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SYMPOSIUM OF VERTEBRATE PALAEOLOGY
& COMPARATIVE ANATOMY

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LYME REGIS 2011

Abstracts of Presentations

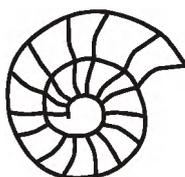


**59th Annual Symposium of Vertebrate Palaeontology and
Comparative Anatomy**

**20th Symposium of Palaeontological Preparation and
Conservation**

Geological Curators' Group

held in



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SPPC Papers

Bringing sea dragons back to life: 200 years on from Anning, Conybeare and De la Beche.

Mark Evans

New Walk Museum and Art Gallery, 53 New Walk, Leicester, UK, LE1 7EA

The Geological Galleries at New Walk Museum, Leicester, are being redisplayed. The main objective of the new gallery is to present examples of the evidence and methodology underlying the reconstruction of extinct organisms, focussing on charismatic dinosaurs and marine reptiles. Harking back to Henry Thomas De la Beche's *Duria Antiquior*, reconstructions of the living organisms and their environments were to be a vital part of the gallery's interpretation. We commissioned palaeoartist Robert Nicholls to produce paintings and reconstruction drawings which produced a valuable collaboration between artist and curator.

However, the expectations of the modern museum visitor have been raised. We therefore decided to produce a computer generated animation of the Oxford Clay. Robert Nicholls sculpted maquettes of 7 animals from the Oxford Clay and these were subsequently laser scanned. Our initial idea was to commission an animated video which would be played on a loop and projected onto an overhead screen, so that the visitor becomes immersed in the environment. However, Leicester-based virtual reality specialists Maelstrom suggested an alternative where the scene is rendered in realtime so that the visitor never sees the same sequence of events. The system also allows for extra interpretation on the animal in focus to be displayed on a separate monitor, and for multiple views of the scene to be rendered. The visitor can control an interactive display and zoom in and out. Sample footage will be presented.

Accessing Palaeontology in a Local Museum

Philip Hadland

Canterbury City Council Museums Service

Kent is a region of surprising geological heritage and a diverse range of fossil deposits can be found within the county. Canterbury's Museums feature fossil collections, dating back to the early days of palaeontology reflecting the spectacular variety of collecting opportunities available. For several years Canterbury's Museum service has exploited a variety of ways to engage the public with their local geology and the science of palaeontology. More recently, work has been undertaken to enhance the accessibility of palaeontological collections held by Canterbury's Museum Service.

The UK Continental Shelf on the move: transferring two major core and sample collections.

Mike P. A. Howe

British Geological Survey

The British Geological Survey (BGS) manages the national borehole archive, with corestores at Keyworth, Nottingham, holding samples and cuttings from over 15,000 onshore boreholes, including 250 km of core. The marine corestore at Loanhead, Edinburgh, held 12,000 metres of core and 15,000 seabed samples, and the UK Continental Shelf corestore at Gilmerton, Edinburgh, contained DECC's UK seaward hydrocarbon well cores and samples from over 8,000 wells, with 300 km of core and 4.5 million samples of cuttings.

In 2009, the decision was taken to consolidate the core holdings into a single "state of the art" facility at Keyworth. Because of the importance of the Gilmerton material to Britain's energy security, the BGS worked closely with a group of advisors to develop and monitor a safe transfer methodology. The move required 125,000 boxes of core and 47,000 boxes of cuttings to be packed into caged pallets and transferred to Keyworth within 18 months. Every box of core (often containing three internal boxes) was opened, the contents photographed (7216x5412 pixels) and additional conservation grade packaging added to protect the material during transit. Adoption of a production line technique, coupled with the extensive use of barcodes and database systems, is enabling the transfer to proceed on target. It has also provided a unique opportunity to audit 100% of the core, adding metadata or conservation issues to the database. QC inspection of the core on arrival at Keyworth has failed to detect any transfer damage.

Resourcing Palaeontological Collection Care in a Time of Crisis: The Legacy of the Earth Science Review, Twenty Years On

Jeff Liston

Division of Environmental & Evolutionary Biology, University of Glasgow

The current round of cuts resulting from the global financial crisis once again places museum collections in a vulnerable position in terms of resource allocations from funders national, regional and private. Often, cuts in institutional funding are proposed in the context of being intended to reshape an organisation for a more streamlined role, better designed to meet the challenges of the future. But however well museums are redesigned, they rarely escape being

viewed as legitimate targets for funding cuts whenever a new round of belt-tightening comes up. The inherent implication of the language of institutional reshaping is that a certain amount of protection, if not immunity, will be conferred on the museum come the next round – but that rarely happens. This is true from all ranges of funders: it is simply hard in political terms for funders to justify resources going to cultural preservation instead of hospitals or nursery education.

Within museums, geological collections traditionally have a particularly hard time in terms of funding and justifying their existence. Whereas artworks, archaeological, historical or ethnographic objects appear to have an intuitively obvious value to external assessors, arguing the case for natural science in general, and geology in particular, has always been an uphill struggle.

This presentation will review how an unusual manifestation of this phenomenon in the late 1980s - the Earth Science Review, when cuts in funding actually led to an increase in long-term funding for some geological museum collections - has survived to the present day.

How Long? Preparation of the Weymouth Bay Pliosaur.

Scott Moore-Fay

Wavecut Platform Ltd

Between 2002 and 2006 a large quantity of bones and bone bearing concretions (more than 32) were found washing out of a landslip in Weymouth Bay and collected, mainly by a single collector, Kevan Sheehan. These pieces, some weighing as much as 80kg, were subsequently identified by Richard Edmonds as the skull of a huge pliosaur and were purchased by Dorset County Council using funds provided by the Heritage Lottery Fund.

Scott Moore-Fay (freelance preparator) successfully bid for the contract to prepare and mount the skull and lower jaws. Find out how long it takes to prepare a 2m pliosaur skull? Where do you start? What tools do you use? Were there any problems? What information has the preparation helped reveal?

The finished skull is now on display in the Geology Gallery at Dorchester County Museum.

Acid Preparation of a pond turtle from the Eocene Mo clay formation of northern Denmark

Frank Osbæck

Museernes Bevaringscenter i Skive

In 2010 an extremely well preserved Pond turtle (*Owenemys* sp.) was prepared at the preparation laboratory of Museernes Bevaringscenter i Skive. In 2011 it was returned with the request to prepare the specimens ventral side, exposing the plastron, a crucial diagnostic element.

The preparation produced a 3 dimensional prepared specimen, with a perfectly preserved plastron and more than 27 new bones including a femur, fibia, several bones from the foot and 6 tail vertebra. Together with the previously prepared dorsal side with the skull, large parts of the extremities, neck and tail vertebrae (57 in all), the specimen represents one of the best preserved Eocene turtles from the London Clay period.

The preparation of the ventral side was documented with stop motion technique showing the matrix, consisting partly of calcareous concretion known as cement stone, partly of calcium bound volcanic ash, slowly "disappearing" during preparation.

The specimen has not yet been described, but will undoubtedly give a unique new insight into Eocene Pond turtles.

Simplifying extraction and cross sectioning of microfossils in unlithified sediment

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Preparing micro-fossils can be a slow and costly affair because of difficulties in preparation and/or the need of expensive laboratory equipment. Here we present a low-tech solution to extract microfossils from unlithified sediment and preparation of cross sections.

The Late Miocene (late Serravallien and Tortonien) Gram Formation in Southern Denmark is well known for its many whale fossils. However, many other vertebrates and invertebrates are found in the Gram Clay leaving e.g. coprolites, tests, denticles, shells, bone- and teeth-fragments of micro-scale behind as fossils. The sticky, grey-brownish clay makes it difficult to spot fossils of sizes less than a few millimetres and wet sieving of the sediment is necessary for extraction. A nest of sieves with mesh sizes 1-0.063 mm and a mechanical shaker is traditionally used. Extracting the microfossils and fragments from the clay sediment using an old washing machine and a pair of nylon stockings have also proven to be an effective method and is a cheap and easy supplement to wet sieving.

A method for producing cross sections of crystals has been adapted to simplify the preparation process when making cross sections of microfossils and small fragments. Specimens are mounted on a compact disc using special double-sided adhesive film. A completely plane surface is thereby obtained minimizing the grinding afterwards. The flexible CD is easily

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removed after hardening of the epoxy. A CD can also be used as base when producing moulds of small fossils.

The Bristol Dinosaur Project – Preparation Methods

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The Bristol Dinosaur, *Thecodontosaurus antiquus*, lived on small islands in a Rhaetic transgression environment about 200 million years ago amongst other animals. Much of the associated fauna remains are often very small ($\leq 1\text{mm}$) and have been found in karstic fissure fills alongside *Thecodontosaurus*.

These micro fossils are sometimes overlooked; this is for many reasons, i.e. low budgets, the need for fast results for publication, among others. Although much of the microfauna from this fissure has been described in earlier publications by David Whiteside, much more remains to be prepared, sorted and studied. The Bristol Dinosaur Project (BDP), now funded by the Heritage Lottery Fund, aims to retrieve more of the minute fossil remains from all those reptiles and fishes that co-habited the islands with *Thecodontosaurus*. This is no small task and a preparator is hired to achieve these results, recruit and supervise volunteers to work through much of the remaining estimated 4 tonnes of fossiliferous rock.

Due to their nature, microfossils are very fragile elements and cannot be removed from the rock with the "traditional" methods of preparation, such as hammers and chisels or even air scribes. Instead the rocks are acid prepared, using acetic acid. In this paper we describe in detail the whole process of acid digestion at the BDP, the retrieval of all the microelements from the rocks and how they are treated subsequently until they are made available for handling for research. The process of preparation is actively contributing to the research value of the material.

SPPC Posters

Building Conservation Grade Support Systems for the Long-Term Storage of Fossil Vertebrates

E Vervenioutou, A Bernucci, and L Allington-Jones
The Natural History Museum (London, UK)

This poster presents the fabrication of support systems for long-term storage of vertebrate palaeontological specimens. The conservation unit in the Palaeontology department at the Natural History Museum, London UK, is regularly presented with opportunities to develop mounts for heavy, complex-shaped and often fragile specimens. The mounts have to be both strong and light-weight. They must fully support the specimen without applying pressure to weak points and allow maximum access with minimal handling. Using the laminating epoxy paste Epopast 400 as a primary material, the poster presents various support solutions that meet the above criteria and combines user-friendly, space-efficient and functional design features. The use of Hexlite (aluminium honeycomb board) and Plastazote (polyethylene foam) in combination with the use of Epopast 400 is discussed and practical information for the construction of the mounts is given. The long-term stability of the materials presented in this poster is established through the application of modified Oddy testing carried out by the conservation unit of the Palaeontology department. The project concludes that these materials are suitable for long-term storage solutions and Epopast 400 is a versatile support medium, especially suited to fossil vertebrates.

A very primitive tetrapod from the earliest Famennian of South Timan, Russia

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Three field seasons collecting in the Sosnogorsk Formation, a basal Famennian lacustrine or lagoonal deposit from present-day South Timan, Russia, has yielded an extensive collection of cranial, mandibular and some postcranial stem-tetrapod bones.

All bones are attributable to a single previously unknown species, on the basis of a shared distinctive ornament and close morphological match between duplicate elements. The material also includes an articulated snout and several articulated skull tables, enabling us to present a provisional but fairly well constrained skull reconstruction. We tentatively identify it as a tetrapod *sensu stricto*, i.e. a taxon with limbs rather than paired fins, because a cleithrum + partial scapulocoracoid shows a characteristic tetrapod morphology, similar to *Ichthyostega* and quite different from *Panderichthys* or *Tiktaalik*. However, the material shows a number of primitive characteristics suggesting that it is the least crownward of known tetrapods. The snout does not have the typical tetrapod spade shape, vomeral morphology is intermediate between the elpistostegid and tetrapod conditions, the pterygoids are separated by the parasphenoid, the braincase has a well-developed crista parotica attached to the skull roof, the postorbital separates the squamosal from the supratemporal as in *Tiktaalik*, and the cleithrum carries dermal ornament.

The Sosnogorsk Formation tetrapod will thus provide important data for character polarization among stem-group tetrapods. Notably, its otoccipital braincase differs from those of *Ichthyostega* and *Acanthostega*, themselves very different from each other, but represents a pattern that could be antecedent to both.

Owen's pterosaurs, old fossils shedding light on new clades

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The Natural History Museum, London, has one of the oldest and largest collections from the over two-hundred years of pterosaur discovery. New discoveries are still being made in these collections that date back to the establishment of the museum.

In 1884, Sir Richard Owen presented a partial pterosaur skull to the museum from the Middle Jurassic of Stonesfield, Oxfordshire. The relationships of this specimen have been a mystery until the current study likely due to its enigmatic characters. The combination of characters found in this specimen was unknown in other pterosaurs until the recent discovery of the wukongopterid pterosaurs in China. Through use of the Natural History Museum's Imaging and Analysis Centre, CT-scans reveal the morphology of the alveoli and palate hidden in matrix and confirm that this specimen is the oldest wukongopterid. However, Owen's specimen and others he reported from Stonesfield that are also referable to the Wukongopteridae lack the elongate skull and cervical vertebrae thought to unite the wukongopterids with the pterodactyloids in a group named the Monofenestrata. These and other characters were used to argue that the pterodactyloid skull and neck evolved first in the wukongopterids and were a separate module from the body and limbs. Phylogenetic analysis of these specimens confirms that they belong to the Wukongopteridae in a monophyletic Monofenestrata. The pterodactyloid skull evolved first in phylogeny, and modules were present in pterosaur evolution but were smaller and more numerous than two large modules dividing the body into craniocervical and postcervical regions.

Dental eruption in Southern Placental Mammals

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Relative to most mammals, xenarthrans (sloths, anteaters, and armadillos) have a very distinctive dentition. Anteaters lack teeth completely; armadillos and sloths show homogeneous, peg-like teeth, often characterized as lacking both enamel and diphyodonty. In fact, the armadillo genus *Dasypus* exhibits both a narrow layer of enamel and a replacement generation, and appears to be the only xenarthran with two generations of teeth.

It is not yet known if the pattern of deciduous tooth eruption in *Dasypus*, or replacement of its deciduous set by permanent teeth, resembles patterns exhibited by other clades of mammals. The possibility that "late eruption" of the permanent dentition, as observed among endemic African mammals, also characterizes *Dasypus* has not yet been definitively tested. Here, we present data showing that *Dasypus* reaches adult size prior to the completion of dental replacement, consistent with the hypothesis that it exhibits an afrotherian-like pattern of dental replacement. In addition, we compare data on dental eruption of the deciduous teeth using developmental series of mammalian embryos and fetuses, including *Dasypus*, and ask to what

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extent armadillos and afrotherians exhibit more diversity within vs. among their constituent clades.

A new skull of *Apatosaurus* and its taxonomic and palaeobiological implications

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Complete sauropod skulls are rare, hampering attempts to investigate their palaeobiology and systematics. Here, we report an undescribed skull of *Apatosaurus* from the Brushy Basin Member of the Morrison Formation (Kimmeridgian–Tithonian: Late Jurassic) of Emery County, Utah (Cincinnati Museums Center [CMC] VP 7180).

This specimen is unique among those previously referred to *Apatosaurus* as it was found in direct articulation with a cervical series that unequivocally confirms its identification – all other skulls have been attributed to the genus on the basis of deduction, rather than first-hand observation. The skull of CMC VP 7180 is substantially complete, though the palate is badly damaged and incomplete, and is in articulation with both mandibles, the first to be reported for the genus. The rest of the specimen includes an incomplete cervical series, poorly preserved, incomplete dorsals and other indeterminate fragments. The skull has been CT-scanned, to produce a detailed endocast, that provides substantial information on neuroanatomy and the otic capsule. As predicted previously, the mandible is extremely similar to that of *Diplodocus*, with an elongate craniomandibular joint, supporting the probable use of translational jaw movements. Details of the cervical vertebrae preclude referral of the specimen to *A. louisae*, a conclusion supported by minor differences between the basicrania of this taxon and CMC VP 7180, which probably reflect genuine taxonomic features. Current data suggest a referral of CMC VP 7180 to *A. ajax* is more likely, which would substantially increase the amount of phylogenetic character information available for this species.

High diversity, low disparity and small body size in plesiosaurs from the Triassic–Jurassic boundary

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Sauropterygia is the longest-lived clade of secondarily marine tetrapods. Their derived representatives, Plesiosauria (Jurassic–Cretaceous [199.6–65.5 Mya]) successfully adapted to life in the open ocean with a unique body plan comprising a stiff trunk, four large propulsive flippers, and highly plastic body proportions, including taxa with extremely long necks.

The European record of Early Jurassic plesiosaurians is abundant. However, due to lack of research focus, our understanding of early plesiosaurian evolution is poor compared to that of other marine tetrapods such as ichthyosaurs and cetaceans. We review the earliest plesiosaurian fauna, known primarily from the lowermost Hettangian of Street, Somerset, UK. Three new taxa are identified: a plesiosauroid and two small-bodied rhomaleosaurids. Thus, plesiosaurian diversity was high immediately following the end-Triassic extinction event, comparable to that in younger well-sampled horizons of the Sinemurian and Toarcian of Europe. In contrast, phenetic disparity and range of body plans are low in the earliest Jurassic and increase monotonically through the Lower Jurassic. This suggests adaptive radiation following invasion of the pelagic zone, or possibly following decimation during a Late Triassic extinction event. An increase in maximum and minimum body sizes during the Lower Jurassic suggests a driven trend associated with invasion of the open ocean.

A new phylogenetic analysis recovers Pliosauridae and Plesiosauroidae in a monophyletic Neoplesiosauria that excludes Rhomaleosauridae. Many nodes within Rhomaleosauridae likely split before the Triassic–Jurassic boundary. Pliosauridae and Plesiosauroidae radiated during the Lower Jurassic at the expense of Rhomaleosauridae.

Tetrapod evolution through the Permian and Triassic: rock record, supertrees, and detecting events

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Studies of macroevolution depend on an adequate fossil record, and investigators should ensure that their data are sufficient to test relevant hypotheses. In such studies it is therefore appropriate to assess the data for error, whether from geological (incomplete rock record) or human (variable study effort) failings. Error is relevant only to the question in hand, so a fossil record that works well for one study may be inadequate for another; so, a statement that the dinosaur fossil record is good or bad is meaningless. Some studies of vertebrates through the Permian and Mesozoic have applied inappropriate sampling proxies (SPs) that do little to reveal

whether the record in question is good, bad, or adequate. This is because many popular SPs are redundant with the signal they seek to assess or correct (e.g. 'number of formations' is often correlated with 'number of contained fossils' because the measures are linked).

A key macroevolutionary theme is clade diversifications, whether following a mass extinction, the evolution of an important novelty, or some other cause. In exploring the greatest mass extinction of all time, at the end of the Permian, some investigators have assumed that the tetrapod fossil record is inadequate. However, preliminary studies have shown that the times of lowest diversity in the Early Triassic were times of most intense sampling. Taking this further, we present new evidence on the mass extinction and the recovery from three sources: biodiversity through time; ecosystem or alpha diversity; and disparity (= morphological variance), to explore pre- and post-extinction models. SPs, including number of formations, number of specimens, and specimen completeness are deployed at regional and global scale to monitor error and evenness of sampling in these cases. Recovery from the mass extinction occurred in three phases, with rapid initial filling of ecospace by putative 'disaster' taxa, then building ecosystem complexity, and finally addition of top carnivore taxa, some occupying entirely novel niches. Generally, disparity races ahead of diversity, as taxa explore morphospace and then fill in the gaps.

The Completeness of the Fossil Record of Mesozoic Birds

Neil Brocklehurst¹, Paul Upchurch¹, Philip Mannion¹ and Jingmai O'Connor²

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There have been a great many studies looking at the completeness of the fossil record from a sampling point of view, endeavouring to answer such questions as whether or not we have a nearly complete list of species. However, there have been few looking at the completeness of the specimens themselves.

An assessment is made of the completeness of the fossil material of the 120 species of Aves from the Mesozoic, using a recently proposed character completeness metric which determines the percentage of characters from a list of 655 which can be scored for a particular specimen. These results were plotted against geological time and compared to different diversity estimates, sea level, and environment. The completeness scores were also plotted against latitude to observe the effect of human sampling bias. The completeness scores vary greatly from the late Tithonian to the end of the Cretaceous, with peaks during the late Tithonian, the later stages of the Lower Cretaceous, and the Santonian, and troughs during the Cenomanian-Turonian and the Maastrichtian. The completeness metric correlates more strongly with a residual diversity curve based on the number of dinosaur bearing formations than with the raw taxic diversity curve. There is no correlation of completeness with sea level, the number of fluvial/lacustrine localities or the character completeness metric of Sauropodomorpha. The poor completeness of specimens found during the Upper Cretaceous calls into question interpretations of avian evolution based on the fossil record.

A ctenochasmatid pterosaur from the Stonesfield Slate (Bathonian) of Oxfordshire, England.

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Pterosaur remains from the Stonesfield Slate (Taynton Limestone Formation, Middle Bathonian) of Oxfordshire were first identified by Buckland in 1829. Following work by Huxley (1859) and Seeley (1880), it was long accepted that only the single genus *Rhamphocephalus* Seeley, 1880, a rhamphorhynchid, was present in the Stonesfield Slate. Re-examination of the anterior end of a lower jaw bearing numerous long slender teeth in the Oxford University Museum of Natural History, originally described by Phillips (1870) and referred by him to the crocodylian *Teleosaurus subulatus*, shows that it actually belongs to a pterosaur clearly different from *Rhamphocephalus*, which has a shorter symphysis and fewer and larger teeth. Its characters show that it belongs to a ctenochasmatid pterodactyloid reminiscent of *Gnathosaurus*, from the Tithonian "Plattenkalk" of Germany and the Berriasian Purbeck Limestone of England. A number of isolated teeth from Stonesfield can be referred to this form. It is the earliest known representative of the Ctenochasmatidae, and one of the earliest known pterodactyloids.

The diversity of the pterosaur assemblage from the Stonesfield Slate is higher than previously recognised, comprising at least three taxa: the rhamphorhynchid *Rhamphocephalus*, a *Darwinopterus*-like form briefly mentioned by Steel (2010), and the newly identified *Gnathosaurus*-like ctenochasmatid.

Continuous character states and their impact on the phylogeny of the Pterosauria

David Button, David Unwin and Mark Purnell

University of Leicester

Recent years have seen the publication of numerous cladistic analyses of pterosaurs, but consensus remains elusive. The high proportion of continuous characters in pterosaur analyses offers a potential explanation for this problem. The use of continuous characters in phylogenetics is controversial primarily because there is no reliable or objective method for coding them into discrete states for analysis. Inappropriate and inconsistent delimitation of states may be contributing to the lack of reconciliation between analyses.

In order to test this possibility two recent contrasting analyses of Pterosaurs were repeated in TNT, which is capable of handling raw values, circumventing the need to delimit states. Experimentation with continuous character inclusion and exclusion indicates that whilst continuous characters do provide some phylogenetic signal, many such characters and the majority of character states are irrecoverably flawed. Varying the treatment of continuous characters demonstrates no significant role in the conflict between pterosaur phylogenies, this instead owing to fundamental differences in general character selection and coding between analyses. Some theoretical and practical issues with continuous characters, especially for groups with small sample sizes such as pterosaurs, prevent their use from being generally recommended. However, as they show some phylogenetic signal, they cannot be omitted outright. Rather than ruling out entire classes of data based on presumed weaknesses it would seem more prudent to critically evaluate all characters on the grounds of the hypotheses of homology they present. Such transparent and thorough reappraisal of character selection and coding will be necessary to reach consensus in pterosaur phylogeny.

A *Crassigyrinus*-like lower jaw, and other vertebrate elements, from the Tournaisian of Scotland.

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The early tetrapod *Crassigyrinus* was a large aquatic predator from the late Early Carboniferous (late Viséan or early Serpukovian) of Scotland, 327–323 MY in age. There are five main specimens: an articulated skeleton, two incomplete skulls and two lower jaws.

Crassigyrinus retains several apparently primitive features of the palatal dentition and lower jaw, and its phylogenetic position is disputed. In summer 2010, as well as rhizodont and lungfish elements, we excavated and prepared a partial tetrapod lower jaw from the Borders Region. These are dated as late Tournaisian, CM palynozone, 348–346 MY in age. Though it lacks dentition, the jaw preserves much of the lower margin, whose external appearance is almost indistinguishable from that of *Crassigyrinus scoticus*. Yet it is dated around 20–25 million years earlier. Internally the jaw shows similar primitive features to *C. scoticus*, as far as can be seen, but these areas are poorly preserved or obscured in all *C. scoticus* specimens. They are under current investigation, to establish how, or if, they differ from the Tournaisian specimen. Apart from external features, all specimens are similar in one other respect: they are all of a similar skull size, to within a 2.5% difference allowing for measurement error.

Considered as more than coincidence in samples so disparate in time, this could indicate a long survival period for the genus, and the possibility that *Crassigyrinus* reached a maximum size. This would further imply determinate growth in this early tetrapod.

Teleost superiority: a foregone conclusion? Patterns of teleost and holostean diversification in the Mesozoic.

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Teleosts are the dominant living group of aquatic vertebrates; they comprise approximately 29,000 species, assume a bewildering array of morphologies, and have come to occupy nearly every environment imaginable. In extreme contrast, their holostean sister group comprises a mere 8 living species, all of which are restricted to the freshwaters of eastern North America. It is this pattern of extreme contrast, gleaned from living taxa alone, which has provided the basis for assertions of teleost 'superiority' and fuelled a series of evolutionary scenarios. However, the fossil record indicates that these groups arose in the Permian, and so around 280 million years of diversification has been largely excluded from the debate.

By reconstructing the historical diversity trajectories for these groups, we can establish the pattern by which teleosts came to dominate. We quantified taxonomic and morphological diversity for holosteans and teleosts from the Permian to Jurassic (spanning 65% of their joint history), with a third measure, functional diversity, to be the subject of future work. Our taxonomic and morphometric dataset suggests that across the 50 million years of the Triassic, holosteans were in fact more diverse than teleosts, both taxonomically and morphologically. However, teleosts expanded their range of morphologies greatly in the Jurassic, and their taxonomic diversity continued to grow throughout this period. This continued teleost

diversification led them to overtake holosteans during the Jurassic, signalling a 'switchover' event at this time.

Chondrenchelys, chimaeroids and early holocephalans

Michael I. Coates and John A. Finarelli

University of Chicago

Living holocephalans (ratfish, rabbitfish, elephant sharks) are being used to investigate fundamental questions about the biology of early gnathostomes. As such, fossil holocephalans provide an essential phylogenetic context within which to understand data and hypotheses derived from these extant subjects. We are re-describing the skeletal anatomy of *Chondrenchelys problematica* (Viséan, Glencarholm, Scotland), perhaps the best-preserved early holocephalan, using three, exceptionally preserved, new specimens, two of which are from S. P. Wood's Mumbie fish quarry excavation. Modern holocephalans display numerous distinctive morphologies, including toothplates and holostylic jaws. *Chondrenchelys* exhibits several of these characteristics, and a recent study of its unusual dentition (including toothplates that are remarkably similar to Mesozoic examples), challenges accepted hypotheses of holocephalan toothplate formation and provides a new perspective on early gnathostome dental development. However, other crown-group synapomorphies are absent. The gill skeleton is not sub-otic, the jaw articulation is posterior to widely-separated orbits, the ethmoid canal is absent, and the axial skeleton is not polyspondylous. Importantly, *Chondrenchelys* highlights the distinctive apomorphies of modern holocephalans, separating the crown group from the late Palaeozoic ratfish radiation. Furthermore, we note that the short postorbital region and high-walled rostrum of *Chondrenchelys* imply that the jaw adductor muscles inserted pre-orbitally, as in extant holocephalans. This suggests that the unique holocephalan masticatory apparatus and the sub-otic position of gill arches are distinct morphofunctional complexes and are not causally linked, as has been hypothesized.

All Yesterdays: Unexpected and Unusual Reconstructions of the Past (That We Don't Know are Wrong)

John Conway and C. M. Koseman

(to be presented as Ice-Breaker, Skittle Alley, 17:00 Tuesday 13th September)

Reconstructing extinct vertebrates can be approached in a strictly methodological way, by weighing likelihoods and piecing together the most probable appearance of any given animal based on what is currently known. However, it is often the case that new information takes us by surprise—animals are often stranger than we would have imagined.

In this presentation, we will take the opposite approach to the one we usually do as paleontological artists, and explore the possibilities rather than the probabilities. Inspired by recent debates in palaeontological art, we took part in an exercise of plausible speculation with novel forms of integument and display structures, as well details of life such as disease, inter-species interaction and play behaviour that is rarely displayed in contemporary palaeontological art.

While we agree that the purpose of palaeontological art is to mainly display the latest knowledge about extinct animals, it can also serve as an arena to propose new hypotheses, rather than repetitively drawing proven theories. In the history of palaeontology, out-of-the-norm images have been crucial in popularising new notions about the appearance and behaviour of extinct animals. While we are aware that some of our reconstructions will probably be falsified, some may actually "hit the spot," or may even look modest when compared to new fossil discoveries.

Patterns in the origin of multicuspid teeth among terrestrial amniotes – early adopters from Devon

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The origin of multicuspid teeth is frequently considered a key evolutionary innovation, especially of mammals. However, multicuspid teeth have independently been acquired by many vertebrates. Here we concentrate on terrestrial amniotes to examine morphological, developmental and ecological patterns shared across these independent origins.

Examining taxa in a phylogenetic and chronological context, we first analysed the Procolophonoidea, a Permian/Triassic (255 to 200 MA) radiation of small reptile-like animals within the wholly extinct clade Parareptilia. All Permian taxa had numerous, conical teeth, but Triassic species evolved a wide diversity of heterodont and/or multicuspid dentitions. To examine dental morphology, we micro-CT scanned lower and upper jaws of the Triassic procolophonid *Kapes bentoni* from the Otter Sandstone Formation, east Devon. Tomographic models of the internal structure of the teeth show an Enamel Dentine Junction (EDJ) and pulp cavity which mirror the shape of the bicuspid molar teeth. We hence consider the teeth of *Kapes* to represent 'true' multicuspid teeth, placing procolophonids among the earliest amniotes with multicuspid dentitions. We then analysed phylogenetically and chronologically early members of

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multicuspid radiations within Synapsida and Diapsida, the other two principal branches (with Parareptilia) of Amniota, including notosuchian crocodiles and early pterosaurs, archosauromorphs, lepidosaurs and synapsids. Despite the disparate taxa, key features of each of these radiations are the relatively similar mode of multicuspal origin, and the relatively small body size of the first multicuspid taxa.

These results indicate that both developmental and energetic factors may have instigated the stereotypic origins of multicuspid teeth.

Biomechanical performance of the rodent skull: sensitivity analyses of finite element models

Philip G Cox¹, Michael J Fagan², Emily J Rayfield³ and Nathan Jeffery¹

¹*Department of Musculoskeletal Biology, University of Liverpool;* ²*Department of Engineering, University of Hull;* ³*Department of Earth Sciences, University of Bristol*

Rodents possess a uniquely specialised dentition and a complex arrangement of jaw-closing muscles. Finite element analysis (FEA) is an ideal technique to investigate the biomechanical implications of these specialisations, but it is essential to understand fully the degree of influence of the different input parameters of the FE model to have confidence in the model's predictions.

This study evaluates the sensitivity of FE models of rodent crania to elastic properties of the materials, loading direction, and the location and orientation of the model's constraints. Three models were constructed of squirrel, guinea pig and rat skulls. Each was loaded to simulate biting on the incisors and the molars, with the angle of the incisal bite varied over a range of 45°. The Young's moduli of the bone and teeth components were varied between limits defined by experimentation. Geometric morphometrics (GMM) was used to analyse the resulting skull deformations. Bone stiffness had the strongest influence on the results, followed by bite position, bite angle and muscle orientation. Tooth material properties had little effect on skull deformation. The effect of bite position varied between species, with the mesiodistal position of the biting tooth being most important in squirrels and guinea pigs, and bilateral versus unilateral biting having the greatest influence in rats..

The results here elucidate which input parameters are most important when defining FE models, and provide interesting glimpses of the biomechanical differences between the three skulls, which will be fully explored in future research.

The Vestibular System in Talpidae

Nick Crumpton

Department of Zoology, University of Cambridge

The mammalian vestibular system has received a large amount of interest in recent years. Variation in this structure has been studied in terms of its function and its phylogenetic use as an anatomical trait. Both of these fields of research have benefited from the use of high resolution CT scanning technology allowing quantification of a hitherto inaccessible morphology. I present an investigation into the inner ear of nine members of the family Talpidae (and non-talpids fossorial mammals) to quantify how the vestibular system varies between closely related species that occupy distinct ecotype, including small fossorial, terrestrial and semiaquatic faunivorous mammals. Morphological variation of virtually reconstructed endocasts was observed via a suite of linear measurements. Variation is reported between species occupying different ecotypes. However, although morphology correlated with behaviour (e.g. an extension of the lateral semicircular canal in semiaquatic species) differences in semicircular canal and cochlear architecture were found between specimens of a single species (10 specimens of *Talpa europaea*). This study confirms previous finds that there is a 'communication' between the horizontal and posterior semicircular canals in *Talpa europaea*, describes a convergent inner ear morphology apparent within distantly related species and highlights an unexpected variation of the inner ear within the family Talpidae.

The revision of the genus *Magyarosaurus*, and titanosaur diversity in the Maastrichtian of the Hateg Basin, Romania - preliminary results

Zoltan Csiki-Sava¹, Rosie Barnes² and Paul Upchurch²

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Magyarosaurus is one of the first named titanosaurs, with a large number of referred specimens (mainly vertebrae and appendicular elements), discovered in uppermost Cretaceous deposits of the Hateg Basin, Romania, from continental, mainly fluvial, deposits spread discontinuously over a relatively small (25 x 10 km) area. The taxonomy of the genus has a rather convoluted history, with as many as three different species being identified by some authors, while other authors have rejected this splitting. Understanding the taxonomy of *Magyarosaurus* is fraught with deficiencies of the original descriptions (undiagnostic specimens, obsolete characters used in diagnoses, unreliable "chimaeric" associations of skeletal elements). It is further complicated by the fragmentary nature of the available fossil material, with few cases of well-documented skeletal associations, and even fewer situations of overlapping diagnostic elements.

In order to clarify the taxonomy of *Magyarosaurus*, we undertook an extensive survey of the existing Hateg sauropod material. This survey reveals the presence of several different morphotypes showing diagnostic features, for most appendicular elements represented by multiple specimens. Vertebral morphotypes are also present, but here differences are more subtle and difficult to interpret. Largest variability is recorded within the humeri (in robustness, shape of deltopectoral crest), suggesting that three (possibly four) titanosaur taxa might be present in the Hateg assemblage. Although this local diversity might appear surprising, it mirrors the sympatric distribution of different titanosaur genera reported previously in other areas and reinforces recent work suggesting that sauropods were not in decline immediately before the end-Cretaceous mass extinction.

The Bristol Dinosaur Project - developing a learning and outreach programme and training research staff and students to help deliver.

Edward Drewitt, Remmert Schouten, Pedro Viegas and Michael J. Benton
School of Earth Sciences, University of Bristol

The Bristol Dinosaur, *Thecodontosaurus antiquus* is a unique dinosaur to the Bristol region and an ideal subject to tell people of Bristol and the west about 'their' very own dinosaur. Recently secured funding for the Heritage Lottery Fund has allowed for a unique project, which employs a Learning Officer and a Fossil Preparator for 3 years. Where the Preparator chases more fossils out of the rock and supervises volunteers assisting him, it is my role as a Learning Officer to utilise the Bristol Dinosaur as an educational tool. Almost a unique position in universities in the UK, my work as a learning officer at the University of Bristol is to develop a learning programme in Bristol so that various audiences, schools, families especially can learn more about a dinosaur which is local and very relevant both to them.

In this presentation I will explore who the Bristol dinosaur was and how we are enabling discoveries and work in the lab to be made accessible at schools and events, in particular how exact models of the bones of the dinosaur and graphic designs of the skeleton are helping children and adults to engage and learn more about it. It provides a great opportunity for developing scientific enquiry skills and enabling people to realise scientific ideas are changing all the time. I will also explore the many positive and unexpected opportunities that have arisen as a result of our learning work.

Review of the West Dorset fossil collecting code of conduct

Richard Edmonds

Jurassic Coast Project Officer

The West Dorset fossil collecting code of conduct has been running for 10 years and was developed through a working party of interested groups with wider consultation. The code was accepted by UNESCO as appropriate management for a rapidly eroding coastline. As part of the Dorset and East Devon Coast Management Plan review, it was agreed that now is the time to undertake a review of the code.

The aim of the review is to examine the effectiveness of the code and to consult widely with organisations with an Earth science and Geoconservation interest although views are welcome from individuals with any background. The paper will examine the state of the coast, the record of important specimens, the issues and includes a discussion on the rationale behind the present management. The review is open to consultation from June to the end of September 2011. Responses to the review will help inform its future development.

First occurrence of neonatal ornithomimid teeth from South America

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The abundance and diversity of South American ornithomimid dinosaurs has increased over the past ten years. Despite these discoveries, the ornithomimid fossil record is still extremely fragmentary. Only *Gasparinisaura cincosaltensis* is represented by individuals from different ontogenetic stages, from older juveniles to adults. The Cerro Fortaleza Formation in southern Patagonia, Argentina has yielded a distinct fauna of ornithomimid (*Talenkauen santacrucensis*), sauropod (*Puertasaurus reuili*) and a nov. gen et sp. titanosaurian currently under study by members of our group), and theropod dinosaurs (*Orkoraptor burkei* and *Austrocheirus isasii*) in addition to numerous microfossils and plant material.

Discrete teeth and bone fragments were recovered during preparation of the holotype of *Talenkauen santacrucensis* (MPM-10001). The minute tooth crowns are 1mm apicobasally tall and 1.7mm mesodistally wide. The crowns are symmetrical and have a centrally located primary ridge on the lingual surface. Secondary ridges lead to five marginal denticles on both teeth. The tooth morphology is consistent with dentary teeth in euiguanodontids. There is no evidence of pitting cracking, or erosion via transport. Thus, the material appears autochthonous with respect to the adult body block of *T. santacrucensis*. Steeply inclined wear facets on the

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lingual surface and associated microstriae indicates that the teeth were post-embryonic. The morphology, size, and wear of the teeth and small bone fragments suggest that the teeth were from a neonatal *Talenkauen santacruzensis*. This is the first record of neonatal ornithopod remains from South America.

The Early Cretaceous Chinese lizard *Yabeinosaurus*: insights from new specimens

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Yabeinosaurus was one of the first tetrapods to be described from the now famous Early Cretaceous Jehol Biota of north-eastern China. However, although it was correctly identified as a lizard its phylogenetic position was misunderstood for decades due to poor preservation, limited access to the material, and the subsequent loss of the holotype during WW2. As the original specimens (and a recently erected neotype) appeared to be weakly ossified, many authors attributed *Yabeinosaurus* to the Gekkota, but the recovery of new specimens from the Yixian and overlying Jiufotang formations (125-120 mya) has changed our perceptions. The type specimens are small with thin bones because they are immature. *Yabeinosaurus* adults were robust and relatively large (~300 mm SVL), probably reaching adult size over several seasons. New phylogenetic analyses place *Yabeinosaurus* and its sister taxon, the near contemporary Japanese *Sakurasaurus*, on the scleroglossan stem.

Importantly, some of the new specimens also provide an insight into the biology of *Yabeinosaurus*. Three preserve vertebrate remains, predominantly fish bones, in the gut. Fish eating is reportedly rare in living lizards, being restricted to the small clade comprising *Shinisaurus*, *Lanthanotus* and *Varanus*, all of which forage in and around freshwater.

High diversity in late Early Cretaceous ichthyosaurs part II: The Cambridge Greensand material

Valentin Fischer

(supported by Jones-Fenleigh Memorial Fund)

Palaeontology Department, Royal Belgian Institute of Natural Sciences, Brussels and Geology Department, Geosciences Centre, University of Liège

Recent and on-going work on Canadian and French Cretaceous ichthyosaurs has unveiled a high diversity of Albian ophthalmosaurids, suggesting the extinction of ichthyosaurs which occurs during the Cenomanian was a much more severe event than previously supposed. Yet the ichthyosaur assemblages from other areas such as the USA and Australia are monospecific, suggesting that the diversity of ichthyosaurs was not universally high.

The Cambridge Greensand ichthyosaur material, which has not been the subject of any thorough study since 1869, consists of about 900 specimens, the vast majority of which are isolated bones. Nevertheless, this abundant material offers a good opportunity to assess the diversity of the ichthyosaurs that roamed the western England Sea during the late Albian–Early Cenomanian interval. In order to assess this diversity, diagnostic bones such as basioccipitals, stapes, humeri and femora were compared to that of other ophthalmosaurids. Several morphotypes, some represented by 10+ specimens are recognized. Articulated specimens were used to unite cranial and appendicular bone morphotypes to a taxon. An extremely diverse assemblage of at least 5 distinct taxa is recognized in the Cambridge Greensand Formation: *Platypterygius* sp., two new genera that have representatives in southeastern France and Germany, a *Brachypterygius/Aegirosaurus* morphotype, and the long-forgotten but diagnostic *Cetarthrosaurus walkeri*, for which we found a second and better preserved specimen. The diversity of the 'mid' Cretaceous ichthyosaurs from Europe now matches that of the Early Jurassic, a period sometimes seen as the 'Golden Age' of post-Triassic ichthyosaurs.

Form, function and phylogeny: Virtual reconstruction of the inner ear of plesiosaurs

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(supported by Jones-Fenleigh Memorial Fund)

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Plesiosaurs, are extinct marine diapsids spanning almost 140 million years (Jurassic–Cretaceous). They represent an excellent study group for comparisons of semi-circular canal form and function due to their conspicuous range of body plans, suggesting wide variation in the range of angular motion of the head within Plesiosauria. Nonetheless, the vestibular system of plesiosaurs has not been examined in any detail.

In the present study, 3D reconstructions of semicircular-canals in five distantly-related plesiosaurs were created using Micro-CT scan data. These included two plesiosauro-morph taxa

Microcleidus homalospondylus (Lower Jurassic) and *Libonectes morgani* (Late Cretaceous), one pliosauroform taxon *Peloneustes philarchus* (Middle Jurassic) and two taxa with intermediate body plans, *Macroplata tenuiceps* (Early Jurassic) and *Nichollsaura borealis* (Early Cretaceous). Three possible drivers of canal morphology were investigated: (i) body proportions (as a proxy for locomotory style), (ii) spatial constraints, conferred by skull size, and (iii) phylogeny. Canal lengths and angles between perpendicular canals were measured to obtain quantitative descriptions of canal shapes. Cluster analyses indicate that taxa with similar body proportions do not have similar canal forms. Instead, a strong phylogenetic influence is evident. Regression analyses show a significant relationship between linear measurements of the canals and total skull length. This indicates that spatial constraint selectively effects semicircular-canal size.

Our results are consistent with studies of other groups, which detect a strong form-function relationship only in comparisons of closely-related taxa. We predict that focused study of restricted plesiosaurian clades may reveal such a relationship.

Synchrotron tomography reveals three-dimensional gill-arch structure in a stem gnathostome from the Hunsrück Slate

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Although jaws are considered to have a special anatomical relationship to gill arches, remarkably little is known about the branchial skeletons of crownward members of the gnathostome stem.

To address this issue, we have targeted the exceptionally preserved, but phylogenetically enigmatic 'placoderms' of the Hunsrück Slate of Germany. Due to pyritization, these fossils are particularly amenable to x-ray studies. To acquire high-resolution, three-dimensional data, we used powerful synchrotron light tomography at the Diamond Light Source in Oxfordshire, UK with considerable success. Here we report on the endocranium and branchial arches of *Paraplesiobatis heinrichsi*. We compare it with preliminary results on the anatomy of so-called 'stenioellids', to which it has sometimes been assigned. Our data on the endocranium support petalichthyid relationships for *Paraplesiobatis*. Branchial arch data refute earlier shark-like reconstructions of petalichthyid pharynx morphology in favour of an agnathan-like organization of the branchial chamber situated beneath the braincase and orbits.

The data have several implications for early gnathostome phylogeny. First, they provide additional corroboration for a stem-gnathostome placement of 'placoderm'-grade vertebrates. Second, they yield rich character data that can be used to polarize gill-arch characters within the gnathostome crown. Finally, and perhaps not unexpectedly, they confirm that the 'stenioellids' are a polyphyletic wastebin assemblage. From a technical side, this work serves as a valuable proof of concept for the power of x-ray tomography to yield significant new anatomical data from even very flattened specimens.

Skeletogenesis in the African elephant.

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The elephants show by far the longest gestation length of all mammals (623-729 days in the Asian and 640-673 days in the African elephants). Here, we provide unique data on elephant skeletal ontogeny.

We focus on the sequence of cranial and postcranial ossification events during growth in the African elephant (*Loxodonta africana*). Previous analyses on ossification sequences in mammals have focused on monotremes, marsupials, boreoeutherian, and xenarthran placentals. Thus, we present here the first data on ossification sequence for an afrotherian mammal. We use two different methods to quantify sequence heterochrony: sequence-ANOVA and event-pairing/Parsimov. These analyses show that elephants significantly differ from other placentals by a late ossification of the basicranium, manual and pedal phalanges, and an early ossification of several elements of the limbs, pelvic girdle, and the spine. Moreover, compared to other the placental mammals, the ossification of the skeleton in elephants starts very early during development, and appears to progress rapidly.

The elephant has attained the same degree of ossification at the end of the one-third of the total gestation period as the mouse and hamster have at the last third. Thus, elephants seem to show a substantial degree of developmental distinctiveness compared to other placentals.

Discovery and recovery of a complete, three-dimensionally preserved ankylosaur from the Early Cretaceous of northern Alberta, Canada

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In March of 2011 a giant excavating machine in the Athabasca tars sands of northern Alberta exposed the rear half of what turned out to be a nearly complete ankylosaur with only the tail

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missing. The specimen is hosted in the Wabiskaw member of the Clearwater Formation and is dated as late Aptian (113Ma).

The specimen was excavated over a three week period in April with the assistance of heavy equipment and staff from the Suncor Millenium Mine. The find is significant for many reasons. It is the oldest known, complete dinosaur from Alberta. It is the first ankylosaur from the Early Cretaceous of Alberta in contrast to the more typical latest Cretaceous forms from the province. It is the first dinosaur from the marine Clearwater Formation (better known for its ichthyosaurs and plesiosaurs), and represents a terrestrial animal that became entombed in a seafloor approximately 200km from the nearest known palaeo-shoreline. It experienced no post-mortem disruption, with all the bones, including phalanges, in three-dimensional articulation. All the dermal armour appears to be undisturbed and present. There are large areas with impressions of scales of alternating diamond and hexagon shapes in close association with the osteoderms on the dorsal surface. There is a large cluster of unusual, pisolith-like bodies (up to 2cm in diameter) in the gut region, and these may represent stomach contents. Unfortunately, the bone is much softer than the concretion containing the specimen, and careful and responsible preparation will take several years.

A new primate (Omomyidae, Microchoerinae) from the earliest Eocene of southern UK: the beginning of microchoerine evolution.

Jerry Hooker

Natural History Museum, London

The Omomyidae are a well-known extinct holarctic family of primitive, possibly tarsiiform, primates that lived mainly during the Eocene. The more completely known taxa sport large eyes and were arboreal leapers like modern bushbabies. They are best known from North America, where a high diversity was produced by explosive evolution in the Early Eocene, before which primates are unknown. The European branch of the family, subfamily Microchoerinae, has long shown a moderate diversity of relatively derived forms. Until recently, no microchoerines were known from the first c.5 million years of the Eocene. In 2007 the genus *Melaneremia* was described from c.500 thousand years after the beginning of the Eocene at Abbey Wood, UK. Here I report the discovery of a new species of *Melaneremia* from the Woolwich Formation of Croydon, UK, extending the record of Microchoerinae earlier to within the first 170 thousand years of the Eocene, within an interval known as the Paleocene-Eocene Thermal Maximum.

The new species is represented by a lower jaw with five cheek teeth and three lower molars belonging to different individuals. Most adequately known microchoerines apart from *Melaneremia* show enlarged incisors and reduced premolars and the subfamily has previously been thought to be nested well within the North American subfamily Anaptomorphinae. Importantly, the new species shows little evidence of premolar reduction. Cladistic analysis shows a very early divergence for Microchoerinae within the Omomyidae and supports a sister group relationship with Anaptomorphinae plus Omomyinae.

James Frederick Jackson (1894-1966). An Extraordinary Geologist.

Cindy Howells

National Museum of Wales

James Frederick Jackson came from humble origins in North Wales, yet this poorly educated boy wrote a geological guidebook to Hunstanton, Norfolk at the age of 15, and was hailed as a Boy Genius. His passion for geology and collecting was to rule his life thereafter. Unable to obtain a permanent scientific job in any institution, he spent his life collecting rocks and fossils from around the UK, over 20,000 of which were sent to the National Museum of Wales for just the cost of his expenses.

He was a truly extraordinary gentleman whose breadth of knowledge, and skill in interpretation and identification far surpassed many professionals today. He had an eye for unusual finds and was the first to discover the fossil insects in the Lower Lias Flatstone nodules, as well as collecting an articulated juvenile Scelidosaur from Lyme. In the 1920s he published a paper on the stratigraphy of the Lower Jurassic Junction Bed of Dorset, and later formed a major stratigraphic collection of Dorset fossils.

Despite his constant ill-health and poverty he managed to amass collections of significant scientific importance, and described his years of collecting as 'a labour of love'. This talk will illustrate his background, his life and his collecting, and will help to ensure that his work is never forgotten.

Lizard calibration points the the problem of *Tikiguania*

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Fossils regarded as the "earliest known record" of a major clade are often heavily relied on to establish the timing and broad picture of evolutionary history. More recently, such fossils have become pivotal in studies using DNA sequence data as calibration points for molecular clocks.

Tikiguania estesi, from the Late Triassic Tiki Formation of north-central India, is based on a partial mandible interpreted as the earliest member of Acrodonta (which includes the living agamids and chameleons), and thus the earliest crown squamate (lizards and snakes). However, we find that the characters used to justify the recognition of *Tikiguania* as a separate genus establish that it is indistinguishable from the living subfamily Draconinae, the main agamid lineage of modern India and South-East Asia. This relationship is supported by explicit phylogenetic analysis of morphological and molecular data. A 216-million-year period of "stasis" would be an unlikely explanation for an apparently modern lizard in Triassic sediments; it is more conceivable that *Tikiguania* is a reworked Tertiary or Quaternary draconine, a conclusion that is compatible with the superficial exposure of the Tiki Formation over a considerable area. A number of studies have already employed *Tikiguania* as a reference point for evolutionary, palaeobiogeographical, and molecular clock inferences concerning the evolution of Squamata and Acrodonta. We conclude that *Tikiguania* is an unreliable choice as a reference point for such studies.

Evolution of elasmobranch (Chondrichthyes) dentitions

Zerina Johanson¹, Moya Smith² and Charlie Underwood³

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Patterns of tooth initiation in modern chondrichthyan dentitions are still poorly understood. As sister group to other living gnathostomes, an understanding of chondrichthyan tooth development is critical to the study of the evolution of teeth and jaws.

Teeth develop in the dental lamina, where tooth size, shape and polarity and number are regulated, from the symphyseal tooth. Among elasmobranchs, both shark clades (Galeomorphi and Squalomorphi) have a fixed number of tooth families once the first two rows form in the embryo. However, the embryonic condition in rays (Batoidea), the sister clade to the living sharks, is poorly known. We show that some rays have a more shark-like condition with initially a large number of tooth families but no subsequent proximal addition along the jaw (Rhinobatidae), while other rays have a reduced initial number of families and add new ones throughout development (Torpediniformes). Contrary to previous observations, 'file splitting' is not characteristic of the ray dentition (only occurring in certain taxa) and is more generally restricted to certain elasmobranchs. The relationship between tooth development and phylogeny in the rays is unclear. For example, the Torpediniformes are resolved as sister group to all or most extant batoid groups but have a derived mechanism for establishing tooth family number. In contrast, the Rhinobatidae are considered a more derived family, but share dental (and skeletal) characters with early fossil batoids and sharks. Thus, these observations on dentition development conflict with current chondrichthyan phylogenies.

Shearing in *Sphenodon* and related character acquisition in Mesozoic Rhynchocephalia (Diapsida: Lepidosauria)

Marc E.H. Jones¹, Neil Curtis², Paul O'Higgins³, Michael J. Fagan², Susan S. Evans¹

¹University College London; ²University of Hull, Hull; ³University of York

Amongst living tetrapods, the shearing mechanism of the New Zealand tuatara (*Sphenodon*) is unique. The lower jaw closes between the maxillary and palatine tooth rows before sliding forward to tear food apart like a steak-knife. Nevertheless, manipulation of dry skeletal material can give the impression that occlusion is crude and that most tooth wear is the result of food-on-tooth wear. Using a detailed computer model of a *Sphenodon* skull, details of jaw movement were investigated with Multibody Dynamics Analysis.

Results show that the shearing mechanism is more sophisticated than previously appreciated. Facilitated by the shape of the articular surface and symphysis, the anterior movement of the lower jaws is coupled with a long axis rotation: initially shearing occurs between the anterolabial flanges on the dentary teeth and posterolingual flanges of the maxillary teeth whereas near the end of the shearing phase it occurs between the anterolingual flanges of the dentary teeth and the posterolabial flanges of the palatine teeth. Fossil rhynchocephalians, such as the Early Jurassic *Cynosphenodon*, show that many of the anatomical features associated with the *Sphenodon*-mode of feeding were acquired early in the clade's evolution. Moreover, the Upper Jurassic-Late Cretaceous eilenodontines seem to have elaborated on the mechanism found in *Sphenodon* by transverse expansion of the dentary and palatine teeth to form a single occlusal surface. This example contradicts previous suggestions that the specialized jaw arrangement found in *Sphenodon* is an evolutionary dead end.

Filling a gap in Palaeozoic vertebrate diversity: the Wayne Herbert osteostracan fauna

Joseph Keating, Robert Sansom and Mark Purnell

University of Leicester, Geology Department

The jawless Osteostraci were an important constituent of vertebrate ecosystems during the Middle Palaeozoic. They were a diverse group comprising over 200 species, but rudimentary taxonomic understanding of the British fauna is impeding analyses of the diversity, interrelationships and palaeobiology of this group, and more broadly, the circumstances surrounding the evolution of jawed vertebrates from jawless ancestors. Principal among British

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faunas is a well preserved but undescribed Early Devonian fauna from Wayne Herbert Quarry, Herefordshire. This fauna is the focus of the taxonomic study presented here. From anatomical observations of the character-rich head-shields combined with measurements from high resolution digital photographs we have recognized a number of discrete morphogroups which can be compared with established taxa. This approach ensures that species identification accurately reflects intra- and inter-taxon variation within the fauna and indicates that two new species of Zenaspidae and two new species of Cornuata incertae sedis are present. High fidelity preservation of osteostracan material from Wayne Herbert reveals centrifugal addition of tissue to existing dermoskeletal tesseræ, addition of new tesseræ and fusion of units into larger plates, providing support for models of indeterminate growth in Osteostraci. These new taxonomic results and anatomical data enable a better understanding of the diversity and development of the Osteostraci and will help to elucidate the evolutionary diversification of this intriguing group.

Bean bags, modules, systems and the evolvability problem: reflections on how major new vertebrate taxa arise

Tom Kemp

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The major vertebrate taxa such as teleosts, tetrapods, ichthyosaurs, birds and mammals, resulted from long evolutionary treks through morphospace, involving large changes in many characters. This raises an evolvability problem, because highly integrated systems consisting of many functionally linked parts should be resistant to significant evolutionary change. R.A. Fisher's 'cost of complexity' argument implies that only small changes are possible in a complex organism, while J.B.S. Haldane's 'cost of selection' argument implies that only a relatively small number of traits can be undergoing natural selection simultaneously.

To attack the problem, a simplified, tractable model of the phenotype is necessary, and currently there are three kinds in use. The Bean Bag Model of cladistic methodology, in which characters are assumed to be independent of one another, takes simplification to an unrealistic extent and so is of little help. The Modularity Model, in which the organisms are assumed to consist of semi-independent modules, has relevance for shorter term evolution, but modules are too overlapping and too transient to account for the major transitions. The Correlated Progression model, which assumes that organism consists of functionally but flexibly interlinked characters, offers the most realistic resolution of the evolvability paradox, certainly at the higher taxonomic level.

There are important ecological implications associated with these models for the frequency, direction, and rates of evolution of the trends that resulted in new higher taxa.

A basal pliosaurid (Reptilia, Sauropterygia) from the Oxford Clay Formation (Callovian, Middle Jurassic) of Bedfordshire: evidence for a gracile, longirostrine grade of Early-Middle Jurassic pliosaurids

Hilary Ketchum and Roger Benson

A partial skeleton including cranial, axial and appendicular material from the *Sigiloceras enodatum* ammonite Subzone (early Callovian, Middle Jurassic) of the Oxford Clay Formation of Quest Pit, near Stewartby, Bedfordshire, UK represents one of the basalmost Middle Jurassic pliosaurids.

The new taxon possesses a longirostrine snout, and seven autapomorphies, indicating clear distinction from other Oxford Clay pliosaurids. The primitive nature of the new taxon allows reassessment of pliosauroid relationships. This demonstrates that the Lower Jurassic taxa *Thalassiodracon hawkinsii*, *Hauffiosaurus* spp., and possibly also *Attenborosaurus conybeari*, are successively more derived basal representatives of Pliosauridae. This shows that a longirostrine snout was acquired among Early Jurassic pliosaurids (such as *Hauffiosaurus*), but that these early taxa had small body size, a long neck, and gracile skull and limb bones relative to the contemporaneous rhomaleosaurids, which were robust, large-bodied macropredators. The pliosaurid lineage only acquired its 'characteristic' large size, robust skull and short neck in the late Middle Jurassic after the extinction of Rhomaleosauridae.

Effects of the late Permian extinction on Permian-Triassic shark faunas

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An apparent radiation of fish families across the Permian/Triassic (P/Tr) boundary has suggested that sharks (top predators) were relatively unaffected by the late Permian mass extinction. Other evidence shows that chondrichthyan diversity may instead have followed the late Permian decline and Early Triassic recovery in other aquatic organisms. Correlation of elasmobranch records from P-Tr oceanic basins and comparison of preservation and biodiversity—allowing quality assessment of the fossil record, identification of changes in the global shark community and ultimately significant evolutionary developments—is needed to ascertain true events.

Data on elasmobranch faunas were obtained from a comprehensive literature survey, with additional field data collected from the previously unstudied P-Tr of Oman (western Neothethys), from Japan (Panthalassa), and East Greenland (Boreal). The middle Permian fauna of Oman contains *Glikmanius* and one new ctenacanthiform, four new hybodontiforms and two unidentified taxa (hybodontiform and ?eugeneodontiform). The Omani Early Triassic fauna also contains hybodontiforms (but generically different) and is dominated by synchodontiforms. Japanese Permian and Triassic records also share no genera, but middle Permian faunas of Oman and Japan are similar, with *Glikmanius* in common. The East Greenland middle Permian-Lower Triassic record is eugeneodontiform dominated, has *Hybodus* and *Janassa* in common with Japan but currently no genera with Oman.

This new analysis expands knowledge on global distribution and diversity, and currently shows a clear divide between local Permian and Triassic communities, suggesting at least some influence of extinction on evolutionary patterns.

Skeletal Taphonomy of Pterosaurs from the Late Jurassic of Germany

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The Solnhofen exceptional biota (Late Jurassic, Southern Germany) preserves large numbers of pterosaur fossils. The most common are *Rhamphorhynchus* (a member of the paraphyletic assemblage of basal pterosaurs called 'rhamphorhynchoids') and *Pterodactylus*, a member of the derived pterodactyloid clade.

There are obvious skeletal differences between the two groups, and as such, between these genus (e.g. the size of the head, and the length of the neck and tail). It can be assumed that there are also soft tissue differences although these are difficult to elucidate.

We assessed the skeletal taphonomy of each species using the semi-quantitative method devised by Beardmore et al. in prep. The skeletal system is divided into 9 units (skull, neck, dorsal, ribs, tail, left and right front limbs and hind limbs) and the completeness and degree of articulation of each coded.

Specimens of each taxon are preserved in the same lithologies and the sedimentary context each occurs in is reconstructed as similar. The null hypothesis tested is therefore that systematic variation in the skeletal taphonomy of the two taxa represent physiological differences in vivo and how this impacts on their post mortem decay, not differences in the depositional environment. *Pterodactylus* exhibits consistently higher values for completeness and articulation, especially in the body region. In contrast, the head and neck units of both species disarticulated equally, and *Rhamphorhynchus*' tail unit disarticulated less than that of *Pterodactylus*. The differences suggest that the soft-tissue architecture of the body was more robust in *Pterodactylus* - i.e. musculature was more extensive, and ligament and tendon attachments stronger.

The Strange Case of the Jurassic Ichthyosaur

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A report is given on the four decades of unpublished research on a novel ichthyosaur taxon from Iraq. Found in 1952 by field workers for Iraq Oil, it was donated to the Natural History Museum (London), then borrowed by the late Robert M. Appleby at University College, Cardiff. Appleby aimed to complete a full description of the specimen; his final manuscript also included an extensive discussion of the stratigraphic provenance of the specimen, its phylogenetic affinities, and speculations on its possible ecology. During his investigation, a broad collaboration ensued with members of the universities of Reading and Cambridge and HV Dunnington & Associates (exploration and resource appraisal consultants), as Appleby attempted to constrain the precise age of the specimen within the Jurassic Sargelu Formation. However, the manuscript resulting from this collaboration (submitted to the journal *Palaeontology* in 1979) was not deemed to have satisfactorily addressed that outstanding question. Although Appleby continued to work widely on ichthyosaurs up until his death in 2004, he was unable to resolve this problem.

Subsequent work by the first two authors, incorporating archival research and a revisiting of earlier laboratory techniques, has led to a conclusive resolution of this issue, making it possible for a manuscript describing the specimen to finally be acceptable for publication. Resulting from one of several pieces of Appleby's unpublished research, the new Iraq taxon has major implications for our understanding of ichthyosaurian diversity, phylogeny and distribution across time and space.

From Archimedes to *Archaeopteryx*: Trace metal mapping with Synchrotron Rapid Scanning X-Ray Fluorescence.

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A chemical analysis of *Archaeopteryx* has never been completed, despite its iconic status. Ideally such analysis would measure and map the chemistry of bone, soft tissue structures, and the embedding rock matrix. Mapping the fossil in situ would place constraints on mass transfer between the limestone and specimen, and therefore aid in distinguishing taphonomic processes from original chemical zonation remnant from the *Archaeopteryx* itself. Conventional nondestructive analytical methods face serious problems in this case and most recent technological advances have been targeted at developing nanometer-scale rather than decimeter-scale capabilities.

However, the recent development of Synchrotron Rapid Scanning X-ray Fluorescence (SRS-XRF) now allows large palaeontological specimens to be non-destructively analyzed and imaged using major, minor, and trace element concentrations. Here we present high-resolution maps covering an entire *Archaeopteryx* specimen, along with large sections of the limestone matrix for Si, P, S, Cl, Ca, Ba, Mn, Fe, Zn, Cu, Br, and Pb.

Our results unequivocally show that the feathers in this *Archaeopteryx* specimen are not simply impressions. Several rachises are clearly visible in maps of both phosphorous and sulfur; thus, indicating that feather chemistry has been partially preserved. Furthermore, zinc and copper levels in the bone are similar to concentrations in extant avian species. We therefore conclude that part of the original bone composition is preserved in these critical macronutrients. Curation artifacts have also been resolved. These results indicate that SRS-XRF provides a new and powerful non-destructive tool for the study of ancient life.

A freshwater teleosaurid in the Late Jurassic of northeastern Thailand

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The name *Thalattosuchia* means 'marine crocodiles' and refers to their frequent occurrence in proximal and pelagic deposits of the Early Jurassic–Early Cretaceous interval. They are therefore not expected to occur in continental deposits but rare reports indicate that they actually do. Hitherto, the teleosaurid *Machimosaurus hugii* has been reported from brackish deposits of the Late Jurassic Guimarota coal mine in Portugal. A definite freshwater occurrence is that of *Peipehsuchus teleorhinus* in the Middle Jurassic Ziliujing Formation of Sichuan in China. In addition, fragmentary teleosaurid remains have been reported from Late Jurassic continental deposits of peninsular Thailand.

Here, we report and describe three teleosaurid skulls from the newly discovered vertebrate locality of Phu Noi in the Phu Kradung Formation (Late Jurassic–Early Cretaceous) of northeastern Thailand. The fossiliferous deposit is part of a pedogenetic horizon located at the base of an alternating fluvial series of silts and sandstones. Paleogeographical reconstructions show that Phu Noi was located far inland, implying that these teleosaurids were able to durably live in such an environment. The recovery of three skulls of different sizes as well as postcranial elements indicates that their occurrence in fluvial deposits is not incidental and that a population was established there. We discuss whether the ability of teleosaurids to colonize freshwater habitats is a secondary adaptation or whether it is plesiomorphic and reminiscent of terrestrial or freshwater-adapted ancestors.

A choristodere from the late Paleocene of France

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Choristoderan reptiles form a clade of freshwater aquatic reptiles with a temporal record extending from at least Middle Jurassic to Miocene and a strictly Laurasian distribution. The large Cretaceous–Eocene neochoristoderes *Champsosaurus* and *Simoedosaurus* are the most familiar taxa, but many smaller representatives have since been recognised. Large neochoristoderes disappeared from the fossil record in the Eocene, but the group survived into the European Neogene in the form of the small, superficially lizard-like, *Lazarussuchus*.

Lazarussuchus was originally described from the Late Oligocene of France but has since also been recorded from the Early Miocene of the Czech Republic. Similar jaws are also known from the Oligocene of Germany. Despite its age, most phylogenetic analyses place *Lazarussuchus* at or close to the base of the choristoderan tree, implying a very long unrecorded history. However, part of that hiatus has now been filled.

The Late Paleocene (Thanetian) locality of Menat in the Auvergne region of France has yielded an assemblage of mammals, birds, crocodylians, lizards, turtles, amphibians, fish, insects and plants preserved in diatomite beds within a lacustrine environment. More recently, the locality has produced the skeleton of a small choristodere. This is identified as an early representative of *Lazarussuchus*. The genus was thus present in the waterways of Western Europe for at least 30 million years, and was probably considerably more widespread than current records suggest.

Robert Appleby's ichthyosaur legacy

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For five decades, Robert M. Appleby (1922-2004) worked on the biology, evolution and diversity of ichthyosaurs. Appleby's main published contributions are his articles on ophthalmosaurid cranial morphology and his description of the controversial Protoichthyosaurus. However, Appleby's published output far from reflects the prodigious amount of research he performed on this group. An enormous quantity of unpublished material, including correspondence, illustrations and draft manuscripts is archived. While Appleby's views on ichthyosaur phylogeny and taxonomy are anachronistic, much of his research remains novel and worthy of salvage. Plans to complete the Encyclopedia of Paleoherpétology volume on ichthyosaurs were unfortunately never fulfilled; a second, substantial manuscript on ichthyosaur diversity and evolution was also drafted. The authors have attempted to reconstruct this manuscript as best as possible and a version is currently scheduled for publication.

Appleby seemingly abandoned drafts of several individual manuscripts after receiving reviews of the sort that (to modern eyes) appear about normal in their degree of negativity for a first submission, and a requirement for perfectionism slowed his revision of these works. Unpublished manuscripts include those on tail evolution and function, ichthyosaur sensory abilities, and on two new Cretaceous taxa, both of which have major implications for interpretation of ichthyosaur phylogeny and diversity. This renewal of interest in Appleby's work coincides with a resurgence of interest in ichthyosaur diversity and phylogeny; the early stages of an 'ichthyosaur research renaissance', in parallel with that currently occurring in plesiosaur research, now seems underway. Rather than being destined for redundancy, Appleby's unpublished projects will appear posthumously in the literature.

The histology and structural performance of pterosaur wing bones

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The wing bones of pterosaurs are thin walled and have a complex trabecular structure. Historically, the internal structure could not be quantified in detail, but CT scanning now makes this possible. Specimens of pterosaur wing bones in the Natural History Museum collection have been scanned using the museum's XTH225 CT facility. The results reveal the detailed internal structure for the first time.

The cross section shape, cortical thickness and trabecular geometry along the full length of the BMNH OR 41637 ornithocheiroid first wing phalanx specimen were analysed and visualised. The data were used in a model of the wing spar to predict deflection under load, susceptibility to local buckling and structural safety factors.

Morphometric analysis predicts that the complete wing was 2.63m long and recent methodologies predict an animal mass of around 25kg for this wing size. Assuming an ideal, elliptical lift distribution and a wing mass fraction of 40% results in a wing tip deflection of 0.55m. While this may be aerodynamically feasible, the structural safety factors are less than 3 in many locations. The safety factors increase to between 3 and 6 if either a less efficient (but aeroelastically more likely) triangular lift distribution or lower animal mass in line with earlier estimates is assumed.

Thus it appears that either pterosaurs were significantly lighter than recent predictions or that the natural aeroelasticity of their membrane wings reduced distal lift distribution and limited the bending moments experienced by the wing bones.

New vertebrate fossils from the Lower/Middle Jurassic Kota Formation of Pranhita-Godavari valley, peninsular India

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The Lower – Middle Jurassic Kota Formation of Pranhita-Godavari valley, peninsular India has been a source of rich and diversified vertebrate fossils for a long time. Initially, holostean fish, crocodylian and pterosaur remains, and sauropod dinosaurs were described from this formation. In the last two decades, application of bulk screen-washing techniques has substantially increased the vertebrate faunal diversity of the Kota Formation. As a consequence, many vertebrate groups viz., amphibians, turtles, lizards, sphenodontians, and mammals were added to the faunal list. During the current study, intensified search for micromammals in the Kota Formation has led to the discovery of additional vertebrate fossils from an ossiferous section of the Kota Formation exposed southwest of Paikasigudem village in Adilabad district, Andhra Pradesh state (India).

The new microvertebrate fauna from this site includes two isolated teeth of haramiyid mammals, one snake dentary, and 10 ornithischian and 30 theropod dinosaur teeth. This fauna is being reported for the first time from the Kota Formation. In the former Gondwanaland, haramiyid mammals are known from the Upper Jurassic Tendaguru beds of Tanzania and the Upper Cretaceous Deccan intertrappean beds of peninsular India. The new haramiyid mammals from the Kota Formation, therefore, represent the oldest Gondwanan record of this group. So far, no fossil snake and ornithischian and theropod dinosaur have been documented from this formation. This work deals mainly with the phylogenetic and biogeographic relationships of the new finds.

The neodiapsid *Lanthanolania ivakhnenkoi* from the Middle Permian of Russia, and the initial diversification of diapsid reptiles

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The evolutionary history of Diapsida during the Palaeozoic Era is remarkably poor. Following the reclassification of the Early Permian *Apsisaurus witteri* as a synapsid last year, only a handful of taxa span the large temporal gap between the oldest known diapsid *Petrolacosaurus kansensis* and the Late Permian neodiapsid *Youngina capensis*. These include two Middle Permian neodiapsids, the recently described *Orovenator mayorum* from Oklahoma, USA, and *Lanthanolania ivakhnenkoi* from the Mezen region, northern Russia. A recently collected, nearly complete skeleton of *Lanthanolania* permits a thorough reexamination of the phylogenetic relationships of these two taxa.

Phylogenetic analysis of 188 characters and 30 diapsid taxa positions these two small forms as stem saurians and the oldest known neodiapsids (recently redefined by the authors as the sister taxon of Araeoscelidia). Interestingly, our results suggest that the lower temporal bar was lost by the ancestral neodiapsid relatively soon after the evolution of the diapsid temporal morphology, and conversely, that the temporal configuration of the Late Permian *Youngina capensis* is a secondary condition. In addition, the skeletal anatomy of *Lanthanolania* provides evidence of limb proportions that suggest that this small reptile is the oldest known bipedal diapsid.

Cranial anatomy and palaeopathology of an Upper Jurassic (Kimmeridgian) pliosaur (Reptilia: Sauropterygia) from Westbury, Wiltshire

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The cranial and mandibular anatomy of a large, Upper Jurassic pliosaur (Reptilia: Sauropterygia) from the Kimmeridge Clay Formation of Westbury, Wiltshire is described and reconstructed. The specimen is crushed and has some cranial roof elements missing, but the palate and mandible are exceptionally well preserved. The specimen (BRSMG Cd6172) was initially identified as *Pliosaurus brachyspondylus*, but could only be referred to the genus *Pliosaurus* because of the lack of rigorous modern descriptions for members of that genus. Indeed, the genus *Pliosaurus* may include forms that require their own generic designations. In general, the classification of Kimmeridgian pliosaurs is in need of revision.

Comparison of BRSMG Cd6172 to another pliosaur from the same locality (BRSMG Cc332) showed the two animals have quantifiable features in common. Marked differences in the snout and parietal crest are interpreted as sexually dimorphic. The size, extent of sutural fusion and the presence of pathologies in BRSMG Cd6172 indicate an ageing individual. An arthrotic condition of the articular glenoid apparently eroded the hinge joint and led to a prolonged lateral jaw misalignment, confirmed by dental pathologies. A transverse fracture on the right articular may be taphonomic or may have occurred in the last few weeks of the animal's life.

Interpreting these palaeopathologies as integrated events contributes to a reconstruction of part of the pliosaur's life history and behaviour.

Sauropod necks: how much do we really know?

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Despite recent studies on the anatomy, function and posture of the necks of sauropod dinosaurs, much of what we think we know rests on very shaky foundations.

1. Incomplete fossils. For most sauropod genera there are no complete necks, and multiple necks are known from only a handful of genera. Even "trusted" specimens like the Carnegie *Diplodocus* are damaged and possibly incomplete.
2. Distorted fossils. Even the few complete necks are invariably crushed and otherwise distorted. This is almost inevitable due to the fragile construction of sauropod cervicals.
3. Unpreserved cartilage. Extant animals show that it is impossible to understand the vertebral column in the absence of intervertebral and zygapophyseal cartilage -- even neck length cannot be determined.
4. Ignored soft tissue. As palaeontologists, we tend to concentrate on bones, but animals are also made of muscle, ligament, skin and other organs. We have yet to see a realistic attempt to restore the soft tissue of a sauropod neck: all neck mass estimates are whistling in the wind.

In summary, many palaeobiological studies of sauropod necks are based on soft-tissue-free models of cartilage-less bones that are distorted and do not constitute complete necks.

These problems are difficult, but not wholly intractable. The way forward is to apply data from extant animals in a phylogenetic context. Recently, work on cartilage, skeletal pneumaticity and neck posture of extant archosaurs has been applied to sauropods with good effect. Much more is needed.

A Combined Analysis Approach to the Phylogeny of the Talpidae (Mammalia: Lipotyphla).

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The family Talpidae, consisting of 17 extant genera, exhibits some of the most pronounced apomorphies amongst mammals. Although best known for their fossorial specialisations, a number of genera exhibit semiaquatic adaptations (*Desmana*, *Galemys*, *Condylura*) or possess a more generalized body plan (*Urotrichus*, *Neurotrichus*, *Uropsilus* and *Dymecodon*).

Here, an existing detailed morphological study of the Talpidae is supplemented with new morphological characters, continuous morphological variables and an eight locus molecular alignment in order to produce the most robust Talpid phylogeny to date. A number of extinct taxa are added to this extant dataset, including *Eotalpa*, the oldest confirmed talpid from the Late Eocene of the Isle of Wight. Both parsimony and model-based methods are used to produce phylogenetic hypotheses for the Talpidae, allowing both the timing and evolution of talpid locomotor habits to be assessed.

The integration of molecular phylogenetic data with traditional morphological approaches is key to the future study of systematics; allowing fossil taxa to influence large combined topologies should improve the positioning of such taxa for studies of both dating and phenotypic evolution.

Palaeoenvironmental setting of the marine Eocene vertebrate faunas of the Fayum, Egypt.

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The marine to marginal marine rocks of the Fayum region of Egypt have provided holotypes for species of sharks, rays, teleosts, crocodylians, chelonians, cetaceans, sirenians, proboscidians and diverse small land mammals. This association of marine and non marine taxa within the same stratigraphical successions, and a general lack of detailed recording of the context of fossils, has resulted in confused and often contradictory interpretations of the stratigraphy and palaeoenvironments.

Extensive fieldwork has allowed a reinterpretation of these rocks. Offshore mudstones of the Gehannam Formation yield diverse sharks as well as sirenians and some whales. Above these are shallow water sandstones of the Birket Qarun Formation, the lower three bodies of which thin and pass laterally into offshore mudstones within a short distance. Both sandstones and mudstones contain common marine vertebrates, with archaeocete whales being especially obvious. A dark mudstone drapes the underlying units and appears to represent a sudden influx of sediment, above which shallow water sandstones reappear. Progressive shallowing brings in lagoonal and deltaic sediments of the Qasr el Sagha Formation, which are cut by frequent large tidal channels. Shallow marine vertebrates, including small whales, as well as (possibly amphibious) proboscidians are present in the lagoonal sediments, with some deeper water taxa

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in the channels. Most non-marine fossils, such as those within the famous site of BQ-2, are within the channels and are the result of transport by tidal and fluvio-tidal currents.

A new dimorphodontid pterosaur from the Lower Jurassic of Dorset, southern England

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The rate of discovery of new species of pterosaur is currently at an all time high, but shows marked variation within particular intervals. During the last decade Lower Cretaceous rocks have yielded more than 20 new species, whereas it is now 40 years since a new pterosaur was described from any Lower Jurassic sequence, and over a century since this last occurred in the UK. Consequently, the recovery of a fossil from the Lias of Dorset, representing a new pterosaur, is noteworthy. The material, associated remains of the rostrum and mandibles, was found in a nodule near Seatown and appears to be Pliensbachian in age. The relatively deep rostrum and extreme size dimorphism in the dentition show clear similarities to *Dimorphodon*, also from the Lias of Dorset, and phylogenetic analysis supports a close relationship with other dimorphodontids. The distinctive dentition, in which the first four pairs of rostral teeth and two pairs of mandibular teeth are relatively large and fang-like, while the remaining teeth are remarkably small and short, prompted a re-evaluation of dental morphology in other pterosaurs. It appears that this pattern of size distribution represents the plesiomorphic condition for pterosaurs as it is present in all basal forms: *Preondactylus*, *Austriadactylus*, dimorphodontids and campylognathoidids (although among the latter *Raeticodactylus* and *Caviramus* have three large mandibular teeth). Anurognathids lack this pattern – further evidence that this clade is relatively derived rather than basal to all other taxa

A re-evaluation of Wealden sauropod faunas: implications for the evolution of sauropod dinosaurs during the Cretaceous

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Sauropod dinosaurs from the Early Cretaceous Wealden Supergroup are known from numerous fragmentary specimens. Recent studies regard most named taxa as invalid and have suggested that Wealden sauropod faunas displayed low diversity and were dominated by brachiosaurids. However, phylogenetic research has yielded a wealth of comparative data that facilitate a re-evaluation of the affinities and validity of Wealden sauropods.

This re-evaluation suggests that five valid monospecific genera can be accepted at present, and specimens such as the 'Barnes High sauropod' and the Isle of Wight rebbachisaurid, indicate the potential for recognising several new genera. The Hastings Beds Group was dominated exclusively by titanosauriforms. In contrast, the Wessex Formation was more diverse, comprising a rebbachisaurid, a brachiosaurid, a basal titanosauriform, two advanced titanosaurs, a possible non-titanosauriform macronarian or a non-neosauropod, and either a flagellicaudatan or a non-neosauropod. Thus, a conservative estimate of the diversity of the Wessex Formation sauropod fauna would be a minimum of six genera. The presence of a flagellicaudatan is unexpected given the current view that diplodocids became extinct at the Jurassic/Cretaceous boundary, and that dicraeosaurids were restricted to South America at this time. These UK faunas include some of the earliest known members of important Cretaceous clades such as Lithostrotia (advanced titanosaurs) and Rebbachisauridae.

Thus Wealden sauropods are important because of the insights they yield into the nature of Early Cretaceous sauropod faunas during the recovery from the Jurassic-Cretaceous boundary extinction and the onset of the titanosaur radiation.

Whale meat again: the forensic microvertebrate palaeontology of a *Basilosaurus* skeleton from Wadi Al-Hitan (Zeuglodon valley), Egypt

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The Fayum oasis to the west of Cairo, Egypt is well known to vertebrate palaeontologists for its rich marine mammal faunas. To its west, the Wadi Al-Hitan UNESCO World heritage site, known also as "Zeuglodon Valley", is famous for its abundant and well-preserved fossil whales and sirenians.

Many of the larger species of sharks and rays were published in the late 19th century. These records were generally based on teeth associated with marine mammals or surface-collected. They often lack a reliable stratigraphic and geographical context. Fieldwork by the authors between 2005 and 2009 in collaboration with members of the University of Michigan yielded large numbers of undescribed or previously unrecorded shark and ray species, more than trebling the previous records. These were generally obtained by acid-concentration and wet screening of unweathered and partially unconsolidated sediments and by surface collecting wind-ablated surfaces.

As the prevailing opinion was that large numbers of sharks' teeth were associated with marine mammal skeletons, samples were taken both close to carcasses and relatively whale-free sites in the Birket Qarun and from the deeper-water coeval Gehannan formations. In all, more than 40 samples were taken within a number of different facies. Separate to the Egyptian fieldwork, at University of Michigan in Ann Arbor, Michigan, USA, the sediment surrounding a large skeleton of *Basilosaurus isis* in the Birket Qarun Formation was sieved.

It was found that there was a relationship between facies related diversity and the presence or absence of a whale bones but that the great majority of the shark and ray species collected were not directly predated the carcass.

A *Diplodocus*-sized bipedal basal sauropodomorph from the Late Triassic of South Africa

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A partial skeleton of a basal sauropodomorph from the Lower Elliot Formation (mid to late Norian) of South Africa represents an animal of unprecedented size for that place and time.

Available material includes dorsal and caudal vertebrae, a dorsal rib, a chevron, an ulna, and a pedal ungual, with additional elements under preparation. All of the elements are exceptionally large, on average 1.9 times the linear size of the largest individual of the contemporary *Aardonyx*. *Aardonyx* was previously the largest known non-sauropod from the Lower Elliott Formation, with a femur length of up to ~800 mm. Cross-scaling from other basal sauropodomorphs suggests a femur length of ~1500 mm and a mass of 10-15 metric tons for the giant Elliot form. These estimates are comparable to the femur length (1540 mm) and estimated mass of CM 84/94, the holotype of *Diplodocus carnegii*. The ulna is unusually short and robust, 20% shorter than expected based on the other elements, and its morphology suggests that, like some other large basal sauropodomorphs, the giant Elliot form was an obligate biped. This is opposite to the trend of forelimb elongation in quadrupedal basal sauropods.

The giant Elliot form represents the largest known non-sauropod sauropodomorph and one of the largest bipedal animals of all time. It demonstrates that basal sauropodomorphs achieved very large body size despite lacking most of the presumed key innovations of sauropods, such as quadrupedal stance, columnar limbs, and extensive skeletal pneumaticity.

The pectoral girdle of *Dimorphodon macronyx* (Pterosauria, Dimorphodontidae) and the terrestrial abilities of non-pterodactyloid pterosaurs

Mark P. Witton

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A handful of studies conducted across the 1980s and 1990s have concluded that non-pterodactyloids were sluggish, sprawling quadrupeds or, perhaps, were bipedal. Reassessment of non-pterodactyloid limb girdles and proximal limb bones, principally those of the Lower Jurassic pterosaur *Dimorphodon*, suggest that early pterosaurs were actually capable of using parasagittal, quadrupedal gaits like those suspected for pterodactyloids, albeit with relatively restrictive shoulder mechanics. The glenoid fossa of *Dimorphodon* is comprised of two laterally-prominent buttresses that permit a great range of lateral and aft humeral motion. The dorsal glenoid buttress is larger and more posteriorly-prominent than the ventral, providing support for a parasagittal limb and allowing the adducted humerus to rotate forward to a subvertical position. The buttress configuration dictates that the forelimb must be rotated somewhat posteriorly before a parasagittal pose can be assumed, with the curved humeral head then pronating the forelimb to facilitate parasagittal movement. Arguments that the hindlimb permitted an erect, bipedal pose can be applied to this model, permitting parasagittal use of the legs along with the arms. Elongate preacetabular processes are also indicative of columnar hindlimbs in most early pterosaurs. Claims that the relatively extensive membranes of non-pterodactyloids would hinder terrestrial locomotion ignore the probable elasticity of these structures and the possible use of asymmetric gaits. The glenoid morphology described for *Dimorphodon* is common to all non-pterodactyloids, indicating these postures could be assumed by all early pterosaurs.

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Preliminary results of acid etching limestone containing bone fragments from the Middle Jurassic (Bathonian) Kilmaluag Formation at Cladach a' Ghlinne, Isle Of Skye, Scotland.

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In 2009, a field trip (organised by Liston as part of the 69th annual Society of Vertebrate Paleontology conference, held that year in Bristol), visited a locality on the Isle of Skye, near Elgol, an outcrop on the foreshore at Cladach a' Ghlinne. This is by no means a new locality with early workers identifying the Middle Jurassic sediments as early as 1986.

Recent work by Barrett and field team in 2004 identified a sauropod tooth from this locality, the first to be described from Scotland. Barrett has also indicated that this area was significant for its microvertebrate fauna consisting of sharks, fishes, salamanders, turtles, crocodylians, various squamates, synapsids, early mammals and a choristodere.

In addition to the femur of a small ornithopod dinosaur (discovered by Kelly, and under description by Liston), approximately 1 kilogram of bone bearing limestone was collected and processed through hydrochloric acid (5-10% strength, with the etchings rinsed in fresh running water) by Berrell, in an attempt to retrieve microfossils. This resulted in many very small isolated bone fragments (lodged with the National Museums of Scotland, as per the agreements for permission to collect during the SVP field trip), currently pending identification. This demonstrates that the procedure is effective at extracting microfossils from this matrix. It is likely that a larger sample size would yield better material. All these finds confirms this locality's importance for better understanding the fauna of the Middle Jurassic of Scotland.

Extant xenarthrans inner ear diversity

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The Xenarthra, which include the extant armadillos, anteaters and sloths, and a rich diversity of fossil taxa, constitute one of the four major extant placental clades. Their living representatives cover a large diversity of locomotor habits varying from exclusive burrowing to arboreality. They also present different degrees of activity like the cursorial three banded armadillo and the almost inactive sloths. Here we present the first detailed study investigating the morphology of the bony inner ear in most of the extant xenarthrans. Our large sample allows us exploring the relationships of the inner ear morphology in relation with phylogeny, locomotor behavior, ontogeny and allometry. We took a number of measurements including angles between the different semicircular canals and the cochlear basal plane, perimeter, radius, diameters, thickness of the semicircular canals, number of coils, length, height and width of the cochlea. The Xenarthra are notably characterized by a putative plesiomorphic pattern of the cochlea in placentals, with the first basal turn often widely separated from the following turns. Besides, the variation of the measured metric values shows a strong correlation with the phylogenetic pattern, but less with the locomotor behavior and allometry. Concerning ontogeny, the location of the semicircular canals in the petrosal appears to be set up before the volumetric growth of the bony labyrinth is completed. This study will also allow recognizing isolated xenarthran petrosal bones in the fossil record.

Reptiles from the Lower Lias of the Dorset Coast and the Mary Anning Connection

Sandra Chapman and Lorna Steel

Natural History Museum, UK.

The Lower Lias is famous for its assemblage of marine and terrestrial reptiles. This iconic marine reptile fauna includes numerous ichthyosaur and plesiosaur specimens and the rare primitive pterosaur *Dimorphodon*, some rare, fragmentary, theropod material and the ornithischian *Scelidosaurus*. Mary Anning is most famously connected with the first discoveries of the ichthyosaur *Temnodontosaurus platyodon*, the plesiosaur *Plesiosaurus macrocephalus* and the pterosaur *Dimorphodon macronyx* between 1810 and 1840. The *Temnodontosaurus* skull displayed in Lyme Regis Museum was discovered by Mary's brother Joseph in 1810, and Mary found the cervical vertebrae in 1811 when she was 12 years old.

In the Natural History Museum collections there are 13 ichthyosaur specimens that were collected by Mary, three plesiosaurs, three pterosaurs and two coprolites. There are also a few invertebrates and a shark dentition that she collected. Most of these specimens were purchased by the British Museum from collectors such as Thomas Hawkins, and William Cole (Earl of Enniskillen), who had purchased them from Anning, but some were purchased directly from

Mary and her mother 'Molly'. Many other reptile specimens came from other Lower Lias collectors such as Mr R. Damon, Mr H. Marder and Mr J. Marder, Mr B. Wright, Hon. R. Marsham, Mr F. Harford and Mrs M. Dollin.

The Lower Lias has a long history of collecting, but discoveries can be made in museum collections too. In the NHM fossil reptile collections, these include four articulated thalattosuchian vertebrae, the only record from the Lower Lias, and isolated theropod material.

James Harrison (1819-1864) and the discovery of the dinosaur *Scelidosaurus* from the Early Jurassic (Sinemurian) (Liassic Cliffs) of Charmouth, Dorset, UK.

Sandra D. Chapman and Timothy A. M. Ewin

Natural History Museum, London

James Harrison, a "medical gentleman" who resided in Charmouth from 1850 to 1864, is an unsung hero of vertebrate palaeontology. Between 1856 and 1861 Harrison made his most lasting accomplishment; he found the world's first complete articulated dinosaur near Charmouth, Dorset in what is now known as the Charmouth Mudstone Formation (Lower Sinemurian, Lower Jurassic).

These remains were sent to Richard Owen who, in a series of papers (1859; 1861; and 1863), identified the remains as a new dinosaur species. Owen named it *Scelidosaurus harrisoni* in 1861 in the collector's honour. In addition to the completeness, these remains were also significant in that they included the first complete dinosaur skull and gave further support for Owen's 1842 dinosauria which, as a concept, had been under threat in 1858. These remains are now even more significant as they are the earliest British ornithischian dinosaur and are located in a key area in the phylogeny of Thyreophoran dinosaurs. Sadly, Harrison died in 1864 only a year after Owen's final publication on *Scelidosaurus*.

This work charts Harrison's discovery and the history of his other collections (which also included cephalopods, fish and other reptiles) based on his correspondence with many leading scientists of the time including; Sir Richard Owen, Dr Thomas Wright, Dr S. Woodward and Henry Woodward and Sir Philip Edgerton, as well as other documents. Also noteworthy is Harrison's juvenile *Scelidosaurus* figured by Owen and held in the Lyme Regis Museum.

An almost complete, articulated specimen of the lungfish *Ctenodus interruptus* from the Viséan of Scotland.

E. L. Sharp and J. A. Clack

University Museum of Zoology, Cambridge

The skeleton of the lungfish *Ctenodus interruptus* presented here is the most complete Carboniferous lungfish from the United Kingdom ever found. Only a few examples of articulated lungfish specimens are known anywhere, most Carboniferous specimens consisting of isolated tooth plates, isolated cranial or postcranial elements, and a few showing more or less complete skull roofs or palates.

The taxonomy of *Ctenodus* has thus been uncertain for well over a century. Recent work has shown that there are four valid species, separated stratigraphically, in the UK, and a fifth new species remains to be described. The Viséan *C. interruptus* was formerly known only from isolated tooth plates, but the discovery of this new specimen provides much new information about the skull and postcranium not just of *C. interruptus*, but of *Ctenodus* species generally. *Ctenodus* can now be placed more securely in the context of lungfish anatomy, phylogeny and evolution. The specimen shows, in both external and internal views, cheek and circumorbital bones previously unknown for *Ctenodus*. It also shows that it retained the primitive condition of distally segmented and bifurcated lepidotrichia in the caudal fin, although it is not clear whether it shows the primitive state of a separate first dorsal fin, or the derived condition of a continuous dorsal and caudal fin. The closest anatomical comparisons can be made between *Ctenodus interruptus* and the Late Devonian *Scaumenacia*, the Viséan *Straitonia*, and the Late Carboniferous *Sagenodus copeanus* from North America, which are also known from articulated material.

Possible theropod footprints from the Lower Greensand *Mammilatum* bed of Folkestone

Philip Hadland

The Cretaceous Lower Greensand *Mammilatum* bed is well exposed on the foreshore at Folkestone Warren. They reveal what appear to be three closely grouped two toed footprints of a large vertebrate. Two of the prints are of such similar form that it cannot be denied that they are indeed footprints made by an animal. Specimens of presumed 'footcasts', some of which resemble the form of an ostrich foot have also been found in close proximity to the footprints and collected. The footcasts are of comparable sizes to the prints and also indicate two toes. Based on the shape of the footprints it can be reasonably assumed that the animal that made them was bipedal. One can only speculate about the exact kind of animal that made them but it is possible that they were created by a kind of theropod. It is hoped that in the future body fossils will come to light revealing the identity of the animal.

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Investigating the buoyancy and floating posture of pterosaurs

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Most pterosaur specimens are known from marine settings and there is strong evidence that some taxa were pelagic. Specimens found over a hundred kilometers from palaeo-coastlines suggest that some species may have been trans-oceanic, while others are known with fish as gut contents. It is reasonable to expect that some pterosaurs would be forced to the water's surface on occasion while feeding or during poor weather conditions. However, pterosaurs lack a strongly flexible neck and have wing membranes that link the fore- and hindlimb suggesting that they were unable to adopt a resting posture on water in the manner of seabirds. Using digital models of both pterodactyloid and non-pterodactyloid pterosaurs, and computational dynamics, we tested the buoyancy and floating posture of a number of pterosaurs. In all cases the body floated high on the water, but the head was positioned at, or partially below, the surface. Repositioning the wings or neck did not improve this posture. Thus it would seem that a pterosaur forced down to the water would likely drown unless it could take-off again quickly. A recent study suggests that pterosaurs could launch from the water, so a sea surface touchdown would not necessarily be fatal, but could prove difficult for the animal. The problematic posture and vulnerability does strongly suggest that pterosaurs (like tropicbirds) would have avoided landing as much as possible and the 'surfing' style of locomotion suggested for some species would be unlikely.

Maximum bite force and its relationship to biting substrate and mechanoreceptors in lizards

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Bite force is an important ecological attribute in lizards that can both facilitate and limit dietary breadth, feeding strategy, and reproductive success. It is thus an important driver of cranial evolution. To date bite force has been measured from conscious animals using a bite force transducer in over 50 studies. For results to be comparable across studies it is necessary to obtain maximum voluntary performance. However, previous studies vary with regards to the biting substrate on the transducer bite surface (e.g. leather, rubber, metal). Using a phylogenetically diverse sample of lizards (e.g. *Crotaphytus*, *Eublepharis*, *Gekko*, *Elgaria*; n = 10 taxa), we examined the effect of bite substrate (i.e. cowhide leather, balsa wood, stainless steel) on maximum bite force. The experimental design was such that the lizards' experience biting on different substrates was accounted for in the analysis.

We found that bite-force performance was significantly lower on hard substrates than it was on more pliable substrates. This constraint on bite force probably arises through feedback from mechanoreceptors in the tongue, teeth, bone, jaw joints, and/or sutures that serve to limit risk of damage to the feeding apparatus (e.g. teeth) during loading. The extent of the difference in bite force is particularly pronounced in iguanians, perhaps due to more sensitive mechanoreceptors and a greater need to protect the teeth from damage. We suggest that in future studies researchers standardize bite substrate so that comparisons across studies can be more informative.

A new longirostrine ichthyosaur (Reptilia) from the Toarcian of France broadens the ecological diversity of the genus *Temnodontosaurus*

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The ichthyosaur genus *Temnodontosaurus* has always been viewed as a top predator of the Early Jurassic marine environments, while other contemporaneous ichthyosaurs such as leptonektids and stenopterygiids were occupying the lower trophic levels. We describe here an almost complete skeleton of this successful genus from the middle Toarcian (Lower Jurassic) of the Beaujolais foothills near Lyon, France, and assign it to a new species of *Temnodontosaurus*. This specimen exhibits cranial peculiarities such as a thin, elongated, and likely edentulous rostrum, as well as a reduced quadrate. Such morphological combination indicates dietary preferences that markedly differ from other species referred to as *Temnodontosaurus*. Despite a conservative postcranial skeleton, we propose that *Temnodontosaurus* is one of the most ecologically diverse genera of ichthyosaurs, including apex predators, small and soft prey longirostrine hunters, and generalized forms. Ammonites collected along the described specimen indicate that the new species is younger (*bifrons*

ammonite zone) than most known Toarcian ichthyosaurs and therefore slightly postdates the severe environmental changes and marine invertebrate extinctions that occur during the Toarcian Oceanic Anoxic Event. The present study hence raises the question whether the speciation of *Temnodontosaurus* towards a new ecological niche, may have been a consequence of the post-crisis marine ecosystem reorganization.

A new species of *Ichthyosaurus* from the Pliensbachian of the Charmouth area.

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(supported by Jones-Fenleigh Memorial Fund)

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A well preserved ichthyosaur (DONMG:1983.98) from the palaeontology collection of the Doncaster Museum and Art Gallery was recently "rediscovered". The incomplete, laterally flattened skeleton includes a skull, articulated dorsal and cervical vertebrae with ribs, a nearly complete pectoral girdle, and an articulated forelimb. A specimen of the Pliensbachian belemnite *Bairdowius junceus*, preserved on the same slab as the ichthyosaur, indicates that the specimen originated from the Stonebarrow Marl Member of the Charmouth Mudstone Formation. Morphology of the shoulder girdle and forelimb suggest that this specimen is an *Ichthyosaurus*, thus extending the range of the genus to the Pliensbachian. Preliminary examination of skull proportions and tooth morphology suggest that the specimen represents a new species, but work is ongoing. Of additional interest are preserved gut contents of cephalopod hooklets found among the ribs of the specimen.

Function of palatal dentition

Ryoko Matsumoto^{1,2} and Susan Evans¹

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Any consideration of feeding in extinct vertebrates will include detailed discussion of the marginal dentition, but far less attention has been paid to the palatal dentition. Although there is a general acceptance that the palatal dentition is plesiomorphic for amniotes, its evolutionary history and function are not well understood. During feeding, the tongue and palate cooperate in gripping, intra-oral transport, and swallowing, thus modification of the palatal dentition should reflect changes in feeding behaviour and/or changes in the anatomy of the oral soft tissues. Potentially, therefore, a better understanding of the role of the palatal dentition may provide an additional source of information on the biology of extinct tetrapods.

This study focuses on variation and changes in the palatal dentition through the evolutionary history of amniotes. On the phylogenetic tree, the palatal dentition is discussed on the basis of literature review, as are ideas on the function of palatal teeth. There are differences between groups with respect to the arrangement of the palatal dentition and pattern of loss. Palatal teeth may be considered as having an important role in the action of holding and manipulating food within the mouth (although they may occasionally contribute to food reduction). The challenge is then to provide an explanation for the subsequent loss/reduction of this important gripping surface in derived members of most major tetrapod lineages. The hypothesis is that this loss/reduction was linked, in each case, with functional, anatomical, or lifestyle changes that rendered a palatal gripping surface less important.

Virtual reconstruction of the brain and sinuses of the basal marine crocodylomorph

Pelagosaurus typus

SE Pierce^{1,2}, ME Williams¹ and RBJ Benson³

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Fossil crocodile brains and associated sinuses are poorly studied, but potentially offer valuable functional paleoneurological and evolutionary insights. Recent acquisition of micro-CT scan data of the skull of *Pelagosaurus typus*, a Jurassic thalattosuchian, provides an excellent opportunity to reconstruct the endocast of a basal marine crocodylomorph. Results indicate a suite of unique and functionally intriguing anatomical features including: 1) dorsally positioned paranasal sinuses – allowing the snout to develop a circular cross section conferring a constant mechanical bending strength in all directions; 2) enlarged cerebrum – possibly correlated with more complex cognition and behaviours; 3) bulbous pituitary – potentially increasing water absorption and reducing dehydration in a marine environment; 4) sizable oculomotor nerves – consistent with large orbits and suggesting the ability to process large quantities of visual information; 5) dorsoposteriorly expanded longitudinal venous sinuses – indicative of increased blood flow through the brain; 6) semicircular canals as high as long – closer in shape to more terrestrially adapted archosaurs; and 7) a wide and ventromedially extended cochlear duct – potentially increasing the range of detectable sound frequencies. Taken together, the morphology of the brain and associated sinuses in *Pelagosaurus* implies that this basal crocodylomorph was a highly visual and active marine predator that may have had increased social complexity. However, the data also suggests that *Pelagosaurus* was most likely only

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semi-aquatic in habit, presumably communicating and interacting on land and hunting in the water.

The Carboniferous Derbyshire Riviera, a chondrichthyan paradise

K. R. Richards and J. A. Clack

University of Cambridge

Derbyshire's Cawdor Limestone is Viséan in age and a member of the Eyam Limestone Formation. It is dark gray to gray and forms lenses of knoll-reef limestones and thin-bedded black limestones with shale. Rapid facies changes indicate a frequently changing environment and the rich invertebrate fauna includes spriferid, productid and gigantoproductid brachiopods, corals, trilobites, foraminifera and ostracods. The vertebrae and scales of palaeoniscid actinopterygians have previously been recorded and first reports of the Derbyshire chondrichthyans documented 25 species, with recent publications adding a further 7 species. Carboniferous near-shore sites are numerous worldwide and include sites in Montana, Poland, Russia, Belgium and Iran. Historical publications are fraught with collection bias and a lack of adequate locality descriptions, consequently the current picture of the Derbyshire palaeoenvironment is incomplete and biased. In this study, limestone material representing four localities, within 10km of each other, was acid digested and the micro and macro fossils recorded. The fauna of all four sites are dominated by chondrichthyans and shares many taxa with Bear Gulch, Montana and Bearsden, Scotland, as well as with Polish, Russian and Iranian sites. The large range of particular species and groups, such as the Stethacanthids, raise questions as to species vagrancy and species boundary recognition in the fossil record. Tentative comparisons are made between the nearshore environment of Derbyshire with the bay deposits of Bear Gulch in Montana.

A new procolophonoid parareptile from Australia (Arcadia Formation, Early Triassic)

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Procolophonoidea is a group of small- to medium-sized parareptiles that had a high survival rate during the P/Tr extinction event. It is traditionally divided into two clades, the Owenettidae and Procolophonidae. Unequivocal Permian procolophonoid records are limited to owenettids from Africa and a single procolophonid from Russia. During the Triassic, procolophonids had a global distribution, whereas owenettids are known only from Africa, Madagascar and South America. Here we report a new procolophonoid from Australia, represented by a partial skull. The study of the specimen was supplemented by high resolution CT scans. It was found by Dr Anne Warren at the Tank Locality, a vertebrate fossil site within the Early Triassic (Griesbachian) Arcadia Formation of Queensland. The formation is dominated by red-brown overbank mudstones interbedded with channel sandstones, and was deposited by meandering river systems in a warm to semiarid climate with seasonal rainfall.

The new specimen displays a unique combination of primitive parareptilian and derived procolophonoid characters, along with some autapomorphies. Inclusion of the taxon in a phylogenetic analysis with well-known procolophonoids supports placement within Owenettidae, but a basal procolophonid position cannot be excluded.

The Arcadia Fm has been correlated with the *Lystrosaurus* Assemblage zone (AZ) of South Africa with which it shares common faunal components, although the Arcadia fauna differs in being dominated by temnospondyls rather than synapsids and reptiles. The new procolophonoid increases the known diversity of the Arcadia reptilian fauna and, if confirmed as an owenettid, would provide another link with South Africa.

The taxonomy of '*Germanodactylus*' *rhamphastinus* (Wagner, 1851)

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The Late Jurassic pterodactyls, *Germanodactylus cristatus* (type species of genus) and '*G. rhamphastinus*' from the Solnhofen platenkalk of Bavaria, Germany, present a number of taxonomic and phylogenetic problems. The genus *Germanodactylus* was erected by Young (1964) to accommodate a specimen of *Pterodactylus kochi* (Wagner, 1837) that had been renamed *P. cristatus* by Wiman (1925), characterised by an edentulous beak tip and remarkably straight dorsal surface of the skull when viewed laterally. Young (1964) placed *Germanodactylus* in Dsungaripteroidea on account of distal edentuly. Later, Wellnhofer (1970) placed *Pterodactylus rhamphastinus* (Wagner, 1851) in *Germanodactylus* on account of its robust dentition and headcrest. *G. rhamphastinus* possess teeth distally in its jaws and thus is regarded to be plesiomorphic. Bennett (2006) reassessed the systematics of *Germanodactylus* and evaluated the diagnosis of the genus provided by Wellnhofer (1970).

In two cladistic analyses (Unwin 2003, Kellner 2003) *Germanodactylus* falls out in two distinct positions in a cladogram for all Pterosauria. In the analysis of Unwin (2003), Dsungaripteroidea is recovered, where *Germanodactylus* is a monophyletic genus that is sister taxon to Dsungaripteridae. However, in the analysis by Kellner (2003), *Germanodactylus* is recovered in

the Archaeopterodactyloidea. Within the Archaeopterodactyloidea, *Germanodactylus* spp. form a monophyletic clade in a polytomy with *Pterodactylus* spp., forming a sister group relationship with an unnamed clade containing Ctenochasmatidae and *Gallodactylus* (= *Cycnorhamphus*). Such a major difference in phylogenetic modelling clearly demonstrates that these taxa require scrutiny. Arguments for the reassessment of the taxonomic divisions for BSP AS I 745 & BSP 1892 IV 1 are presented.

John Whitaker Hulke, a neglected palaeontological pioneer

Simon Wills

Natural History Museum, London

John Whitaker Hulke (1830–1895) was one of the early pioneers of vertebrate palaeontology whose work is now somewhat forgotten. At various times he was President of the Geological Society, President of the Royal College of Surgeons, President of the Clinical Society and President of the Pathological Society. He was also a Fellow of the Royal Society and Consulting Surgeon at Moorfields Eye Hospital. His initial research into dinosaurs was based around specimens collected by Mr Mansel Pleydell of Blandford in Dorset with whom he appeared to have struck up a friendship. Eight out of twelve papers published by Hulke between 1869 and 1874 concerned specimens from the Kimmeridge Clay of Dorset and included the first descriptions of two of the three known Dorset sauropods. He also developed a close friendship with the Reverend William Fox on the Isle of Wight and for a time Hulke had almost exclusive access to this collection. The sauropod *Ornithopsis hulkei* was named in his honour by his friend Harry Govier Seeley in 1870. Hulke described and named a number of dinosaurs including *Eucamerotus*, *Cumnoria* (= *Iguanodon*) *prestwichii* and *Lexovisaurus* (= *Omosaurus*) *durobrivensis*, amongst others. Hulke attempted the first complete skeletal reconstruction of the small ornithopod dinosaur *Hypsilophodon foxii*. He is also credited with the first detailed description of *Polacanthus foxii*. His personal collection was donated to the British Museum by his widow Julia and is now stored in the Natural History Museum, London.

Additional details on the skull of *Istiodactylus latidens* and the palaeoecology of istiodactylid pterosaurs

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Examination of the holotype of the Wealden Cretaceous pterosaur *Istiodactylus latidens*, a partial skeleton and fragmentary skull, has revealed a 'missing' jaw fragment that completes the jaw length of this animal and permits a new skull reconstruction. The skull has a proportionally tall and elongated orbital region angled relatively high to the jawline, and a comparably robust dorsal extension of the premaxilla. This morphology is interpreted as further specialisation towards the scavenging foraging method proposed for some istiodactylids. Elongation and forward rotation of the jaw adductors lessen muscle fatigue and increase mechanical advantage during jaw adduction and the tall, dorsally-braced skull resists dorsoventral bending in the same plane of motion regularly used by group-foraging avian scavengers. Additional scavenging adaptations are seen in the mechanically-strong circular cross-section formed by the closed jaw tips, broad dental rosette of 'cookie-cutter' teeth and (inferred from other istiodactylids) enlarged m. posterior pterygoideus, permitting an unusually powerful bite compared to other pterosaurs. Istiodactylids also appear well-adapted for flight, another requirement of habitual scavengers: their deltopectoral crests and sterna are indicative of unusually strong m. pectoralis, suggesting strong takeoff and flapping abilities. With long wings, their flight seems ecomorphologically comparable with that of modern soaring birds. Istiodactylids lack the expanded scapulae and elongated flight musculature characteristic of water-launching pterosaurs, however, suggesting they preferred terrestrial habitats. The discovery of istiodactylids in exclusively non-marine strata is consistent with this interpretation.

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Programme

Monday 12th September

12:00	Registration opens in Marine Theatre	
14:00-14:10	Welcome to the SPPC/GCG Conference	
	Session 1 - Chair: Mark Evans	
14:10-14:30	Frank Osbaeck	Acid Preparation of a pond turtle from the Eocene Mo clay formation of northern Denmark
14:30-14:50	Mike P. A. Howe	The UK Continental Shelf on the move: transferring two major core and sample collections.
14:50-15:10	Philip Hadland	Accessing Palaeontology in a Local Museum
15:10-15:30	Jeff Liston	Resourcing Palaeontological Collection Care in a Time of Crisis: The Legacy of the Earth Science Review, Twenty Years On
15:30-15:50	<i>Tea/coffee</i>	
	Session 2 - Chair: Mike Howe	
15:50-16:10	Mark Evans	Bringing sea dragons back to life: 200 years on from Anning, Conybeare and De la Beche.
16:10-16:30	Trine Sørensen and Martin Abrahamsson	Simplifying extraction and cross sectioning of microfossils in unlithified sediment
16:30-16:50	Pedro A. Viegas , Remmert Schouten, Ed Drewitt and Michael J. Benton	The Bristol Dinosaur Project – Preparation Methods
16:50-17:10	Scott Moore-Fay	How Long? Preparation of the Weymouth Bay Pliosaur.

Tuesday 13th September

9:00-9:10	Notices etc	
9:30-12:30	Workshop visits in Lyme Regis and Charmouth	
12:30-15:30	Field Trip - Classic Lyme Regis localities	
16:00-16:10	Welcome to SVPCA	
	Session 1 - Chair: Jeff Liston	
16:10-16:30	Cindy Howells	James Frederick Jackson (1894-1966). An Extraordinary Geologist.
16:30-16:50	G.V.R. Prasad , Varun Parmar, P. Yadagiri & Deepak Kumar	New vertebrate fossils from the Lower/Middle Jurassic Kota Formation of Pranhita-Godavari valley, peninsular India
16:50-17:10	Charlie Underwood , David Ward and Chris King	Palaeoenvironmental setting of the marine Eocene vertebrate faunes of the Fayum, Egypt.
17:10-17:30	David J. Ward , Charlie J. Underwood and Chris King	Whale meat again: the forensic microvertebrate palaeontology of a <i>Basilosaurus</i> skeleton from Wadi Al-Hitan (<i>Zeuglodon</i> valley), Egypt
18:00-19:00	<i>Public Lecture:</i> Michael Benton. The end-Triassic mass extinction and its role in resetting ichthyosaur and dinosaur evolution	
19:00-21:00	Icebreaker in Skittle Alley:	

Wednesday 14th September

9:00-9:10	Welcome to SVPCA	
	Session 1 - Chair: Per Ahlberg	
9:10-9:30	John Clarke and Matt Friedman	Teleost superiority: a foregone conclusion? Patterns of teleost and holostean diversification in the Mesozoic.
9:30-9:50	Michael I. Coates and John A. Finarelli	Chondrenchelys, chimaeroids and early holocephalans
9:50-10:10	Matt Friedman , Martin D Brazeau and Robert Atwood	Synchrotron tomography reveals three-dimensional gill-arch structure in a stem gnathostome from the Hunsrück Slate

Programme

10:10-10:30	Zerina Johanson , Moya Smith and Charlie Underwood	Evolution of elasmobranch (Chondrichthyes) dentitions
10:30-10:50	<i>Tea/Coffee</i> Session 2 - Chair: Matt Friedman	
10:50-11:10	Joseph Keating , Robert Sansom and Mark Purnell	Filling a gap in Palaeozoic vertebrate diversity: the Wayne Herbert osteostracan fauna
11:10-11:30	Martha B. Koot , Richard J. Twitchett, Gilles Cuny and Malcolm B. Hart	Effects of the late Permian extinction on Permian-Triassic shark faunas
11:30-11:50	Per E. Ahlberg , Pavel Beznosov, Ervins Luksevics and Jennifer A. Clack	A very primitive tetrapod from the earliest Famennian of South Timan, Russia
11:50-12:10	J. A. and R. N. G. Clack	A <i>Crassigyrinus</i> -like lower jaw, and other vertebrate elements, from the Tournaisian of Scotland.
12:10-12:30	Poster Session	
12:30-14:00	<i>Lunch</i> Session 3 - Chair: Ian Corfe	
14:10-14:30	Susan E. Evans & Yuan Wang	The Early Cretaceous Chinese lizard <i>Yabeinosaurus</i> : insights from new specimens
14:30-14:50	Mark N. Hutchinson , Adam Skinner and Michael S. Y. Lee	Lizard calibration points the the problem of <i>Tikiguania</i>
14:50-15:10	Marc E.H. Jones , Neil Curtis, Paul O'Higgins, Michael J. Fagan, Susan S. Evans	Shearing in <i>Sphenodon</i> and related character acquisition in Mesozoic Rhynchocephalia (Diapsida: Lepidosauria)
15:10-15:30	Robert Reisz and Sean Modesto	The neodiapsid <i>Lanthanolania ivakhnenkoi</i> from the Middle Permian of Russia, and the initial diversification of diapsid reptiles
15:30-15:50	<i>Tea/Coffee</i> Session 4 - Chair: Susan Evans	
15:50-16:10	Michael J Benton and Marcello Ruta	Tetrapod evolution through the Permian and Triassic: rock record, supertrees, and detecting events
16:10-16:30	Ryoko Matsumoto , Francois Escuillie Eric Buffetaut and Susan Evans	A choristodere from the late Paleocene of France
16:30-16:50	IJ Corfe , LK Säilä, A Kallonen, K Hamalainen, and J Jernvall	Patterns in the origin of multicuspid teeth among terrestrial amniotes – early adopters from Devon
16:50-17:10	Jeremy E. Martin Eric Buffetaut, Romain Liard, Komsorn Lauprasert1,5 and Varavudh Suteethorn	A freshwater teleosaurid in the Late Jurassic of northeastern Thailand
17:10-17:30	Poster Session	
18:00-19:00	<i>Public Lecture:</i> David Norman. Scelidosaurus from Lyme Bay, the world's first complete dinosaur	
19:00-20:00	Reception in Lyme Regis Museum	
20:00-22:00	Auction in Skittle Alley	

Thursday 15th September

9:00-9:10	<i>Notices for the day</i> Session 1 - Chair: David Unwin	
9:10-9:30	David Button , David Unwin and Mark Purnell	Continuous character states and their impact on the phylogeny of the Pterosauria
9:30-9:50	Mark P. Witton	The pectoral girdle of <i>Dimorphodon macronyx</i> (Pterosauria, Dimorphodontidae) and the terrestrial abilities of non-pterodactyloid pterosaurs
9:50-10:10	Eric Buffetaut and Paul Jeffery	A ctenochasmatid pterosaur from the Stonesfield Slate (Bathonian) of Oxfordshire, England.
10:10-10:30	E. Lawlor , S. Beardmore, D. Hone and P. Orr	Skeletal Taphonomy of Pterosaurs from the Late Jurassic of Germany
10:30-10:50	<i>Tea/Coffee</i> Session 2 - Chair: Eric Buffetaut	
10:50-11:10	Brian Andres , Lauren Howard and Lorna Steel	Owen's pterosaurs, old fossils shedding light on new clades

11:10-11:30	David M. Unwin	A new dimorphodontid pterosaur from the Lower Jurassic of Dorset, southern England
11:30-11:50	Colin Palmer	The histology and structural performance of pterosaur wing bones
11:50-12:10	Valentin Fischer	High diversity in late Early Cretaceous ichthyosaurs part II: The Cambridge Greensand material
12:10-12:30	Poster Session	
12:30-14:00	<i>Lunch</i>	
	Session 3 - Chair: Roger Benson	
14:10-14:30	Jeff Liston , Darren Naish and ?? ??.	The Strange Case of the Jurassic Ichthyosaur
14:30-14:50	Darren Naish and Jeff Liston	Robert Appleby's ichthyosaur legacy
14:50-15:10	Tom Kemp	Bean bags, modules, systems and the evolvability problem: reflections on how major new vertebrate taxa arise
15:10-15:30	Hilary Ketchum and Roger Benson	A basal pliosaurid (Reptilia, Sauropterygia) from the Oxford Clay Formation (Callovia, Middle Jurassic) of Bedfordshire: evidence for a gracile, longirostrine grade of Early-Middle Jurassic pliosaurids
15:30-16:30	<i>Bus to Dorchester</i>	
16:30-16:40	Welcome to Dorchester County Museum	
	Session 4 - Chair: Richard Forrest	
16:40-17:00	Richard Edmonds	Review of the West Dorset fossil collecting code of conduct
17:00-17:20	Roger B. J. Benson , Mark Evans and Patrick S. Druckenmiller	High diversity, low disparity and small body size in plesiosaurs from the Triassic-Jurassic boundary
17:20-17:40	Judyth Sassoon , Leslie F. Noè and Michael J. Benton	Cranial anatomy and palaeopathology of an Upper Jurassic (Kimmeridgian) pliosaur (Reptilia: Sauropterygia) from Westbury, Wiltshire
18:00-19:00	<i>Public Lecture:</i> Richard Edmonds and Richard Forrest - The Weymouth Bay pliosaur	
19:00-21:00	Reception in Dorchester County Museum	
	21:00 <i>Buses back to Lyme Regis</i>	

Friday 16th September

9:00-9:10	<i>Notices for the day</i>	
	Session 1 - Chair: Tom Kemp	
9:10-9:30	SSY Foo , SE Pierce , PM Barrett , PS Druckenmiller, RBJ Benson	Form, function and phylogeny: Virtual reconstruction of the inner ear of plesiosaurs
9:30-9:50	Neil Brocklehurst , Paul Upchurch, Philip Mannion and Jingmai O'Connor	The Completeness of the Fossil Record of Mesozoic Birds
9:50-10:10	Zoltan Csiki-Sava , Rosie Barnes and Paul Upchurch	The revision of the genus <i>Magyarosaurus</i> , and titanosaur diversity in the Maastrichtian of the Hateg Basin, Romania - preliminary results
10:10-10:30	Edward Drewitt , Remmert Schouten, Pedro Viegas and Michael J. Benton	The Bristol Dinosaur Project - developing a learning and outreach programme and training research staff and students to help deliver.
10:30-10:50	<i>Coffee/Tea</i>	
	Session 2 - Chair: Paul Barrett	
10:50-11:10	Victoria M. Egerton , Fernando E. Novas, Peter Dodson and Kenneth J. Lacovara	First occurrence of neonatal ornithomimid teeth from South America
11:10-11:30	Donald M. Henderson	Discovery and recovery of a complete, three-dimensionally preserved ankylosaur from the Early Cretaceous of northern Alberta, Canada
11:30-11:50	Phillip L. Manning , Roy A. Wogelius , William I. Sellers , Holly E. Barden , Nicholas P. Edwards, and Uwe Bergman	From Archimedes to <i>Archaeopteryx</i> : Trace metal mapping with Synchrotron Rapid Scanning X-Ray Fluorescence.
11:50-12:10	Michael P. Taylor and Mathew J. Wedel	Sauropod necks: how much do we really know?
12:10-12:30	Richard S. Thompson	A Combined Analysis Approach to the Phylogeny of the Talpidae (Mammalia: Lipotyphla).

Programme

12:30-14:00	<i>Lunch</i>	
	Session 3 - Chair: Don Henderson	
14:10-14:30	Paul Upchurch , Philip D. Mannion and Paul M. Barrett	A re-evaluation of Wealden sauropod faunas: implications for the evolution of sauropod dinosaurs during the Cretaceous
14:30-14:50	Paul M Barrett , Glenn W Storrs, Mark T Young and Lawrence M Witmer	A new skull of <i>Apatosaurus</i> and its taxonomic and palaeobiological implications
14:50-15:10	Mathew J. Wedel and Adam M. Yates	A <i>Diplodocus</i> -sized bipedal basal sauropodomorph from the Late Triassic of South Africa
15:10-15:30	L. Hautier and R.J. Asher	Skeletogenesis in the African elephant.
15:30-15:50	<i>Tea/Coffee</i>	
	Session 4 - Chair: Don Smith	
15:50-16:10	Robert Asher , Martin Ciancio, Mariela Castro, Fernando Galliari, Alfredo Carlini, David Pattinson and Lionel Hautier	Dental eruption in Southern Placental Mammals
16:10-16:30	Philip G Cox , Michael J Fagan, Emily J Rayfield and Nathan Jeffery	Biomechanical performance of the rodent skull: sensitivity analyses of finite element models
16:30-16:50	Nick Crumpton	The Vestibular System in Talpidae
16:50-17:10	Jerry Hooker	A new primate (Omomyidae, Microchoerinae) from the earliest Eocene of southern UK: the beginning of microchoerine evolution
17:10-17:30		
18:00-19:00	Public Lecture: Mark Witton	
	Pterosaurs: the Leathery Winged Revolution'	
19:30-11:30	Conference dinner in Marine Theatre	

Saturday 17th September

09:30 Field trips leave from Lyme Regis

17:30 Latest return from field trips

Previous Venues

2010	Cambridge-University Museum of Zoology
2009	Bristol-University of Bristol (joint meeting with SVP)
2008	Dublin-University College Dublin and National Museum of Ireland (Natural History)
2007	Glasgow-University of Glasgow IBLs/Hunterian Museum
2006	Paris-Ecole Nationale des Mines
2005	London-The Natural History Museum
2004	Leicester-University of Leicester and New Walk Museum
2003	Oxford-University Museum of Natural History
2002	Cambridge-Sedgwick Museum and Dept. Earth Sciences, Cambridge University
2001	York-The Yorkshire Museum
2000	Portsmouth-University of Portsmouth
1999	Edinburgh-National Museums of Scotland
1998	Bournemouth-University of Bournemouth
1997	Derby-University of Derby
1996	London-University College
1995	Newcastle upon Tyne-The Dental School, University of Newcastle upon Tyne
1994	Le Havre
1993	Cambridge-University Museum of Zoology
1992	Bristol-University of Bristol
1991	Oxford-University of Oxford
1990	Milton Keynes-The Open University

1989 Leicester-University of Leicester
1988 Boulogne sur Mer-
1987 London-British Museum (Natural History)
1986 Belfast
1985 Manchester
1984 London-University College
1983 Bristol
1982 Cambridge
1981 Cardiff
1980 Kingston upon Thames
1979 Oxford
1978 Reading
1977 Newcastle upon Tyne
1976 London-University College
1975 Edinburgh-The Royal Scottish Museum
1974 Manchester
1973 Leeds
1972 London-British Museum (Natural History) and Royal Holloway College
1971 Bristol
1970 Cambridge
1969 Newcastle upon Tyne-
1968 Reading
1967 London-Queen Elizabeth College
1966 Edinburgh-The Royal Scottish Museum
1965 London-Royal Holloway College
1964 Bristol
1963 Cambridge
1962 Newcastle upon Tyne
1961 London-University College
1960 Oxford
1959 London-Royal Holloway College
1958 Bristol
1957 Cambridge
1956 Newcastle upon Tyne
1955 Oxford
1954 London-University College
1953 Cambridge

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