Concluding from the differences in size and morphology, the Glamorganshire *Morganucodon watsoni* material exhibits a taxonomic diversity similar to that of *Kuehneotherium*. This represents further evidence of diversity in the earliest mammals, aided by changes in developmental dental patterning, which permitted subsequent ecological diversification.

Eliminating Romer's Gap: new tetrapods from the basal Carboniferous of the Scottish Borders

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Romer's Gap at the base of the Carboniferous is characterised by a world wide break in the fossil record of early tetrapods. It immediately follows the Hangenberg mass extinction. Hitherto, tetrapod material has only been described from Horton Bluff, Canada and Dumbarton, Scotland. In 2009, we announced the discovery of new tetrapods in the Tweed Basin at Coldstream and Burnmouth. Here we report a further discovery in Whiteadder Water near Chirnside. The new locality lies within the Courceyan stage of the Tournaisian. Four separate fossil horizons have been discovered and four tetrapod taxa have been identified so far: two large forms, similar in size to *Pederpes* and two small forms with skulls c20-30 mm long. The associated fauna comprises a variety of fishes and arthropods including myriapods and scorpions. The discovery of a diverse fauna of tetrapods and arthropods at the base of the Carboniferous shows that their radiation had not been constrained by the low levels of atmospheric O₂ at that time. The new discoveries at Willie's Hole help fill a major gap in our knowledge of the morphology and relationships of early tetrapods and provide further insight into their radiation following the Hangenberg mass extinction.

A taxon-free model for brain size determination in Mammalia

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Mammals occupy various niches across almost every environment on Earth. Their evolutionary success has been linked to behavioural and life history traits, many of which are closely tied to brain size. Tracing the evolution of brain size would thus improve understanding of the history of typically mammalian cognitive traits. However, except in circumstances of exceptional preservation, fossil brain sizes are nearly impossible to determine. In the first study of its kind to cover all mammalian orders, 476 adult specimens from 200 species, covering 99 out of 133 families, were used to develop an allometric equation that relates endocranial volume to simple external measurements of the skull, using multiple regression and independent contrasts. The model was developed using only primary data and can be used to

determine brain size from fossils of extinct mammals of all sizes, from all mammalian clades except Cetacea. Model-predicted volume correlates strongly with measured volume ($R^2=0.9925$). Correlations show that there are no significant differences of model formulae between clades. Study demonstrated that the model cannot be applied with high accuracy to therapsid synapsids, but could be used to gain a first-order approximation of endocranial volume, or relative brain sizes within therapsid subgroups.

Evolution of gulp-feeding in baleen whales

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Rorquals feed by engulfing large gulps of prey-loaded seawater that are sieved over the baleen. Several osteological features related to advanced gulp-feeding can be traced in the fossil record of mysticetes. These include a broad and shallow glenoid process suggesting high mobility of the mandible and a broad rostrum. The coronoid process of the mandible of early balaenopteroids is well developed and bent laterally like in balaenopterids where this structure is involved in jaw rotation during the gulp-feeding cycle. A slightly hooked distal part of the coronoid process suggests the presence of a maxillomandibular cam articulation. In balaenopterids, the coronoid process articulates to the suborbital plate of the maxilla enabling a tight close of the mouth, enhancing craniomandibular stability during normal swimming and likely optimizing the timing of deployment of the feeding apparatus. However, stem balaenopterids lack a depressed supraorbital process and thus probably possessed a less massive temporalis muscle and perhaps also lacked the frontomandibular stay associated with gulp-feeding in recent balaenopterids. This combination of early balaenopteroids possessing features related to gulp-feeding, while lacking others, indicates that they did gulp-feed but not yet in a way as advanced as present day balaenopterids.

Sauropodomorph long bone histology through time and ontogeny

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Sauropods grew to be the largest terrestrial animals to ever roam the earth. However, the ancestral sauropodomorphs started out as relatively small animals. The evolution of sauropodomorph body size and growth rate can be observed in the microstructure of their long bones. We studied the change from cortical zones of fibrolamellar bone with LAGs in early sauropodomorphs like *Saturnalia*, *Thecodontosaurus* and *Plateosaurus* to an uninterrupted bone cortex of fibrolamellar bone in the earliest sauropods. Fibrolamellar bone tissue is present in the earliest dinosaurs and dinosaur ancestors, and is also seen in mammals and birds, which have high metabolic rates and are generally endothermic. Some sauropods secondarily evolved small body sizes. *Europasaurus* from the Late Jurassic of Germany, and *Magyarosaurus* from the Late Cretaceous of Romania are believed to be island dwarfs. We observed two distinct growth rate reductions in the long bone histology of these taxa. Preliminary results suggest a strong negative correlation between sauropodomorph osteocyte lacuna density and body mass, similar to extant mammals. However, lacuna density is much higher in sauropodomorphs than in mammals of similar body mass. This feature deserves more attention as it may provide further insights into local bone apposition rates, growth rates and physiology.

Neck posture in extant and extinct vertebrates II: Computational modeling of range of motion

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A representation for the space of possible poses of a vertebrate neck is introduced and applied. For a neck with K cervical vertebrae, and intervertebral joints with 2 degrees of freedom (mediolateral and dorsoventral flexion), the full configuration space has a computationally-unwieldy $2 \cdot K$ dimensions. But regarding the neck as permitting the head to reach to a specific location from a specific direction of approach, the configuration space reduces to a 6-space (3 positional, 3 directional). As the neck extends to reach increasingly far from the body, the range of approach directions (at the atlas) diminishes. In the limit, the "reachability envelope" (RE) is a surface defined by the points of greatest radial distance reachable without stepping. Vertebrate necks vary considerably in RE area, and the directional flexibility within the volume bounded by the RE (the swan, e.g., can preen points on its own neck from various directions). A computational model explores how neck flexibility (both RE and directional flexibility) is affected by factors including

vertebral count and the distribution of centrum length and intervertebral flexibility along the neck. The flexibility observed in representative vertebrates is replicated, and implications for sauropod dinosaurs are derived.

The first records of amphibians, lizards and maniraptoran dinosaurs from the Lower Cretaceous Hastings Group of south-east England

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Prior to the 1960s the only small tetrapod remains to be reported from the Berriasian – Valanginian Hastings Group of the Wealden Supergroup of mainland Britain were a tooth and tooth fragment of the multituberculate mammal *Loxaulax valdensis*. Commencing in 1960 a comprehensive search of mainland Wealden Supergroup strata for new mammal remains was undertaken by a team led by Kenneth Kermack. This resulted in the recovery of specimens representing new Mesozoic mammals but no mention was made of any co-occurring small tetrapod taxa. To date the only record of small tetrapods from the Wealden Supergroup of mainland Britain is that of a salamander, frog and lizards from the Hauterivian part of the Weald Clay Group exposed at Keymer Tileworks in West Sussex. However, examination of Mesozoic mammal specimens accessioned in the collections of the Natural History Museum, London, has revealed the existence of an un-catalogued salamander atlas among material obtained by Kermack in the 1960s. More recently, excavations and bulk screening of samples from Valanginian Hastings Group horizons exposed at Ashdown Brickworks near Bexhill, East Sussex, has produced more small tetrapod remains including those of salamanders, a frog, lizards and small theropods including maniraptorans.

Why giraffes have such short necks

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The necks of sauropod dinosaurs were by far the longest of any animals, exceeding 15m. Four clades with very different cervical morphologies (mamenchisaurids, diplodocids, brachiosaurids, and titanosaurians) evolved 10m necks. By contrast, the neck of the giraffe, the longest of any extant animal, reaches only 2.4m. Those of theropods and pterosaurs attained at most 3m. (Even among aquatic animals, the record is only 7m for elasmosaurs.) Four factors contributed to sauropod neck length: the sheer size of the animals, their distinctive vertebral architecture, air-sacs, and heads that merely gathered food without processing it. Cervical vertebral innovations included: extreme pneumatization, which lightened the neck and increased bending resistance; elongate cervical ribs, which allowed hypaxial muscles to shift posteriorly; and, in several clades, bifid neural spines, which aided stability by shifting epaxial tension elements laterally. Bifid cervicals evolved at least four times among sauropods and were never secondarily lost; they are otherwise found only in Rhea. However, other aspects of sauropod cervical anatomy remain puzzling: low neural spines reduced the moment arm of epaxial tension members; ventrally displaced cervical ribs increased bulk; and epiphyses were not posteriorly elongated. These apparent flaws suggest our understanding of sauropod neck mechanics remains incomplete.

An adult-egg association and its implications for pterosaur reproductive biology

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An individual of *Darwinopterus* from the Jurassic Tiaojishan Formation of China, preserved in direct association with an egg, provides critical new insights into the reproductive biology of pterosaurs. The presence of a cranial crest in some individuals of *Darwinopterus*, but its absence in the new find, evidently a female, provides the clearest support yet for the hypothesis that these structures, widespread in pterosaurs, are sexually dimorphic. Although the new find shows some evidence of osteological maturity it is significantly smaller than other mature individuals of *Darwinopterus* suggesting that, as in extant reptiles, sexual maturity preceded final adult size. The egg, preserved immediately posterior to the pelvis, is oval, seemingly soft shelled and relatively small compared to the adult. Preliminary estimates of egg/adult mass are similar to those of reptiles, notably squamates, and less than half the value for adult birds of

corresponding size. A significant degree of water uptake post oviposition seems likely. These and other findings such as evidence for hyper-precociality in hatchlings suggest that the reproductive biology of pterosaurs was much more like that of reptiles than birds or bats, but offered important advantages (such as mass reduction) to these flying vertebrates.

New insights into the interrelationships of the *Halitherium*-species-complex

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The systematics of sirenians is obscure. The Dugongidae and the therein included Halitheriinae are a paraphyletic assemblage, as is the genus *Halitherium*. However, in recent studies these groups are considered, conversely, to be monophyletic. For a revision of the *Halitherium*-species-complex with focus on the species *H. schinzii*, best sampled from lower Oligocene sediments of Germany, a morphological (re)-investigation of the available skeletal material and a phylogenetic analysis employing cladistic principles is aspired. Beside the late Oligocene *H. christolii* from Austria and *H. taulannense* from the late Eocene of France, the set of taxa is complemented for the first time with the Central and North American species *H. alleni* and *H. antillense*. The status and affinities of several specimens actually considered invalid and synonymous with *H. schinzii* and *H. christolii* is additionally tested. On the basis of this morphological and systematic study, the hypothesis of the presence of two different morpho-species of *Halitherium* at least in the early Oligocene of Germany is corroborated. A specimen consisting of a skullcap with a significant detail morphology, especially in the area of the supraoccipital, and known under the name "*Halitherium bronni*" is supported to be a valid taxon.

Quantitative characterisation of avian brain morphology using X-ray CT approaches

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X-ray computer tomography is increasingly being used by palaeontologists to reveal otherwise inaccessible internal structures in fossils. However, these powerful data are normally used only for comparative morphological analysis; quantitative data collection is usually restricted to simple measurements of linear distance, angles and overall volume. Investigations of vertebrate brain evolution have thus concentrated on overall volume and subjective comparison of brain region size. I describe a new quantitative approach involving characterisation of the avian brain based on brain region volume. Segmentations of the endocranial cavity are first converted from voxel data to polygon mesh stereolithograph (STL) models. Individual brain regions are then separated from the model at their base using mesh editing software. Volume values can then be derived from these separated regions, although these values probably underestimate the true region volume because internal extent of regions cannot be determined in scans of skulls. Brain morphotypes can be characterised by multivariate analysis of these 'partial' volumes as percentages of overall endocranial cast volume. Soft tissue dissections of brains in living species have previously revealed correlations between region volume variation and behaviour. If similar correlations are found using this 'partial' volume approach, behavioural aspects in extinct species can be predicted.

Caudal pneumaticity and pneumatic hiatuses in the sauropod dinosaurs *Giraffatitan* and *Apatosaurus*

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Skeletal pneumaticity is present in the presacral vertebrae of most sauropod dinosaurs, but pneumatic cavities are less common in the vertebrae of the tail: prominent caudal pneumaticity is restricted to diplodocines and saltasaurines. We describe previously overlooked pneumatic fossae in mid-caudal vertebrae of *Giraffatitan* and *Apatosaurus*. In both taxa, the most distal pneumatic vertebrae are separated from other pneumatic vertebrae by sequences of three to seven bilaterally apneumatic vertebrae. These gaps in pneumatization constitute pneumatic hiatuses, which until now were assumed to divide separate pneumatizing diverticula. Caudal pneumaticity is not prominent in most individuals of either taxon, and its unpredictable development means that it may be more taxonomically widespread than previously recognized within Sauropoda and elsewhere in Saurischia. The erratic patterns of caudal pneumatization in *Giraffatitan* and *Apatosaurus*, including asymmetry and the pneumatic hiatuses, show that pneumatic diverticula were more

broadly distributed in the bodies of the living animals than are their traces in the skeleton. Together with recently published evidence of subcutaneous diverticula in pterosaurs, this shows that pneumatic diverticula in ornithodirans are underdetermined by their skeletal traces, and suggests that their prevalence has been systematically underestimated.

Mammalian brain evolution: Marsupials vs. placentals

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The evolution of mammalian brain size is directly linked with the evolution of the brain's unique structure and performance. Both maternal investment traits and basal metabolic rate (BMR) seem to correlate with relative brain size, but this has only been researched in-depth in placentals. Here we provide the first direct quantitative comparison of brain size evolution in marsupials and placentals, whose maternal investment traits and metabolism differ extensively. We show that the misconception that marsupials are systematically smaller-brained than placentals is driven by the inclusion of Primates. Marsupials do not exhibit a body-size adjusted residual correlation of BMR with brain size, whereas placentals do. This contradicts suggestions that larger brains require higher BMRs. We suggest that a positive BMR/brain size residual correlation is derived for placentals and related to the intimate physiological mother/offspring contact during gestation. Marsupials instead achieve large brain size through extended lactation. Comparison with avian brain evolution suggests that placental brain size should be constrained due to their relative precociality, as has been hypothesized for precocial bird hatchlings. We propose that this constraint is circumvented in placentals because of their focus on gestation. Marsupials instead represent the less constrained, plesiomorphic condition.

SVPCA Posters

The evolution of body size, stance and gait in Allosauroidea (Dinosauria: Theropoda)

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Allosauroids were a diverse group of non-avian theropods that dominated predatory niches during the Mesozoic. Cladistic analysis reveals contrasts in hindlimb osteology between basal allosauroids and the derived subclade Carcharodontosauria. Myological reconstructions indicate that carcharodontosaurian synapomorphies are not associated with restructuring of hindlimb musculature. Body mass and muscle moment arm predictions across allosauroids suggest mass distribution and 3D muscle mechanics remained fundamentally unchanged. Femoral diameters show isometry, while hip extensor moment arms exhibit positive allometry, aiding limb support as mass increased. Horizontally orientated femoral heads in non-carcharodontosaurians are associated with augmented mediolateral diameters relative to dorsally inclined femora in carcharodontosaurians. These morphological correlations are present in extant bovids, where greater mediolateral diameters reflect higher bending loads incurred from the horizontally orientated head. Inclination of the head may therefore have reduced bending stress in carcharodontosaurian femora. Carcharodontosauria includes the smallest and largest allosauroids, and primitive members of its component clades had intermediate body sizes. Therefore adaptations for improved weight support appeared independent of size changes, prior to the evolution of large multitaxa. Similar changes occurred independently in tyrannosaurids suggesting these features are important and potentially related to body size, as functional requirements or adaptations predisposed by large size.

Geometric morphometrics of skull shape in frogs

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Lissamphibians are characterised as having lighter skulls than their Palaeozoic ancestors, with fewer, smaller cranial bones. This reduction in ossification is associated with a reduction in body size and, at least in frogs, increased agility for predator evasion and the capture of small motile prey. However, some taxa, notably *Ceratophrys* (Ceratophryidae, South America) and *Pyxicephalus* (Ranidae, sub-Saharan Africa), have reversed the trend and have large hyperossified skulls and a sedentary, 'sit and wait' predation strategy. To explore the relationship between skull morphology, lifestyle, and phylogenetic position, we analysed a broad sample of frog skulls in dorsal, ventral and lateral views. Each image was landmarked and, after Procrustes superimposition, landmark constellations were subjected to a principal components analysis. Hyperossified skulls are usually tall with relatively small orbits, but have evolved independently in several phylogenetically distinct lineages. Vertebrate predation is correlated with large size, relatively large adductor chambers, and posteriorly located jaw joints. However, the adductor chambers in members of the highly successful Bufonidae (true toads) are smaller than expected given their size and habits. This may be due to differences in muscle arrangement or to the use of a ballistic tongue mechanism in combination with a less powerful bite.

Morphometric analysis of cranial shape in fossil and recent Euprimates

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This study explores diversity and convergence in cranial morphology across primates using geometric morphometrics. 33 landmarks were gathered from 28 modern and extinct genera of euprimates (382 specimens), including the Eocene adapiforms *Adapis* and *Leptadapis*, and Quaternary lemurs *Archaeolemur*, *Palaeopropithecus*, and *Megaladapis*. Data were treated with Procrustes superimposition to remove all non-shape differences and then subjected to Principal Components Analysis. PC1 divided haplorhines from strepsirrhines and most fossil taxa with long and narrower skulls. PC2 involved a shift from haplorhines such as *Gorilla* and *Pan* from other haplorhines, strepsirrhines and adapiformes with shorter vaults and longer faces. PC3 chiefly showed widening and ventro-dorsal shortening of the vault with tarsiers at one extreme, *Archaeolemur* and *Cacajao* at the other and adapiformes overlapping with most haplorhines and strepsirrhines in the middle. On PC4 *Alouatta* and *Megaladapis* with a narrower and shorter cranial vault are divided from other strepsirrhines and some haplorhines at the other extreme. Although strepsirrhines and haplorhines are generally distinct in morphospace, there is some overlap along the major axes of variation. Most adapiforms fall within or close to strepsirrhine space, while Quaternary lemurs deviate from extant strepsirrhines, either exploring unique regions of morphospace or converging on haplorhines.

The mysterious early Middle Pleistocene Fallow Deer: a possible link between early Pleistocene 'Pseudodama' and recent *Dama dama*

Marzia Breda and Adrian M Lister
The Natural History Museum

The ancestry of the modern Fallow deer, *Dama dama*, has been tentatively traced back to Pliocene/Early Pleistocene forms referred to '*Pseudodama*', with unpalmed four-point antlers. By the late Middle Pleistocene, *Dama* with palmed antlers occurs, as *D. dama clactoniana*. However, fallow deer from the interim period, the early Middle Pleistocene, are poorly-known. A new specimen from Pakefield (Suffolk, UK), represented by a portion of cranium with a substantial part of both antlers plus a mandible and scapula, is the most complete small deer specimen from the British early Middle Pleistocene. The position and orientation of the basal tine, dental characters and mandibular morphology, are typical of fallow deer. The narrow palmentation is reminiscent of *D. dama clactoniana*. However, the lack of second (and third) tine in an adult specimen differs from both *D. dama dama* and *D. d. clactoniana*, being a primitive character shared with the last representatives of '*Pseudodama*', which, on the other hand, has a circular beam, lacking any palmentation. The presence of both primitive and advanced characters suggests it could be an early member of the stem group of recent Fallow deer. This will be tested by a cladistic study incorporating all skeletal elements.

Differing proportions of the anterior and posterior regions of the frontal bone in green and ocellated lizards

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The frontal bone of lacertids consists of a straight portion anterior to the sulcus interfacialis, and a posterior portion which is expanded laterally. The frontal of *Timon lepidus* (ocelated lizard) can be distinguished from that of *Lacerta viridis* (green lizard) by the differing proportions of the anterior and posterior regions of the frontal bone. The portion anterior to the sulcus interfacialis in *T. lepidus* forms approximately 1/2 of the whole length of the bone. For this reason, the posterior portion is more robust. The proportions of the anterior and posterior portions are approximately 1:1. The portion anterior to the sulcus interfacialis in green lizards is distinctly longer than the posterior one. Their proportions are approximately 3:2, in some individual cases even nearly 3:1. Ocelated lizards can occur together with green lizards (e.g., the Plio-Pleistocene locality Bad Deutsch-Altenburg). These differing proportions of the frontal region help to distinguish these two taxa. Acknowledgements: This project was supported by the Agency of Comenius University in Bratislava, G-10-153-00.

A quantitative comparison of a cranial foramen within extant Talpids: concerning ecological niche partitioning and trigeminal sensitivity.

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The Talpidae (Eulipotyphla) consists of small, insectivorous placentals that express a range of behavioural and environmental preferences including fossorial 'moles', semi-aquatic 'Desmans' and terrestrial 'shrew-moles'. Recent work on extant mammals has suggested that osteological cranial fossae may be used as signals from which we may interpret an organism's ecological niche based on the prevalence of cranio-sensory nervous complexes. In order to test whether the resolution of such methods is adequate on an inter-family scale, skulls from members of each genus within Talpidae were sampled to measure the caliber of the infraorbital foramina, through which the afferent infraorbital nerve exits the cranium and innervates mechanoreceptors on the maxilla. Data on infraorbital foramina area was collected on these 29 species (n=205) in order to elucidate whether closely related species differed in osteological architecture associated with somatosensory innervation. Results indicate infraorbital caliber significantly differs between both terrestrial and semiaquatic species as well as between terrestrial and fossorial species and that the caliber correlates with previously recorded numbers of specialized Eimer's organs on the rhinarium. However, exceptions to this latter result are presented and indicate limitations in fine-scale deductions concerning soft tissue anatomy from some cranial osteological morphologies.

Analyses of ligament tension in long necked animals indicates possible neck movement areas

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The length of the lig. nuchae and lig. flavum between the processus of each vertebra in various cervical joint flexions and the resulting tension of these ligaments give notice of the habitual neck posture and possible usage of the neck. Comparison of ligament tension of *Giraffa camelopardalis*, *Struthio camelus* and *Camelus ferus* shows areas of greater declination or inclination than other areas. The knowledge of these areas is useful to support possible habitual postures of the neck in recent animals or extinct sauropods with a greater database. For *Diplodocus carnegii* the results of the ligament tension analyses shows higher dorsoventral flexibility at the 9th and 8th cervical joint. This indicates that the centrum of greatest flexion lies in the middle of the neck and gives the cranial part a better mobility and consequently an increase in functionality (high browsing, orientation).

New material from the Kimmeridge Clay of England

Steve Etches

No bones about it: the enigmatic Devonian fossil, *Palaeospondylus gunni* reveals a novel vertebrate skeletal histology

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Palaeospondylus gunni (Devonian, Scotland) is an enigmatic vertebrate, assigned to various jawless and jawed groups since its original description. New serial sections allow description of a novel skeletal tissue for *Palaeospondylus*, comprising the entire skeleton, both cranial and postcranial. This tissue is a mineralized cartilage and is characterized by large cell spaces embedded in minimal matrix. A range of individuals of different sizes was examined in which cell spaces vary in size relative to the specimen length and bone is completely absent. Calcium phosphate mineralization has a differential topography of deposition within the cartilage that reflects a biogenic origin, despite subsequent diagenetic modification. This combination of hypertrophied cell spaces surrounded by regionalized mineralized matrix differs from all other cartilage in fossil and extant vertebrates, but compares most closely to endochondral bone in early developmental stages, a type of bone characteristic of osteichthyan vertebrates. Development is halted at this early stage, with no subsequent deposition of bone. Various genes are expressed during these stages, with a potential role of loss of gene regulation responsible for the *Palaeospondylus* skeletal histology.

Geographic variation of lower jaw shape in *Sphenodon* (Rhynchocephalia) from the Holocene of New Zealand

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The tuatara, *Sphenodon*, represents the only living member of Rhynchocephalia, a group that diverged from its sister clade Squamata (lizards and snakes) over 228 million years ago. For much of the Mesozoic, rhynchocephalians were diverse and globally distributed but their extremely sparse Cenozoic record is currently restricted to New Zealand. Nevertheless, the Holocene record (<11,180 ybp) of *Sphenodon* is extensive and shows that this genus was once widespread across the New Zealand mainland. Although recent New Zealand (>250,000 km²) comprises two major islands (effectively separate since 450,000 ybp), and a wide range of environments and biota, Holocene *Sphenodon* assemblages have never been surveyed for geographic variation. We landmarked 125 dentaries from four different localities (North Island: 2, South Island: 2) and following Procrustes fitting performed principal components analyses. Significant differences in jaw shape were found between the localities, for example jaws from Tom Bowling Bay possess a deeper and more curved ventral margin compared to jaws from Marfells Beach. However, a North-South Island divide was unclear. Apparent differences in jaw shape may reflect genetic variation or differences in bone remodeling caused by feeding on prey of different hardness.

The skull of the solemydid turtle *Helochelydra nopcsai* from the early Cretaceous of the Isle of Wight, United Kingdom

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Lydekker (1889) referred a partial shell and some fragments from the Barremian deposits of the Isle of Wight to the Purbeckian (Berriasian) taxon *Tretosternon punctatum*, but Nopcsa (1928) later referred the partial shell to *Helochelydra*. Given that *Tretosternon punctatum* has since been rendered a nomen dubium (Milner, 2004), Lapparent de Broin and Murelaga (1999) coined the name *Helochelydra nopcsai* for the Isle of Wight taxon with the partial shell of Lydekker (1889) and Nopcsa (1928) as the holotype. In 1998, Nick Chase discovered a near complete turtle skull and three associated shell fragments in Barremian sediments exposed on the Isle of Wight, England. Further collecting at the same site by Mick Green produced a mandible and remains of long bones and the pectoral girdle. All remains were

generously donated to Dinosaur Isle Museum, Isle of Wight. Though fragmentary, the shell remains allow confident referral of the new material to *Helochelydra nopcsai*. The purpose of this contribution is to describe the new specimen.

***Pseudohymenochirus merlini*: effects of miniaturization in pipid frogs**

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Miniaturization has evolved numerous times in many different groups of organisms and it has consequences for the morphology and development of species. In anurans, for example, miniature species are more likely to lose skull bones that ossify late during development in other, non-miniaturized anurans. Also, the number of phalangeal elements of the limbs is often reduced. In the present study, I compared the skeleton of the miniature pipid frog *Pseudohymenochirus merlini* to those of the closely related larger species *Xenopus laevis*. Specimens were cleared and differentially stained for bone and cartilage using Alizarin red and Alcian blue and the presence or absence of individual bony elements was recorded. The results confirm developmental differences between the miniaturized *Pseudohymenochirus merlini* and non-miniaturized pipids, for example relatively larger sensory capsules and a reduction in size of some skull elements. Furthermore, *Pseudohymenochirus merlini*-tadpoles are unique among frogs by retaining external gills throughout most of metamorphosis. External gills are only known from larval caecilians and urodeles. This also proves that, contrary to prevailing opinion, the development of *Pseudohymenochirus merlini* does not completely conform with the closely related *Hymenochirus boettgeri*.

The miserable story of *Ptychodus* phylogeny- Will we ever know?

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Ptychodus is an extinct shark ranging from the Albian to Early Campanian. Known only from teeth and limited associated disarticulated post-cranial material, its systematic affinities are debated. Since its discovery in 1822, *Ptychodus* has been assigned to teleosts, cestracionts, myliobatids, heterodontids and hybodonts. Species have been determined based upon dental ornamentation which varies greatly within both conspecifics and individuals. This, plus heterodonty and various dimorphisms, make this method of taxonomic allocation dubious and synonymy undoubtedly rife. The parallel rows and symmetrical pairs of teeth are reminiscent of batoids. However, the medial row is enlarged in the lower jaw and diminished in the upper, a feature found only in heterodonts. Prismatic cartilage in associated vertebrae place *Ptychodus* in the Neoselachii. Conversely, the jaw structure and tooth placement upon the symphysis allies it with hybodonts. As an extinct lineage of large shark, biological and ecological data will further our understanding of marine trophic structures and selachian ecology within the Cretaceous. Elucidating intra-familial and inter-ordinal relationships has implications for the phylogenetics of chondrichthyans as a whole and may provide evidence regarding relationships within basal lineages. This, the most recent phylogenetic study, uses a 'total evidence' approach to solving the riddle.

Skull biomechanics of *Isisfordia duncani* and crocodylian secondary palate evolution

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Recent analyses demonstrate dorso-ventrally flattened (platyrostral) crocodylian rostra are biomechanically sub-optimal at resisting feeding related loading forces and suggest the secondary palate evolved to assist the rostrum resist these loads. This study examines rostral biomechanics of the derived stem/basal eusuchian *Isisfordia duncani* using second moment of area analysis to calculate rostrum resistance to bending and torsion. 20 evenly spaced CT scan slices between the snout tip and palatal fenestrae of *Isisfordia duncani* with and without secondary palate were analysed and compared to equivalent slices from a comparably sized *Alligator mississippiensis*. Slices with secondary palates possessed I and J values greater or equal to slices without. Resistance increases due to the secondary palate are greater in the dorso-ventral plane compared to medio-lateral or torsional planes. In *Isisfordia* the secondary palate gave greater dorso-ventral bending resistance increase whereas the alligator secondary palate gave greater increased medio-lateral and torsional bending resistance. Results support conclusions from previous studies that the secondary

palate assists the rostrum accommodate feeding behaviour generated loading forces. Further biomechanical study of basal taxa is required to examine biomechanics as an evolutionary driving factor during early crocodylian secondary palate evolution.

Comparative biomechanics of the axial skeleton in potential extant analogues for early tetrapod locomotor function

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Morphological variation along the vertebral column, and its correlation with patterns of axial mobility, has been highly understudied in the field of locomotion biomechanics. Past work has primarily focused on proportional changes of the centrum – specifically length, width and height – with little attention paid to other areas of the spine that contain important biomechanical information (e.g. the neural arch, transverse processes and zygapophyses). This study examines a broad selection of phylogenetically disparate aquatic and semi-aquatic animals with very distinct modes of locomotion (e.g., salamanders, crocodiles, otters and seals) in order to tease out morpho-functional differences of the vertebral column. We have chosen these taxa for having aspects of vertebral form and function that might be partly analogous (or even homologous) with those in early tetrapods such as *Ichthyostega* and *Acanthostega*. The ultimate goal of this research is to gain a better understanding of the relationship between morphology and function of the vertebrate axial skeleton and to provide a comparative data base for exploring the locomotion behaviour and evolution of extinct animals such as early tetrapods.

Chondrichthyan skeletal preservation from the Carboniferous of Derbyshire, UK

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Calcified cartilage previously recovered from two localities of the Eyam Limestone Formation in the Peak District of Derbyshire is identified as chondrichthyan. Mechanical preparation of the silty limestone has revealed teeth and associated cranial and postcranial remains with multiple layers of prismatically calcified cartilage. The elements presented here include: cranial elements and a lower jaw attributed to a stethacanthid chondrichthyan on the basis of dental evidence (the former was previously identified as symmoriid), and a pectoral girdle attributed to the same. These are, further, tentatively attributed to *Akmonistion zangerli*, formerly known only from the Serpukhovian limestone of Bearsden, Scotland. Possibly associated distal fin radials exhibit an oval cross section comparable to the commonly non-circular cross sections seen in a wide variety of fossil and extant chondrichthyans. These elements, along with isolated dental remains, ally the Derbyshire fauna of the Lower Carboniferous with that of Bearsden, Scotland and of Bear Gulch, Montana.

Micro-CT scan technology applied to studies of fossil shark dentitions

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The anatomy and internal structure of teeth of the Palaeozoic sharks *Sphenacanthus hybodooides* Egerton, *Diplodoseleche parvulus* (Traquair), *Cladodus* sp., new Euselachians from the Permian of Brazil, together with the Jurassic shark *Hybodus medius* Agassiz were investigated utilizing Micro CT-scan technology. The radiographic images were processed using VG Studio Max software to investigate the capabilities of this relatively new and non-destructive technique on resolving dental features of extinct rare sharks. The micro-CT scan resolves structures larger than 20-30 microns for the size range of the teeth. Our results show that the 3D reconstruction of the dental vascular systems has potential to help define taxonomic groups, as the teeth vary in the size and number of vascular canals and foramina and on the pattern of their vascular networks. The type of dentine, either trabecular or orthodentine is clearly visualized. This technique also allows for the enameloid cover to be measured, although its crystallite ultrastructure cannot be resolved. Generalizations can only be made when further material is CT-scanned to establish if the patterns shown by these teeth are typical for these taxa or whether there are noticeable inter and intra-specific variations to be cautiously considered in systematic studies.

First record of the giant armadillo *Pampatherium mexicanum* from Aguascalientes, Mexico

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The giant armadillo *Pampatherium* is currently known from Pleistocene and Pliocene deposits in the State of Mexico, Puebla, Jalisco and Guanajuato. Recently, a fossil locality in El Cedazo creek, Aguascalientes, has revealed fragmentary remains assigned by its anatomical characteristics to the genus *Pampatherium*. The collected specimen consists of an articulated anterior left fragment of the carapace formed of 23 osteoderms, which possess the distinctive patterning of the genus: collapsed center, attenuated ornamentation, reduced or absent marginal band, as well as a general rectangular shape. There are three described species for this genus, two from South America and one from North America, *Pampatherium mexicanum*. Based on anatomy and geographic occurrence, the new specimen can be assigned to *Pampatherium mexicanum*, making it the first record of this species from the State of Aguascalientes.

The pterosaur collection at the Natural History Museum, London, UK: History, overview, recent curatorial developments and exciting new finds.

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The Natural History Museum's pterosaur collection is not large (approximately 1060 specimens), but has great historical and scientific importance. Pterosaurs from UK localities are well represented, but foreign material is also present as original specimens and as casts. The pterosaur collection was recently re-organised, and the drawers cleaned and re-sized to suit the height of the specimens. Most of the specimens were re-boxed, using clear-lidded specimen boxes. For large specimens, custom-made supports have been constructed using conservation-grade materials (Correx and Plastazote). These curatorial developments ensure that specimens are easily accessible to researchers, but are also protected. During 2009, all of the pterosaur collection was entered into a database (KE Electronic Museum), which is accessible at the Natural History Museum's website (www.nhm.ac.uk). The database includes taxonomic names, descriptions, localities, and stratigraphy. It also holds information relating to conservation treatments, loans, donors and citations. Photographs and PDFs of publications can also be added. Collection users have benefited from easier access to specimens and associated data. It is no coincidence that several important specimens have been recently discovered within the collections, all of which have been unrecognised since the 1800s.

Vertebrate localities in the Upper Cretaceous of Aix-en-Provence Basin (Southeastern France)

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The Aix-en-Provence sedimentary basin (Southeastern France) has been famous since the 19th century for its continental Upper Cretaceous levels characterized by the fluvio-lacustrine series rich in vertebrate remains (dinosaurs, crocodiles, turtles, pterosaurs, mammals, fishes). A number of studies made on the paleontological record of Provence have led to a better understanding of specific taxa or localities but never with the purpose of a broader knowledge at the scale of the basin. Moreover, available faunal lists were considered as a single set, generally dated as Late Campanian-Early Maastrichtian, comparable with those from the other coeval fossiliferous regions of France and Europe (Spain, Transylvania). This study presents discoveries resulting from important recent campaigns of excavations conducted at different new localities in Aix-en-Provence Basin and its surroundings, but also historical and unpublished discoveries. The different faunal assemblages in question are presented in their stratigraphical and palaeoenvironmental contexts which are very different according to the studied area. The compilation of these data provide a better understanding of Late Cretaceous continental vertebrate biodiversity (particularly for morphological variability in titanosaurs), and of the evolution of the assemblages in the Aix-en-Provence Basin in time as well as in space.

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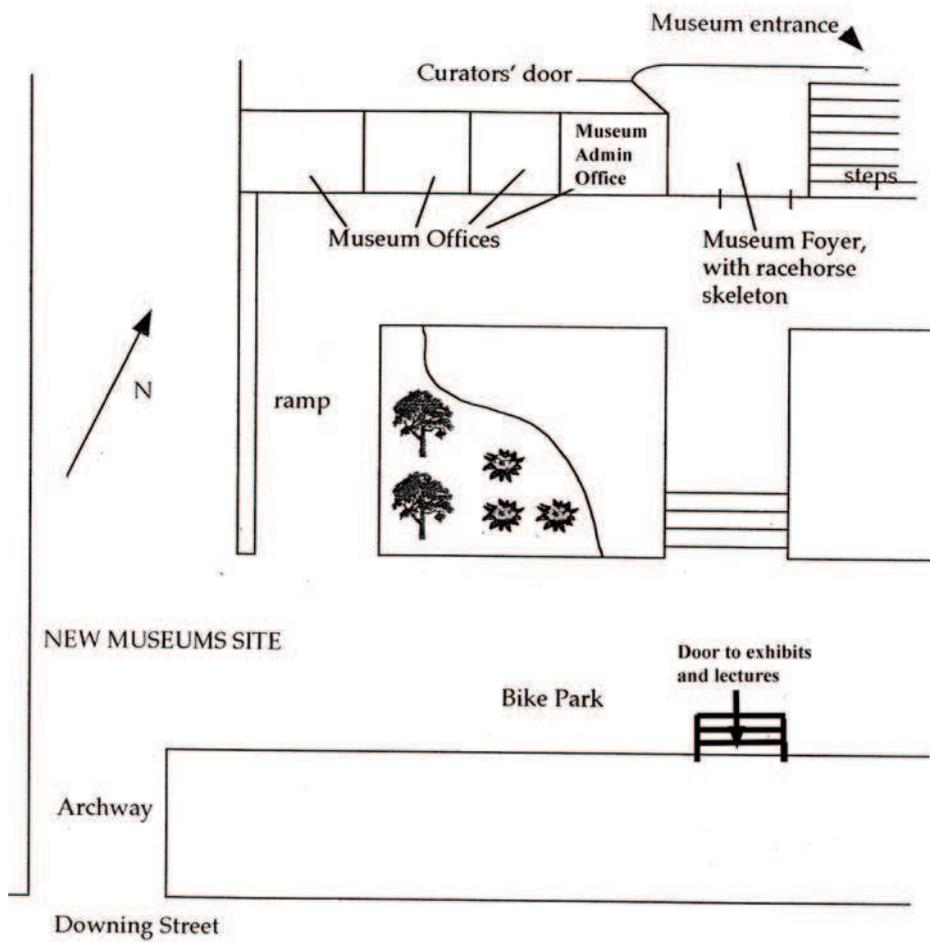
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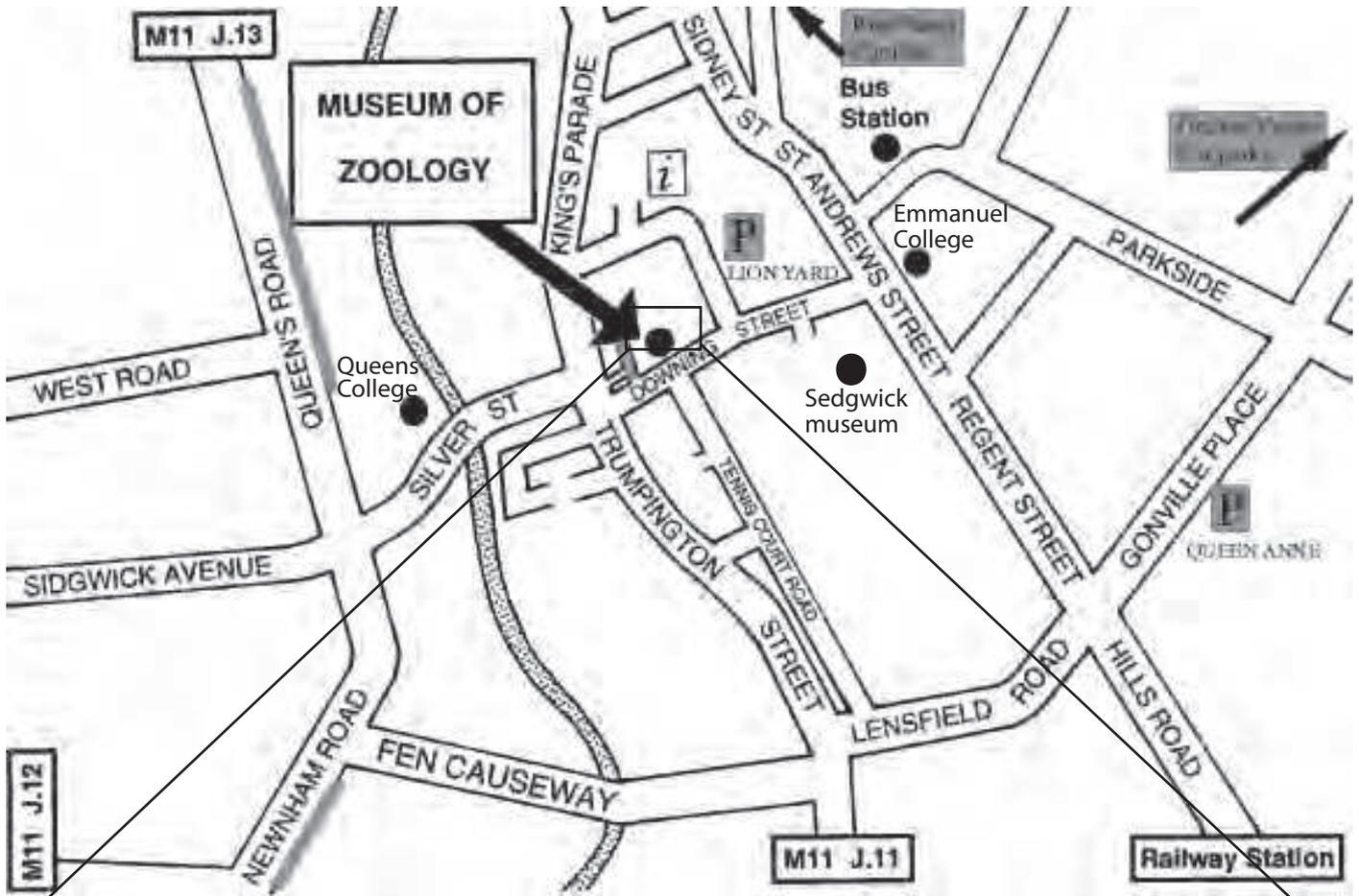
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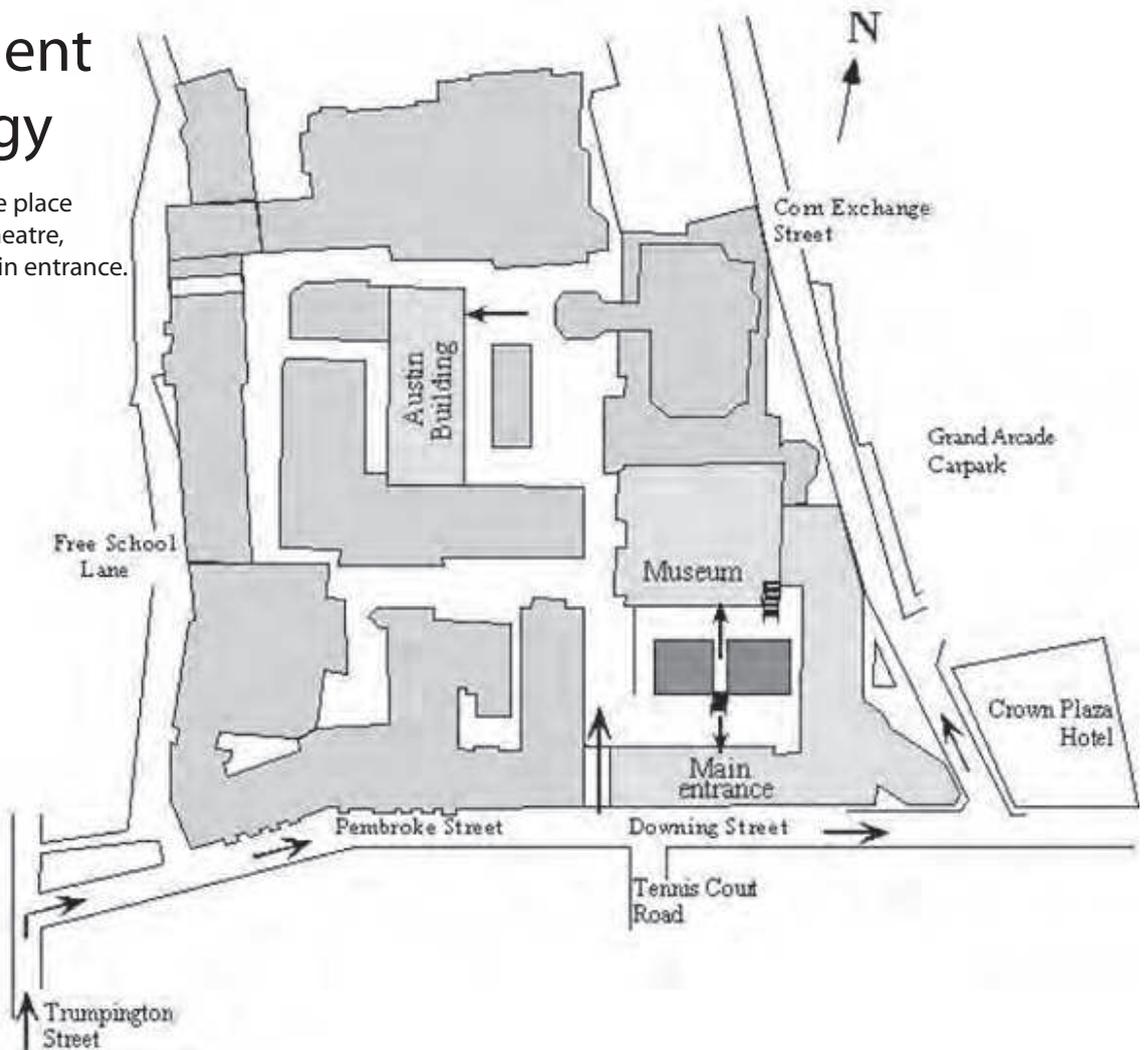
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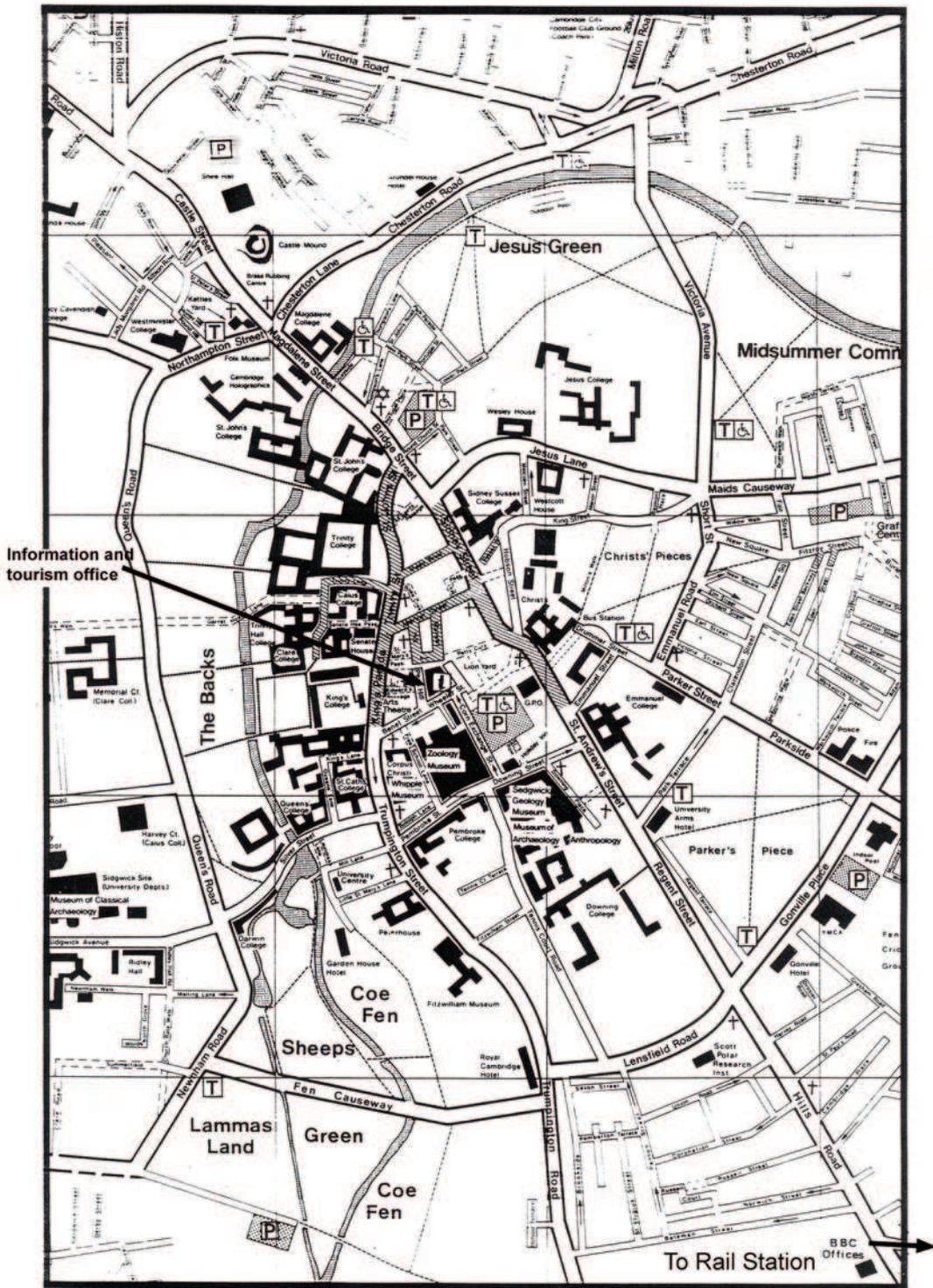




Department of Zoology

Talks and posters take place in the main lecture theatre, accessible via the main entrance.





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