

Progressive Palaeontology 2007



Thursday 12th – Saturday 14th April
Department of Earth Sciences, University of Bristol



Welcome and acknowledgements

We are pleased to welcome you to the Department of Earth Sciences at the University of Bristol for this year's Progressive Palaeontology meeting. This appears to be the best attended and most presentation-packed Progressive Palaeontology on record – we are just shy of 60 delegates and there are 30 presentations in total (24 oral and 6 poster).

As always Progressive Palaeontology's aim is to provide a framework in which to present ideas and discuss work with those at a similar stage in their career. In order to achieve this the Friday presentation session is supplemented by two social events and a field trip. On Thursday evening there is a pre-conference gathering at the Berkeley pub (opposite the department on Queen's Road) and following the presentation sessions on Friday there will also be an evening reception/dinner at Bristol Zoo. This year's field trip will be to Aust Cliff (a site famous for its Late Triassic fish fossils – see the brief guide at the end of this booklet). We are lucky to have two experts on this site joining us on the day and we have scheduled a reasonably late start so please do come along if you have registered!

We would also like to take this opportunity to thank the following individuals who have helped in supporting, preparing and running this year's meeting:

The Palaeontological Association and the University of Bristol Alumni Foundation for providing sponsorship. Blackwell Publishing, Cambridge University Press and Oxford University Press whom all generously offered books to be given away as prizes. Jason Hilton, Alan Spencer and The Palaeontological Association for helping with, and hosting, the website. Michael Benton, Phil Donoghue, Pam Gill, Andrew Hook, David Jones, Susannah Maidment, Nic Minter, Jeremy Philips, Remmert Schouten and Esther Sumner for offering useful advice and help in the planning stages. Phil Donoghue and Mike Bassett for kindly agreeing to do the opening speeches. Mark Bell, Dan Oakley, Ceri Thomas and Mark Young for offering to help out with manning the reception desk and serving tea and coffee. Simon Carpenter and Mike Curtis for offering their expertise to the field trip and the Gee family for giving us permission to visit the Manor Farm locality.

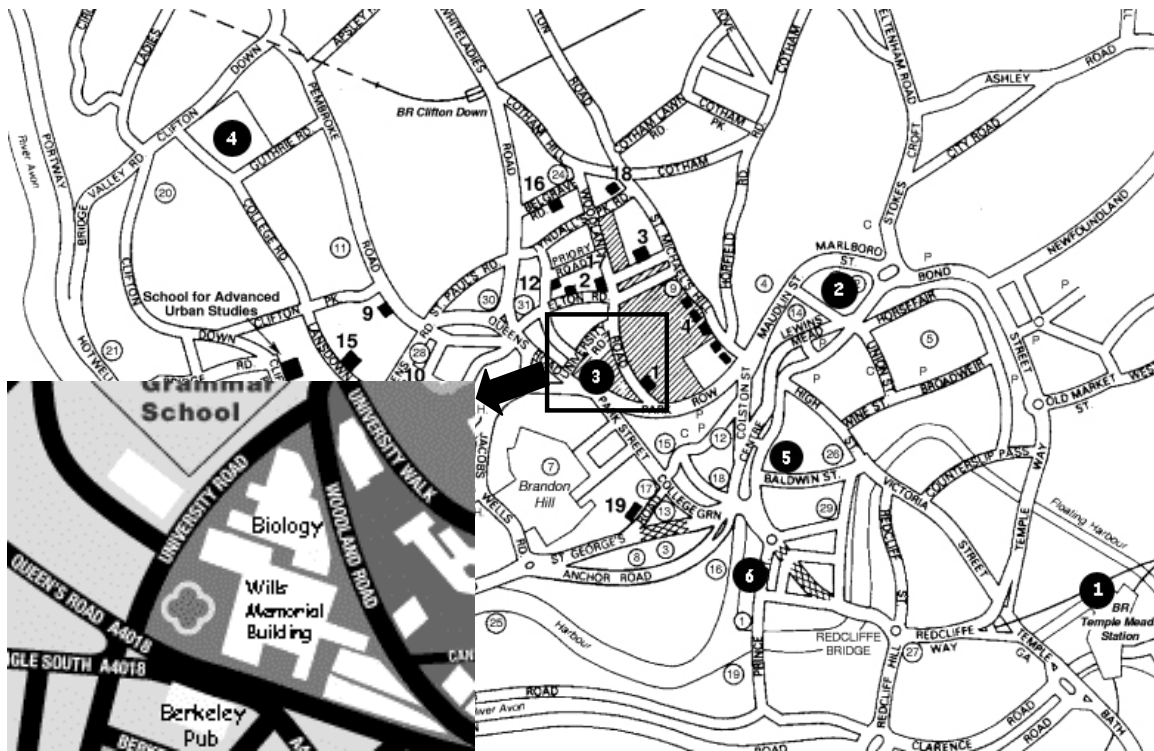
Finally, we would like to wish next year's hosts Manchester the best of luck.

Graeme Lloyd
Ian Corfe
Sandra Jasinowski
Sarda Sahney
Laura Säilä
Manabu Sakamoto
Rob Sansom
James Tarver

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Maps and directions



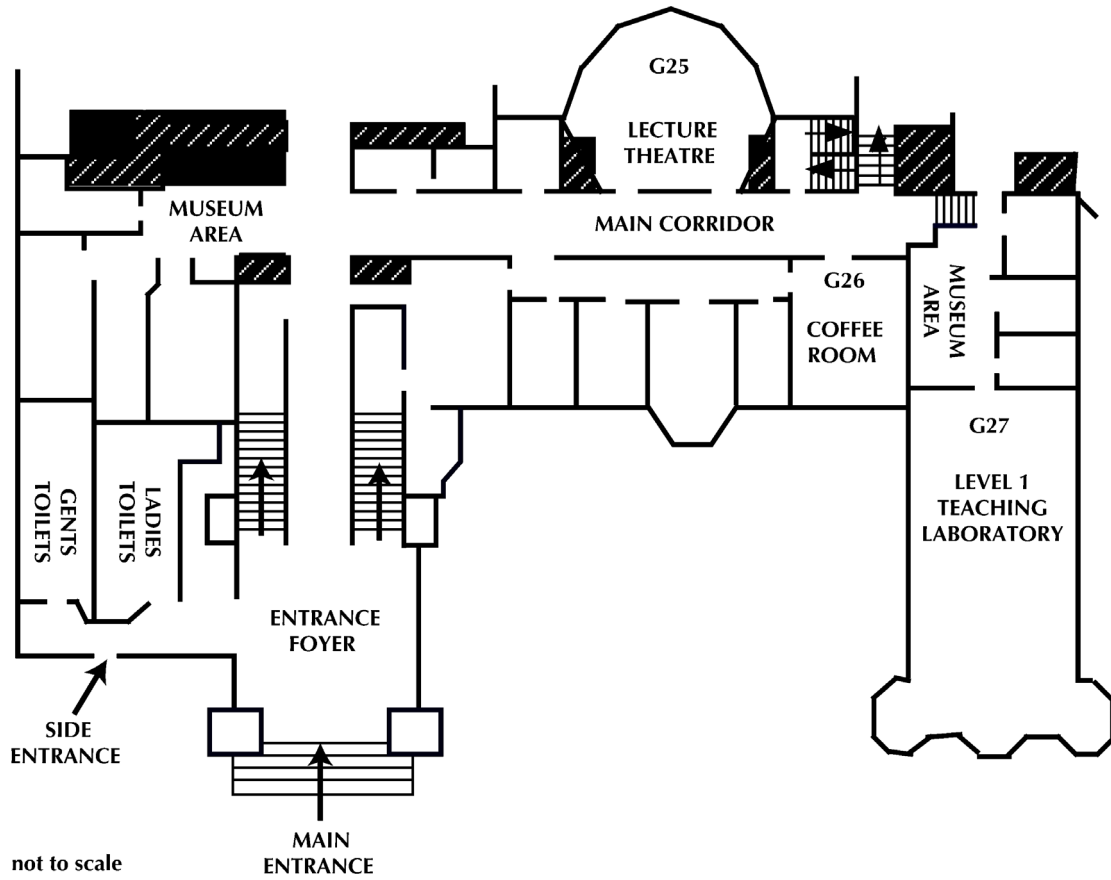
1. Bristol Temple Meads Train Station
2. Bristol Coach Station (Marlborough St.)
3. Department of Earth Sciences (Wills Memorial Building, Queen's Road), The Berkeley Pub (Queen's Road; Thursday evening gathering), Department of Biology (Woodland Road; Saturday field trip pickup point)
4. Bristol Zoo Gardens (Clifton; Friday evening reception)
5. Bristol Backpackers Hostel (17 Baldwin St.)
6. Bristol YHA Hostel (14 Narrow Quay)

The 8(A) and 9(A) buses travel between Temple Meads Station, the Coach Station (Bond St./Penn St. stops) and youth hostels (St. Augustine Parade stop), and the University (Queen's Road, Berkeley/The Clifton Triangle stop) several times an hour. When travelling from the University to the Zoo (Zoo Gardens stop) you should take the 8, and on returning the 9.

The pub gathering on the Thursday evening (at 7pm) will take place in The Berkeley, a Wetherspoon pub across the road from the Department of Earth Sciences.

When arriving on Friday please use the side entrance (map below) as the main doors will be shut. The talk sessions will be held in room G25 and the posters, tea and coffee in G27. We are not providing lunch, but there are plenty of options on Queen's Road and the Triangle (Greggs, Subway, The Berkeley Pub, Rocotillos, The Magic Roll, Pret a Manger, Boulangerie, Café Gusto etc.). Most provide seating, but if you wish you can return to the Department and use our coffee room (G26).

After the talk and poster sessions end at 5pm, we will travel together to the Zoo Gardens by bus. The reception is located in the on the ground floor of the Clifton Pavilion (access is from College Road) and begins at 6pm.



Schedule

Thursday 12th April

19.00 Pre-conference gathering

The Berkeley pub (opposite the Department on Queen's Road)

Friday 13th April

Registration will open at 8.00 and will close at the discretion of the organising committee so please arrive promptly.

After the final session closes at 17.00 we will make our way over to the reception. The evening reception itself will start at 18.00 and will include wine, a selection of soft drinks and a buffet meal. A cash bar will also be available and we can stay until 23.00.

8.50 Welcome

9.00 Decoding the fossil record of embryonic development

Ceri-Wyn Thomas

9.15 Is the diversity of megaloolithid oospecies the diversity of dinosaur species?

Xavier Panades I Blas and Roland Baddeley

9.30 To move, or not to move? Insights into the functional morphology of mitrate appendages

Imran A. Rahman

9.45 Environmental and geological controls on the diversity and distribution of the Sauropodomorpha

Philip D. Mannion

10.00 Taphonomic constraints on understanding early terrestrial ecosystems; integrating palaeobotany and sedimentology from the Lower Old Red Sandstone of South Wales

Jennifer Morris, Dianne Edwards and Paul Wright

10.15 Diversity of sauropod dinosaurs from the Lower Cretaceous Wealden Supergroup of southern England

Michael P. Taylor

10.30 Tea, coffee and posters

11.00 A new *Sphagesaurus* (Crurotarsi, Mesoeucrocodylia) from Brazil and the evolution of the notosuchian crocodylomorphs

Marco Brandalise de Andrade and Reinaldo J. Bertini

11.15 Palaeocene vegetation and climate change from the U.S. Gulf Coast

Phil Jardine and Guy Harrington

11.30 A quantitative approach to the evolution and biomechanics of sauropodomorph dinosaur skulls

Mark Young, Emily J. Rayfield, Paul M. Barrett, Paul Upchurch and Lawrence M. Witmer

11.45 Acropora – piecing together the history of the world’s most important living reef coral

Clare H. White, Brian R. Rosen and Dan W. J. Bosence

12.00 Milankovitch scale cyclicity in the Eocene Southern Ocean – an integrated micropalaeontological and geochemical approach

Catherine E. Burgess and Paul N. Pearson

12.15 Limb bone scaling in dinosaurs

Debi Linton

12.30 Lunch

13.30 The evolution of developmental strategy in spatangoid sea urchins

John A. Cunningham and Charlotte H. Jeffery

13.45 Scaling bite force in predatory animals: bite force is proportional to body mass^{2/3}

Manabu Sakamoto

14.00 Analysis of charred angiosperm woods from the Cenomanian of the Czech Republic

Daniel Oakley and Howard Falcon-Lang

14.15 Variation in the microwear of *Plagiolophus* and *Palaeotherium* from La Débruge, France

Sarah C. Joomun, Jerry J. Hooker and Margaret E. Collinson

14.30 Paleogene calcareous nannofossils from the Kilwa and Lindi areas of coastal Tanzania (Tanzania Drilling Project)

Tom Dunkley Jones and Paul R. Bown

14.45 Allosauroid (Dinosauria: Theropoda) phylogeny: new analysis, comparison, and implications

Stephen L. Brusatte

15.00 Tea, coffee and posters

15.30 Coping with size variation across the Arthropoda

Mark A. Bell, Simon J. Braddy and Richard A. Fortey

15.45 Finite Element Analysis and three-dimensional dinosaur tracks

Peter L. Falkingham

16.00 21st century dinosaur hunters: tracking dinosaurs with LIDAR

Karl T. Bates, Phillip L. Manning, David Hodgetts and Bernat Vila

16.15 Organic preservation in the Early Cambrian Forsteu Formation of western Newfoundland

Thomas H. P. Harvey

16.30 Chewing, chewing all day long: feeding in *Heterodontosaurus*

Laura Porro

16.45 Lower Jurassic pliosaur taxonomy and a skeletal reconstruction of *Rhomaleosaurus*

Adam Stuart Smith

18.00 Evening reception and dinner

Bristol Zoo Gardens

Saturday 14th April

The coach will depart promptly at 9.45 so please don't be late. Delegates registered on the field trip are advised to bring waterproof clothing and sturdy shoes. We should be able to provide hard hats and high-visibility jackets, but if you have your own you are recommended to bring these too. Many of the fossils from these sites are quite small so collecting bags are also recommended.

For the field trip we are lucky to have two experts (Simon Carpenter and Mike Curtis) on the Keuper to Liassic section we are visiting. They will bring examples of some of the material they have found there which should help you 'get your eye in.' Note that collecting at Manor Farm is restricted to the slag pile.

Lunch will be at the Boar's Head pub in Aust. They provide an extensive menu with plenty of vegetarian options.

9.45 Coach departs

Woodland Road (by the Biological Sciences Department)

11.00 Aust Cliff section

Fossil collecting

12.40 Manor Farm pit

Fossil collecting

14.00 Lunch at the Boar's Head pub**15.15 Depart for Bristol****16.15 Arrive at Woodland Road**

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Abstracts of oral presentations

A new *Sphagesaurus* (Crurotarsi, Mesoeucrocodylia) from Brazil and the evolution of the notosuchian crocodylomorphs

Marco Brandalise de Andrade^{1,2} and **Reinaldo J. Bertini**²

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²Instituto de Geociências e Ciências Exatas, Universidade Estadual Paulista, Rio Claro-SP, Brazil

Fossil crocodiles were much more diverse than the semi-aquatic piscivorous extant species. Notosuchians were distinctive terrestrial crocodylomorphs, with terminal naris and lateral orbits, several of them with specialized dental sets. One such notosuchian was *Sphagesaurus* Price, 1950, with a reduced dentition and rotated tooth crowns. A new specimen (MPMA-15/001-90), found in the vicinity of Monte Alto City (Southeastern Brazil), is here described, with notes on notosuchian evolution and taxonomy. Materials were collected in Upper Cretaceous sediments (Bauru Group; Adamantina Formation; Campanian-Maastrichtian). The specimen is the most complete skull of the few *Sphagesaurus* specimens known. Nevertheless, it is assignable to a new species due to the presence of several distinctive features (e.g. possession of an antorbital fenestra). New information for the genus is provided (e.g.: premaxilla development; jugal foramen; pterygoid morphology; mandible robustness and structure; dentition). A preliminary phylogenetic analysis reveals that the new taxon shows a sister-group relationship with *S. huenei*. The genus *Sphagesaurus* could not be assigned to any notosuchian family. Instead, *Sphagesaurus* shows close relationship with *Comahuesuchus* (Upper Cretaceous, South America), Baurusuchidae (Upper Cretaceous, South America and Asia), and *Chimaerasuchus* (Cretaceous, Asia), but especially with Notosuchidae. Although *Sphagesaurus* undoubtedly is a notosuchian, a definition of this group is still under dispute. The traditional definition of Notosuchia clearly shows a paraphyletic but operational group (Gasparini, 1971), while the “phylogenetic” definition (Serenó *et al.*, 2001) does not allow a clear idea about the composition of the most basal genera, such as *Araripesuchus* and *Anatosuchus*. Notosuchians and other basal Mesoeucrocodylia were particularly abundant in South America during the Upper Cretaceous. The Brazilian Bauru Group alone includes 7-10 species, most of them described in the past seven years. Morphological specialization to different diets and niche partitioning could account for the high diversity of the group. The number of species and their specializations show that notosuchians and basal Mesoeucrocodylia were of palaeoecological relevance for the Upper Cretaceous of Brazil.

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- GASPARINI, Z. B., 1971. Los Notosuchia del Cretacico de America del Sur como un nuevo infraorden de los Mesosuchia (Crocodylia). *Ameghiniana*, **8**, 83-103.
- PRICE, L. I., 1950. On a new crocodylian, *Sphagesaurus*, from the Cretaceous of the State of São Paulo, Brazil. *Anais da Academia Brasileira de Ciências*, **22**, 77-85.

SERENO, P. C. LARSSON, H. C. E. SIDOR, C. A. and GADO, B., 2001. The giant Crocodyliform *Sarcosuchus* from the Cretaceous of Africa. *Science*, **294**, 1516-1519.

21st century dinosaur hunters: tracking dinosaurs with LIDAR

Karl T. Bates¹, Phillip L. Manning^{2,3}, David Hodgetts² and Bernat Vila⁴

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⁴*Consorti Ruta Minera, Barcelona, Spain*

LIDAR imaging provides a means to model the 3D geometry of fossil tracks in the field with extremely high accuracy. This represents a considerable methodological advance for the science of vertebrate ichnology, in which traditional field methods suffer from a significant degree of abstraction and lack the resolution required to quantitatively interpret fossil tracks. 3D LIDAR models provide additional morphometric information and allow the application of new analytical tools unique to the digital environment. The method will enable fossil track morphometrics to develop into an iterative process that combines 3D visualization and multivariate statistical methods, effectively blending qualitative and quantitative approaches and allowing track morphologies to be compared holistically.

Modelling of trackways from Fumanya (SE Pyrenees) using LIDAR has provided a preliminary insight into the pedal kinematics and gait of titanosaurid sauropod dinosaurs. Examination of track surface relief suggests multiphase loading of the sediment by the titanosaurid pes, and suggests the possibility of two or three-phase pedal motion during the support phase of the step cycle. The extrapolation of biomechanical information is constrained by quantitative interrogation of morphometric variation in track surfaces and a detailed study of the controls on fossil track formation and preservation at Fumanya. By integrating LIDAR models with other sophisticated modelling techniques (e.g. FEA, forward dynamics gait simulations) within a 3D digital environment it is possible to perform independent tests of these hypotheses and potentially arrive at robust interpretations about fossil tracks and the locomotor mechanics of extinct track-makers.

Coping with size variation across the Arthropoda

Mark A. Bell^{1,2}, Simon J. Braddy¹ and Richard A. Fortey²

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

²*Department of Palaeontology, Natural History Museum, London, UK*

Gigantism within Palaeozoic arthropods has been extensively documented for over a century (i.e. anomalocaridids, eurypterids and trilobites) and is here briefly reviewed. Several mechanisms have been suggested to explain the development of large size in other groups. Firstly, Cope's Rule (the 'active' evolution towards larger size/mass) has

previously been used to explain the occurrence of large vertebrates but has never been quantitatively tested within the Arthropoda. Secondly, Bergmann's Rule suggests a within-species positive association of size with decreasing temperatures seen in higher latitudes.

Cope's Rule is tested here for the first time, within a phylogenetic framework, for the Asaphidae, a family of Cambrian-Ordovician trilobites. Complete adult length was used to reconstruct ancestral sizes across the phylogeny. Several independent comparisons suggested an overall positive trend towards large size, but found an active trend to be unsupported. Size is considered to vary through passive diffusion, rather than an active driving mechanism. Finally, trilobite size variation with palaeolatitude is briefly discussed with reference to key Moroccan localities.

Allosauroid (Dinosauria: Theropoda) phylogeny: new analysis, comparison, and implications

Stephen L. Brusatte^{1,2}

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

²*Department of Geophysical Sciences, University of Chicago, Chicago, USA*

Allosauroid, a clade of large-bodied theropod dinosaurs that ranged from the Middle Jurassic until the Late Cretaceous, has been the subject of extensive phylogenetic study, but little consensus has emerged. Here I analyze allosauroid phylogeny and evolutionary history with a new cladistic analysis, which integrates data from previous studies with information from several new allosauroid taxa currently being described. I find strong support for placing *Sinraptor* as the basalmost allosauroid; *Neovenator* from the Early Cretaceous of the Isle of Wight as the basalmost member of Carcharodontosauridae; and *Acrocantiosaurus* as a derived member of Carcharodontosauridae, not the sister taxon of *Allosaurus* as advocated by many studies. Comparison of my dataset to alternative studies shows that scoring differences, character choice, and taxonomic sampling are all major sources of topological incongruence. My recovered most parsimonious topology shows a strong overall match with the stratigraphic record, and is biogeographically congruent with the breakup sequence of Pangaea, indicating that the fragmentation of this supercontinent was a major driver of allosauroid history.

Milankovitch scale cyclicity in the Eocene Southern Ocean – an integrated micropalaeontological and geochemical approach

Catherine E. Burgess and Paul N. Pearson

School of Earth, Ocean and Planetary Sciences, Cardiff University, Wales, UK

The middle Eocene is a crucial time period in understanding the link between Antarctic ice development and oceanographic systems. Studies suggest that ice had begun to form on Antarctica by the middle Eocene but the extent of the ice and the influence it exerted over local and global ocean currents and marine ecological systems is not well

understood. This study uses an integrated approach combining micropalaeontological and geochemical techniques to address this problem.

The middle Eocene Hampden Formation of New Zealand shows clear sedimentary cyclicity on a Milankovitch timescale. The clay rich sedimentary facies has resulted in excellent preservation of calcareous micro- and nanofossils and of organic walled microfossils. This is key in ensuring that assemblages are as complete as possible and that geochemical results are little influenced by diagenesis.

High-resolution sampling within the Hampden formation has enabled the examination of micropalaeontological and geochemical evidence for environmental and oceanographic change through these cycles.

Studies of faunal assemblages of planktonic and benthic foraminifera, dinoflagellates and calcareous nanofossils have been carried out alongside geochemical analysis of foraminiferal calcite in the same samples. Combining all these lines of evidence enables the reconstruction of variations in current systems, ecology and climate both locally to the site and regionally, through the sedimentary cycles.

The geochemical and sedimentary results show cyclic variability in planktonic and benthic foraminiferal oxygen and carbon isotopes at the same frequency as the sedimentary cycles. The variability in benthic oxygen isotopes is much less than that seen in the planktonic foraminifera thus placing a constraint on the maximum ice volume change through these cycles and indicating that the rest of the planktonic variability is the result of surface water temperature change. These findings are supported by micropalaeontological results, which record ecological changes that indicate a cyclically varying oceanographic regime in the region influencing water temperature, possibly combined with global scale environmental changes.

The evolution of developmental strategy in spatangoid sea urchins

John A. Cunningham and **Charlotte H. Jeffery**

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In a broad study of developmental mode in all sea urchin groups Jeffery (1997, *Geology* 25: 991-994) found that non-planktotrophic (non-feeding) larvae first evolved immediately prior to the Cretaceous-Tertiary boundary and that non-planktotrophy was adopted almost synchronously in five different orders at this time. However, the smaller scale patterns within orders and at lower taxonomic levels remain poorly known. Important questions include: Are there more switches to non-planktotrophy than previously thought? Are switches scattered through time and space or concentrated in particular stratigraphic horizons or geographical areas? Which factors drive switches to non-planktotrophy?

This study addresses these questions by means of an investigation of the Cretaceous representatives of the order Spatangoida (Echinoidea). Developmental modes were determined from the adult test by using either morphological or crystallographic criteria and were then mapped onto a new phylogeny of the group. This method allowed the number, direction and timing of the switches in larval mode to be determined. The

resulting data were then used to determine the temporal and geographic distribution of switches, and to assess which factors drove these switches.

Paleogene calcareous nannofossils from the Kilwa and Lindi areas of coastal Tanzania (Tanzania Drilling Project)

Thomas Dunkley Jones and **Paul R. Bown**

Department of Earth Sciences, University College London, London, UK

Calcareous microfossils from Paleogene hemipelagic clays of coastal Tanzania were first described in the foraminiferal work of Blow and Banner, who described new species of planktonic foraminifers and several biozones from the Lindi area. The Tanzanian Drilling Project (TDP) has returned to this area with the primary aim of recovering pristinely-preserved foraminifera for stable isotope analysis, in order to accurately reconstruct late Mesozoic-Paleogene tropical sea-surface temperatures and pCO₂. In addition to glassy foraminifera the material collected to date has also yielded a spectacularly diverse and well-preserved suite of calcareous nannofossil assemblages, which essentially constitute a long-time-series conservation-lagerstätte. Results so far include the description of 86 new species, effectively doubling the existing diversity estimates for many important Paleogene-Extant families, and revised data on the origination of several extant groups. The high species richness of these samples illustrates the dramatic paleoecological diversity gradient that existed between Eocene shelf and open-ocean assemblages, the most striking in the groups' history. The high diversity and excellent preservation of these assemblages provide the most ecologically representative records of the calcareous phytoplankton through critical intervals such as the Eocene-Oligocene boundary. Initial scanning electron microscope imaging is revealing the exquisite nature of the preservation, with previously unseen grills and bars being observed in many of the well-known taxa, as well as abundant holococcolith material and a high diversity of previously unknown minute taxa (<2µm).

Finite Element Analysis and three-dimensional dinosaur tracks

Peter L. Falkingham

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Historically, dinosaur tracks have been predominantly interpreted as two dimensional surface features, allegedly resembling the form of the track maker's foot. Work by Manning (2004) and Allen (1989), has shown that this is not necessarily the case, and has highlighted the importance of transmitted tracks. These transmitted tracks are formed when sedimentary layers are deformed beneath the surface on which the track maker walked. The mechanical properties of the sediment, the foot morphology, and the limb kinematics affect the way pressures are transmitted through the substrate. Depending on which layer within the substrate is exposed, the visible track may be a transmitted track, and thus vary considerably from the original surface track.

Interpretation is dependant upon track geometry. If a feature is incorrectly interpreted as a surface feature, subsequent analysis (speed, population dynamics etc) will be flawed.

Finite element analysis (FEA) is a tool familiar to many palaeontologists as a method for investigating properties of materials (such as bone) under stress. Here, FEA is proposed to be a valid method for understanding how sediment properties can alter the morphology of a track throughout a three dimensional volume. The results provide a quantitative analysis of the transmission of pressure below a virtual dinosaur foot. This provides insight into surface and transmitted track geometry. The use of FEA in track propagation will provide a robust methodology to undertake repeated and quantifiable track studies.

Organic preservation in the Early Cambrian Forteau Formation of western Newfoundland

Thomas H. P. Harvey

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Siliciclastics of the Early Cambrian Forteau Formation of western Newfoundland yield only a low-diversity 'hard part' macrofauna of trilobites, brachiopods, and hyoliths. Despite this, hydrofluoric acid (HF) maceration of Forteau shales reveals diverse organic-walled microfossils, including many derived from metazoans. These significantly expand the known fauna through the inclusion of non-mineralizing taxa which are usually only identified in fossil Lagerstätten such as the Burgess Shale. For example, the problematic lophotrochozoan *Wiwaxia* is represented by isolated sclerites, and scalidophoran worms are represented by articulated arrays of scalids. Robust organic films are also recovered through HF treatment of the trilobite, brachiopod and hyolith macrofossils. While the precise histological origins of these organics are not yet clear, they have the potential to contribute important palaeobiological and phylogenetic data not otherwise available in the fossil record. Organic constituents of much smaller biomineralized structures have also been recovered, including organic sheaths of hexactinellid sponge spicules, and three-dimensional organic matrices from within the phosphatic cuticular sclerites of palaeoscolecid worms. Together, these studies reveal the utility of organic-walled microfossils in augmenting faunal diversity, in extending temporal and geographic ranges of taxa, in resolving micrometre-scale anatomy of both microscopic and macroscopic organisms, and in providing unrivalled insights into the roles of organics in ancient and sometimes extinct modes of biomineralization.

Palaeocene vegetation and climate change from the U.S. Gulf Coast

Phil Jardine and **Guy Harrington**

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The Palaeocene strata of the U.S. Gulf Coast has yielded a well-preserved pollen and spore record, which represents an extinct paratropical vegetation type. This project aims to use the palynological record to study vegetational changes during the uppermost Cretaceous and Palaeocene in this region. More specifically, the response of the terrestrial ecosystem to the K/P event will be investigated, along with rates of taxonomic diversification during the post-extinction recovery phase, and the impact of climatic changes throughout the Palaeocene. Phylogenetic and environmental controls on pollen morphology will be examined, and patterns of morphological evolution will be compared to taxonomic diversity. The influence of differing pollination strategies (e.g. wind pollinated vs. animal pollinated) on pollen assemblages will also be considered, as will any possible facies controls. By studying the rediversification of a past tropical vegetation type, this project also aims to shed light on the history of the great floral diversity present in the tropics today.

Variation in the microwear of *Plagiolophus* and *Palaeotherium* from La Débruge, France

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La Débruge is a highly fossiliferous mammal site from the Late Eocene of France. It occurs just prior to the mammalian faunal turnover the "Grande Coupure", which significantly affected the endemic European perissodactyls and artiodactyls the earliest Oligocene. The Eocene–Oligocene transition was a period of major climatic change, from greenhouse to icehouse conditions. *Palaeotherium medium* and *Plagiolophus minor* are perissodactyls (family Palaeotheriidae) found at La Débruge, *Palaeotherium* became extinct at the Grande Coupure and *Plagiolophus* survived the Grande Coupure.

Dental microwear is the wear on the tooth which is only visible under a microscope. It commonly takes the form of pits and scratches in the enamel on the surface of the tooth. Microwear is used to determine diet and dietary differences. The feeding preferences of ungulates can be used as an indicator of the palaeoenvironment in which they lived, as they primarily eat plant material.

In order to assess the intra and inter-generic variability of dental wear in a natural population of fossil perissodactyls, quantitative analysis of the dental microwear of *Plagiolophus* and *Palaeotherium* has been carried out using Microware 4.02 software. Initial results show that there is considerable variation within the two genera and that *Plagiolophus* shows fewer microwear features than *Palaeotherium*. The microwear data

will be compared with mesowear and tooth morphology data and will eventually be used to determine whether differences in dental wear across the Eocene–Oligocene transition are significant and therefore to discover whether there was any palaeoenvironmental change across this transition.

Limb bone scaling in dinosaurs

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Previous work by Carrano (2001) compared scaling in the long bones of dinosaurs with those of mammals, to look for describe and explain scaling patterns relating to body size and posture. No attempt was made in that paper to separate the major divisions within the Dinosauria, which could cloud the possible causes of any observed differences with mammalian scaling.

In order to establish whether the posture has a different effect on limb bone scaling within the Dinosauria, Reduced Major Axis regression analysis was performed a dataset consisting of this same data and supplemental measurements obtained separately. Length was regressed against diameter for humeri and femora for the Theropoda, Sauropoda, and three postural groups within the Ornithischia.

Forelimbs tended to scale more negatively for bipedal forms than quadrupedal: lengths increase at a faster rate compared to diameter in bipeds and semi-bipeds than in quadrupeds. This is in accordance with Carrano's observation of the same, but the tendency is more pronounced in theropods than ornithischians.

In the hindlimb, however, the greatest distinction was between the taxonomic groups: saurischian hindlimbs scale more negatively than ornithischian of any posture, implying that there is some sort of taxonomic constraint having a greater effect on the rate of hind limb scaling than simple posture.

Environmental and geological controls on the diversity and distribution of the Sauropodomorpha

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Although research on the Sauropodomorpha is a thriving field, few studies have examined the ecological, geographic & geological factors that controlled their biodiversity & biogeography. This work will examine the possible correlation between such factors as the ecological setting, spatial & temporal distribution, and taphonomy of the Sauropodomorpha, and hypotheses concerning macro-evolutionary patterns. One important hypothesis that will be tested is how their state of preservation is affected by the environment in which they lived; this should help tease apart genuine patterns from taphonomic biases. A large dataset, at the specimen level, will be collected from museum visits, field sites, existing datasets and the published literature. This will then

be integrated into a Geographic Information System, allowing a variety of statistical analyses to be undertaken in order to test possible correlations between parameters. This will provide insights into the evolution & palaeoecology of the Sauropodomorpha as well as enable a better understanding of the taphonomic effects that such large terrestrial vertebrates undergo. In addition, it may also be relevant to our understanding of global change both during the Mesozoic Era and today.

Taphonomic constraints on understanding early terrestrial ecosystems; integrating palaeobotany and sedimentology from the Lower Old Red Sandstone of South Wales

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Palaeobotanical studies on the Old Red Sandstone of Wales have yielded much information on early plant evolution and physiology, whilst sedimentological studies have been successful in understanding fluvial and floodplain processes. However, an integrated approach is required to understand the role of taphonomy in plant fossil distribution and preservation, with the aim of deciphering the environmental settings and ecology of the earliest land vegetation.

Tredomen Quarry (South Wales) provides a unique opportunity for an integrated study through a critical time period for terrestrialisation, via quarry outcrops and cores. Spore assemblages from the quarry surface belong to the lower MN spore biozone, and together with the presence of the Bishop Frome Limestone beneath, indicates an early Lochkovian (Devonian) age.

A number of lithofacies were recognised, and associations represent either a perennial, meandering channel model (e.g. reduced cross-bedded channel sandstones and vertic, calcic palaeosols), or a muddy, ephemeral and anastomosing channel model (e.g. oxidised inclined heterolithics and non-vertic calcic palaeosols), occurring predominately in the upper and lower cores, respectively.

Plant collections occur solely in the reduced perennial channels. The majority of assemblages are allochthonous, either as bedload material (charcoalified *Prototaxites*, *Pachytheca* and fragmentary coalified rhyniophytoids, in conglomeratic channel lag and lower point bar deposits), or as suspended load (fragmented vegetative debris, deposited on upper point bars). Rarer parautochthonous assemblages of well preserved, coalified fertile rhyniophytoids were deposited in minor bar-top channels, after minimal transportation by suspension. Coalified, ordered hyphal fibres maybe *insitu* amongst vegetative debris of the upper point bar, and may represent post depositional fungal activity.

Analysis of charred angiosperm woods from the Cenomanian of the Czech Republic

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Angiosperms are the dominant vegetation type in present-day terrestrial ecosystems, comprising over 90% of global plant diversity. The angiosperms evolved near the start of the Cretaceous, but had their first major diversification across the Cenomanian-Turonian boundary. During this interval they developed between 50 and 80% of their modern diversity and developed woody stems of greater stature than had previously been seen. This marked a gradual transition from forest ecosystems dominated by ferns, conifers and cycads to those of a more modern aspect.

This period of angiosperm diversification is investigated using charcoal from the middle Cenomanian fluvial-estuarine sediments from the Czech Republic. While much work has been conducted on the plant material from these sediments very little of this has utilized the abundant charcoal material present. These charcoal assemblages contain angiosperm, conifer, ginkgo, fern and lycopod remains preserved in superb three-dimensional detail. Charred angiosperm wood from several localities (Pecínov, Hlubětín, Hrousaný and Brník) near Prague have been collected and studied. Wood anatomical data (including measurements of vessel diameter and density, fibre diameter, ray height, width and density and intervessel pitting) was collected and used to establish three morphotypes for the woods present. The validity of the morphotypes was looked at through the use of principle component analysis. The morphotypes were then tentatively identified at the family level, and compared to previously found, non-charred angiosperm material.

Is the diversity of megaloolithid oospecies the diversity of dinosaur species?

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Megaloolithid eggshells are so abundant in several Upper Cretaceous and Cretaceous-Tertiary transitional deposits, that they have been used to interpret the palaeobiodiversity of dinosaurs in America, Asia, and Europe. However, their utility as indicators of dinosaur palaeobiodiversity has not been widely accepted.

Most of palaeo-öologists only accept the attribution of oospecies (species of eggshell) to osteological species by direct association to identifiable osseous remains. However, this level of identification is not necessary just to estimate the diversity of the egg layers; provided that the morphometric analyses on eggshell features can discern oospecies. For example, although each megaloolithid oospecies exhibits a distinct morphology and morphometric range, the oospecies possess similar morphological eggshell

characters and metric continuous variability within egg clutches, as well as great interspecific diversity between eggshells from different localities and ages.

A comparative morphometric model applying biostatistical analyses assessing the inter and intraspecific variation of features of modern oospecies and megaloolithid ootaxa will discern whether the diversity of the oospecies reflects the diversity of dinosaurs or not.

Chewing, chewing all day long: feeding in *Heterodontosaurus*

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Ornithischian dinosaurs were the most diverse and abundant herbivores of the late Mesozoic, developing a range of jaw mechanisms to process vegetation. However, the feeding mechanism used by the primitive clade Heterodontosauridae is poorly understood, although several hypotheses (including long-axis rotation of the mandibles, scissoring of the mandibles, and propaliny) have been proposed. Past limitations in the field of biomechanics and lack of tooth microwear evidence have largely prevented objective testing of these hypotheses. This study uses evidence from skull and dental morphology, tooth wear, and the engineering technique of finite-element analysis (FEA) to approach the problem of feeding in *Heterodontosaurus*. FEA allows visualization of the mechanical behaviour of the skull during the application of loads, allowing determination of the jaw mechanism which best corresponds to skull morphology. Results of this study suggest that mastication involved scissoring of the mandibles with lateral splaying of the posterior skull elements. These results highlight structural changes in the cranium during the transition to eating plants and shed light on the origin and early development of herbivory within Ornithischia.

To move, or not to move? Insights into the functional morphology of mitrate appendages

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Mitrates are a controversial fossil group of Palaeozoic (542-251 Ma) marine deuterostomes. Not only is their systematic position within the deuterostomes contested (were they chordates or echinoderms?), but so too are the functions of their most basic morphological features. One such feature is the long, slender appendage attached to the body, which is currently interpreted as: (i) a feeding arm; or (ii) a muscular locomotory organ.

Here I present four trails associated with specimens of the Devonian mitrate *Rhenocystis*, preserved in the Hunsrück Slate, from Bundenbach, Germany. The co-occurrence of trails and fossils strongly suggests the appendage of *Rhenocystis* was involved in the animal's movement, and therefore should be considered a muscular

locomotory organ, interpretation (ii) above. The recognition of the appendage as being locomotory in function has important implications for the phylogenetic placement of the mitrates within the deuterostomes.

Scaling bite force in predatory animals: bite force is proportional to body mass^{2/3}

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Bite forces of terrestrial predatory vertebrates are shown to scale with increasing body size at a scaling factor of 2/3. This negative allometry indicates that bite force increases less-than-proportional to increase in body mass. This scaling factor of 2/3 can be observed in many instances of scaling: scaling of surface area to its volume in isometric bodies is one obvious example, but more relevant is that of muscle force with body mass. Since the contractile properties of muscle are generally agreed to be constant throughout vertebrates with varying scale, muscle force is most likely proportional to the physiological cross-sectional areas (PCSA) of muscles (length^{2.0}) and since body mass is essentially volume (length^{3.0}), muscle force is proportional to body mass^{2/3}. This coincidence in identical scaling factors enables us to suggest that muscle force, not the lengths of moment arms, is the determining factor of scaling trends in bite forces. A simple biomechanical model is used as an attempt to explain this. The model predicts that scaling factors would be most affected by parameters with the highest dimensions: in this case, body mass (length^{3.0}) and muscle force (length^{2.0}) but not distances (length^{1.0}).

Lower Jurassic pliosaur taxonomy and a skeletal reconstruction of *Rhomaleosaurus*

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The skull of the holotype of the genus *Rhomaleosaurus cramptoni*, a pliosaur from the Toarcian of Yorkshire, has been transported from the National Museum of Ireland in Dublin and prepared by the Palaeontology Conservation Unit in the Natural History Museum, London. The postcranial skeleton is also scheduled for preparation and once completed, the fully prepared specimen is planned to form the centrepiece of a new Earth Science museum in Dublin. The new data has been incorporated into morphometric analyses and phylogenetic analyses of Lower Jurassic plesiosaurs showing that the number of species belonging to *Rhomaleosaurus* is much lower than previous taxonomies suggest. Three species formerly allocated to *Rhomaleosaurus* belong to different or new genera, and *Rhomaleosaurus sensu stricto* contains no more than two species. An interpretation of the newly prepared skull is presented and compared with three contemporaneous specimens. Finally, the new skull data has been

combined with postcranial data from a conspecific specimen (*R. thornstoni*) to construct the first full body skeletal reconstruction of this genus.

Diversity of sauropod dinosaurs from the Lower Cretaceous Wealden Supergroup of southern England

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The Lower Cretaceous Wealden Supergroup of southern England has yielded many fragmentary specimens of sauropod dinosaurs. Wealden sauropod taxonomy is convoluted, with most genera erected on nondiagnostic specimens and most specimens having been referred at various times to many different genera.

To investigate the relationships of Wealden sauropods, I performed a cladistic analysis at the specimen level. I added seven new taxa to the matrix of Harris (2006), six based on dorsal vertebrae and one on appendicular material.

These specimens could be scored for an average of 16.6 characters, only 5% of the total of 331, and for this reason an initial analysis including all seven specimens was uninformative: all but one of the new taxa were in a polytomy at the base of Neosauropoda.

I then performed seven separate analyses, each including just one of the Wealden specimens. In these analyses, the specimens were recovered as representatives of many different groups: Diplodocinae, basal Flagellicaudata, Brachiosauridae, Titanosauria and basal Somphospondyli.

In a third approach, based on Reduced Consensus, the analysis containing all seven new taxa was subjected to seven separate sets of *a posteriori* deletions, each removing all but one of the new taxa. The positions of many of new taxa changed dramatically from the separate analyses: for example, one new taxon jumped from Somphospondyli to Diplodocimorpha while another moved in the opposite direction from Diplodocinae to Macronaria. Only one specimen remained secure under all these analyses: "*Pelorosaurus*" *becklesi* was consistently affirmed as a basal titanosaur, sister to *Malawisaurus*.

These results underscore the care that must be taken in analyzing fragmentary specimens, and show that initial results must not be taken at face value. Resolution will be improved by the addition to the matrix of further characters of the dorsal vertebrae. The presence of an unequivocal titanosaur in the Wealden is noteworthy.

Decoding the fossil record of embryonic development

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Fossil embryos contemporaneous with the dawn of animal life provide a valuable insight into the evolution of embryology and development in early marine organisms. However, the fossil record of embryos across the Neoproterozoic-Cambrian transition is obscured by taphonomic biases that pose a danger to the accuracy of any biological or evolutionary interpretation that could be made.

Phosphatized embryo assemblages are widespread globally, yet their temporal distribution is limited to terminal Neoproterozoic through Lower Ordovician rocks and the level of diversity within this window is low.

Here, the nature and preservation quality of assemblages from the Neoproterozoic Doushantuo, and the Lower Cambrian Kuanchuanpu formations of China are discussed.

Scanning electron microscopy (SEM) and X-ray analyses have been employed to construct a taphonomic profile of the assemblages and extant marine invertebrate embryos have been used to investigate the nature and timing of autolysis within different taxa.

We demonstrate inter-assemblage variations in preservation quality attributable to differences in mineralization chemistry. Moreover, we show that experimental taphonomy of extant marine invertebrates can be employed to elucidate the interplay between autolysis and pore water chemistry and the effect this interplay exerts upon the mineralization potential of the organisms concerned.

These studies form the foundation of future research into the relationships between embryo autolysis, decay and diagenesis, which must be specified and understood if fossilized embryos from this temporal window are to be of true value.

Acropora – piecing together the history of the world's most important living reef coral

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There is widespread concern about recent deterioration of living reef corals, largely related to coral bleaching believed to be the result of global warming. Predictions of the future responses of coral reefs lack data from the past where coral and reef records show that reef coral distribution is highly sensitive to climate change. This project looks at the ancient record of both corals and reefs and how their Cenozoic distribution was highly sensitive to climatic patterns, modulated by availability of suitable habitats. Following the history of one individual taxa, *Acropora*, should demonstrate how one

particular important reef coral genus has responded to global change throughout its geological time-span.

The aim of this project is to establish the stratigraphic, evolutionary, and biogeographical history of one genus, *Acropora*, to provide higher resolution data to test hypotheses on the effects of changing climate and palaeogeography. Detailed sedimentological, taphonomic and geochemical analysis, mainly through stable isotope work, will help to establish the palaeoenvironmental context.

Extraction of *Acropora* records to date from a combination of databases, literature reviews and NHM specimens gives a fuller picture of its changing spatio-temporal distribution through the Cenozoic. This is plotted on 'Boucotgrams' (named for Art Boucot) highlighting (1) latitudinal changes in distribution in response to major climatic trends, and (2) longitudinal changes in distribution, e.g. the relatively late arrival of *Acropora* in the Indo-West Pacific, apparently in response to tectonically-driven rearrangement of Tethyan and Indo-Pacific seaways and land-masses around the end of the Paleogene.

A quantitative approach to the evolution and biomechanics of sauropodomorph dinosaur skulls

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Recent studies of sauropodomorph teeth have provided a thorough understanding of dental morphology, wear patterns, and how they indicate trends in feeding behaviour. However, despite resurgence of interest in functional traits there has been no focus on the actual biomechanics or shape variation of sauropodomorph skulls. This is despite certain of these skulls famously displaying unusual features, such as a retracted external naris, a deep rectangular mandibular symphysis, lateral plates and the skulls importance as being the 'business end' of the animal (responsible for obtaining and to, some extent, processing the plant material required to fuel their enormous bulk). Currently, we lack understanding of how functional characters exhibited by the teeth link to craniofacial morphology and biomechanics; how and why the skull evolved in a particular fashion; the extent of cranial disparity and how this relates to recently established diversity patterns.

The aim of my PhD is to integrate biomechanical and geometric morphometric analyses with phylogenetic inference in order to gain a comprehensive understanding of the cranial evolution within the Sauropodomorpha. To accomplish the categorisation of diversity in sauropodomorph cranial form and to determine the adaptive significance of craniofacial features, novel techniques such as finite element analysis and eigensurface analysis will be employed. In addition to this overview, preliminary finite element analysis results from a CT-scanned *Diplodocus longus* skull will be presented.

Abstracts of poster presentations

The *Chimaerasuchus* paradox: a critical review of a poorly known fossil crocodile

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Chimaerasuchus paradoxus Wu, Sues and Sun, 1995 is one of the most amazing fossil crocodiles known. This species is considered terrestrial, herbivorous, with an unique set of multicusped molariforms. These are combined with an elongated jaw joint that allowed back-to-front (proal) masticatory movements. All these characteristics are unexpected for crocodiles, specially considered the extant eusuchians. The sole specimen (IVPP-V8274) comes from the Wulong Formation (Hubei Province, Central China), usually referred to be Lower Cretaceous. Phylogenetic works always show *Chimaerasuchus* as sister-group to *Sphagesaurus*, and nested within other derived Notosuchia (*sensu* Sereno *et al.*, 2001): Notosuchus, *Mariliasuchus*, *Comahuesuchus* and baurusuchids, all of them proceeding from Gondwanic landmasses, most from South America. The paradox comes from the spatial and temporal distribution of *Chimaerasuchus*: how can a Lower Cretaceous species from China be related to a gondwanic Upper Cretaceous group? Spatial distribution may be explained through dispersion route(s). *Chimaerasuchus* may be the first derived notosuchians to be found outside of Gondwanic territory, but is not the first group to show disjunct distribution through these areas, as many other groups (i. e. titanosaurs) are present at both Gondwanic and Laurasian landmasses. Nevertheless, chronological distribution may be misunderstood. Cladograms from at least six different frameworks do not support the idea of *Chimaerasuchus* as a Lower Cretaceous species. A preliminary review on the geological information from Chinese basins shows that there is little confidence in the age of the Wulong Formation, which may be lower Upper Cretaceous. A critical review of the phylogenetic works on the species was conducted, and two of the major accepted datasets were compared (Pol and Apesteguia, 2005; Jouve *et al.*, 2006). Bootstrap and branch support were applied. Results show that there is little overall support for the phylogenies, and *Chimaerasuchus* may represent in fact a more basal group within Notosuchia. We consider that *Chimaerasuchus* may only be assigned to the Cretaceous, and either is: (i) closely related to *Sphagesaurus* and to derived notosuchians; (ii) or a sister-group to them. The lack of preservation of certain structures (choanae, occipital region, basicranium), may sensibly change future interpretations of this taxon. Nevertheless, the revision suggests a possible predictive biochronological function to phylogenetic analysis.

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Climate change and mid-latitude carbon-sequestration during the pre-glacial Ordovician greenhouse

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The shift towards colder climates during the Late Ordovician (Ashgill, 449-443 Ma) and sudden widespread glaciation of Gondwana in the Hirnantian represent one of the most fundamental reorganizations of the global climate system recognized in the geological record and, was closely associated with the second largest of the three great Phanerozoic mass extinction events. Little is known about the processes leading to glacial inception.

Changes in existing $d^{13}C$, $d^{18}O$ and faunal assemblage data from the Ashgill have been used to define a discrete palaeo- Intertropical Convergence Zone (ITCZ) and to construct a hypothesis in which the re-positioning of this zone resulted in climatic re-organization during the Boda Warm Event. This hypothesis predicts that, at mid-latitudes a concomitant southerly shift of the Sub-tropical High Pressure Belt (STHP) with the ITCZ would have placed the northern margin of Avalonia directly beneath a zone of higher intensity SE trade winds and increased surface water wind stress parallel to the northern Avalonian margin. These would have induced coastal upwelling and eutrophication leading to basin anoxia in the Welsh Basin.

The 'Red Vein' includes four cycles of deposition of organic-rich, laminated hemipelagite under anoxic conditions in the Welsh Basin. These are characterised by negative $\delta^{13}C_{org}$ excursions and high total organic carbon (TOC), indicative of increased productivity, and invariance in continental run-off proxies. An absence of covariance between TOC and run-off proxies excludes a mechanism of black shale formation by salinity stratification from increased continental runoff during climate belt movement as proposed for the formation of Cretaceous ocean anoxic events and Pleistocene sapropels.

The four anoxic events in the Red Vein appear to correlate with four negative $\delta^{13}C_{carbonate}$ excursions in tropical records, suggesting carbon sequestration may have been a global phenomenon and a contributory factor in CO_2 drawdown immediately prior to the

Hirnantian glacial maximum. Our work supports the hypothesis that climate belt reorganisation provides a mechanism to account for global carbon sequestration leading to the onset of the Hirnantian glaciation.

The palynology and palaeoecology of the Eastern European Palaeogene from deposits of the Boltysh post-impact crater, Ukraine

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The Boltysh meteorite impact structure lies in central Ukraine. It is on average 24km in diameter and at its deepest in excess of 1km. Recent Ar³⁹-Ar⁴⁰ dating estimates its age at 65.17 ± 0.64 Ma, placing it within errors of the K/T boundary. After its formation it filled with water to form a crater lake, which, throughout the Palaeocene and Eocene accumulated lacustrine sediment.

Approximately 400m of fine-grained sedimentary rock preserves a wealth of palynomorphs, which are the focus of this study. The primary objective is to reconstruct the regional flora from these spores and pollen and to compare the floral changes and palaeoecology of the area over the period represented. Results so far show few palynomorphs in the beds directly above the melt sheet. This is as expected, as recolonisation of the sterilised area surrounding the meteorite impact would have been limited. Above this, however, in the shales, marls and clays of the uppermost 300m of sediment there is a significant abundance of pollen grains and spores, roughly consistent with Palaeogene taxa of the region.

Of particular interest is the inclusion within the time frame represented of the Palaeocene – Eocene boundary and the global hydrothermal event associated with it (PETM). From the assemblages it is possible to determine the vegetational response to extensive late Palaeocene climatic warming and early Eocene cooling. This is a useful modern analogue. Also possible is to compare records of Cretaceous flora with that of the Boltysh strata and hence the effects of the K/T boundary event on regional ecology.

Deep marine trace fossils record changes in palaeoclimate during the Late Ordovician Boda Warming Event

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Modern analogues show that primary organic productivity in mid-latitude basins is sensitive to climate-moderated changes in the strength of coastal upwelling. Increased latitudinal temperature gradients strengthen the prevailing trade winds allowing nutrient-rich waters to upwell. This promotes increased photic zone primary productivity that leads to the development of oxygen deficiency within the underlying

water column. These conditions are more likely during warmer climate modes, where lower oxygen capacities pre-condition marine waters to anoxia.

The late Ashgill climate is characterized by the transition from the Boda Warming Event into the Hirnantian glaciation. The Boda Warm Event (Rawtheyan Stage) in the Welsh Basin comprises four dark, organic-rich laminated hemipelagites (ocean anoxic events) set against a background of light grey, burrow-mottled oxic sediments. The latter are characterized by a low diversity *Chondrites-Planolites* ichnofauna. The ichnological expression demonstrates the infaunal biotic response to changes in hydrography during a global warming event. A gradual decline in the size, abundance and diversity of the ichnofauna correlates with the onset of the anoxic facies. At a smaller scale the transition into anoxic conditions was characterized by small-scale fluctuations in these parameters. In contrast, the rapid re-colonization of the sediment by the same ichnotaxa marks the termination of anoxia and a return to background conditions.

We conclude the primary ecological control on the ichnofauna was oxygenation at the sediment-water interface. The Boda anoxic events record the response of the deep marine environment to an increased latitudinal temperature gradient, strengthening trade winds and coastal upwelling. Changes in latitudinal temperature gradients are most likely associated with changing orbital configuration and/or developing ice sheets. Ichnofaunas provide an important, but rarely considered, source of palaeo-climate proxies.

Coral diversity across the Oligocene-Miocene boundary in Sabah, Borneo

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The Indo-West Pacific of today is a well-known centre of marine biodiversity, being rich in coral reefs and associated biota. However, it is not known when this diversity first arose. It has previously been suggested that this diversity arose at approximately the Oligo-Miocene (Palaeogene-Neogene) boundary (Wilson and Rosen, 1998).

The following work is a preliminary investigation into the changes in coral diversity across this boundary in facies located in the region of Sukau, Sabah Province in Borneo, as part of my PhD entitled "Global versus local controls on the origins and early evolution of centres of marine diversity".

Dating of localities visited, and identification and comparisons of the different types and numbers of organisms found at each locality have been undertaken. The results are presented here.

Future research will involve a second fieldwork trip, this summer, to Borneo, and will include a more detailed analysis of diversity, and possibly the study of more localities.

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The Cenozoic freshwater molluscs of the Turkana Basin as prime example of punctuated equilibrium evolution: a re-assessment

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The Turkana Basin (Kenya, Ethiopia), presently mainly filled by the endorheic Lake Turkana, preserves a Plio-Pleistocene fossil record of freshwater molluscs with an exceptionally fine resolution (~35,000 years). Peter Williamson, a Ph.D. student at the University of Bristol, investigating the molluscan assemblages at East Turkana, recognized 92 sequential faunas in a sedimentary succession extending from ~4 Ma to ~0.7 Ma and mainly deposited in lacustrine conditions (Williamson, 1981). A morphological/conchometric study of the molluscan faunas led Williamson (1981) to the conclusion that during three geologically brief periods the intensity of the morphological change peaked significantly, while during the long intervals between virtually no change (morphological stasis) could be observed. The evolutionary scenario that was proposed to explain these observations was that of the punctuated equilibrium model (Eldredge and Gould, 1972). Williamson's claim (1981) that the Turkana molluscs formed *prima facie* palaeontological evidence became the subject of a heated debate. Though this debate revealed weaknesses in Williamson's hypothesis, the Turkana molluscs notwithstanding became one of the main empirical foundations, if not the major one, of the punctuated equilibrium paradigm (Kemp, 1999; Benton, 2004). During the last two years the taxonomy and palaeoecology of the Turkana molluscan assemblages, not only from East Turkana but from all parts of the basin, has become part of a comparative study on evolutionary tempo and mode in the malacofaunas of the African rift lakes. In this study, Williamson's findings are being re-evaluated. Though our investigation is far from complete, it has become obvious that several molluscan taxa were misidentified, which led to the establishment of pseudo-lineages. In addition the stratigraphy and palaeolimnology of the Turkana Basin have been soundly revised (Brown and Feibel, 1986, 1991). The present insights suggest several of Williamson's assumptions to be unfounded and eliminate essential arguments on which his evolutionary reconstruction was based. As a result, the application of the punctuated equilibrium model to explain the morphological changes in the Turkana fossil molluscs is no longer tenable.

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Field trip guide

The following is by no means a comprehensive introduction to the sites we will be visiting (Aust Cliff and Manor Farm), but hopefully it will provide a useful background. We are lucky enough to have two experts on these localities with us on the day, Mike Curtis and Simon Carpenter. Simon (who discovered the Westbury pliosaur, now housed next door to the department in the Bristol Museum) has promised to bring along some of his finds from the area to give us a good idea of what to look for. In our dry run of this trip in March we managed to find a vertebra, a tooth, a scale, plenty of coprolites and a couple of bivalves, so we can vouch for the existence of fossils!

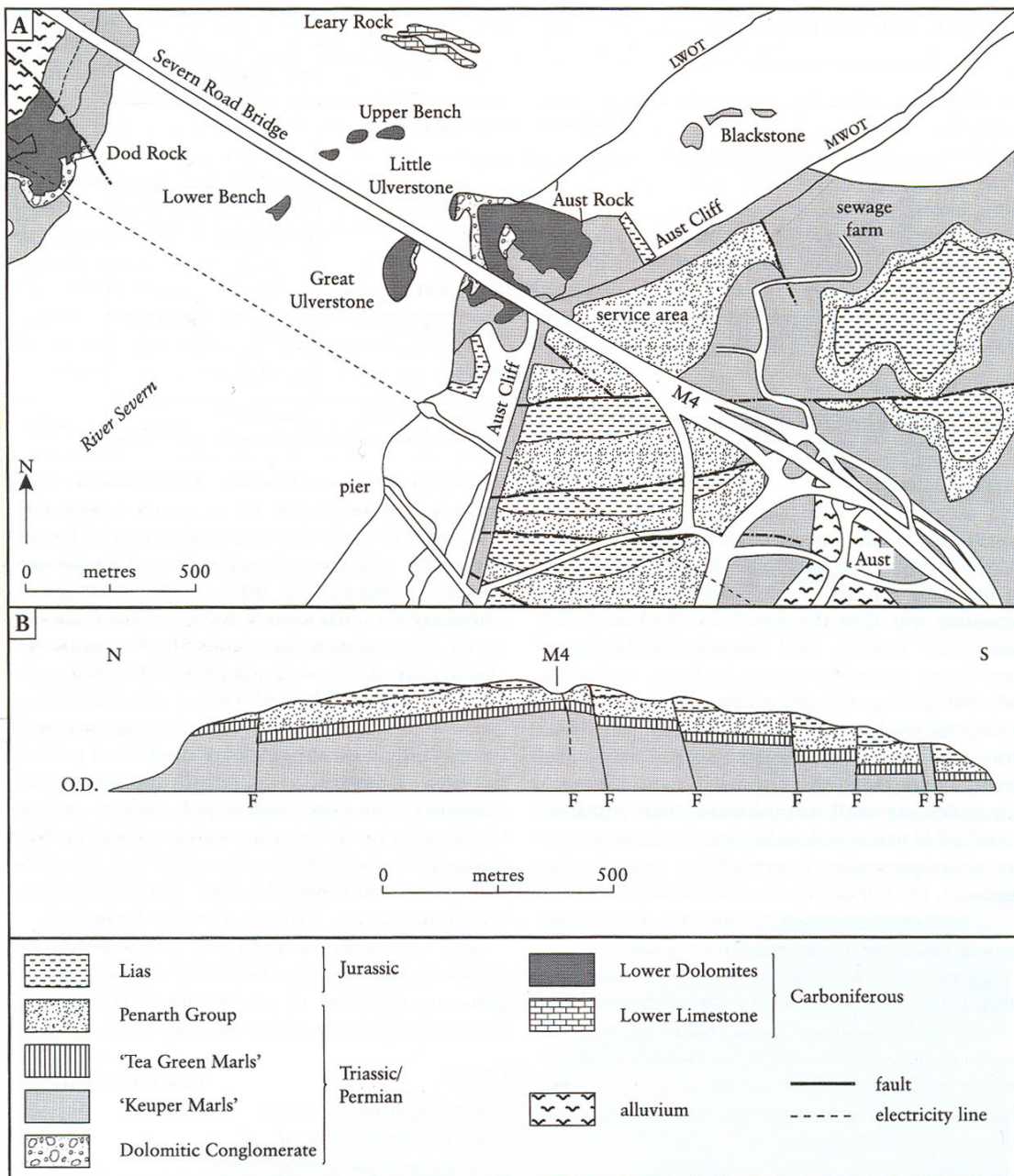


Figure 1 – A. Geological map of the Aust Cliff area. B. Representative N-S line of section showing broad anticline. (From Dineley and Metcalf, 1999; After Hamilton, 1977).

Geology

Aust Cliff (Figure 3) is the best place to see the entire section, especially as the major units are easily distinguished by colour. The red Keuper Marl makes up the bulk of the cliff, and is composed of dolomitic and calcareous clays deposited in a continental, playa flat setting – similar to that seen in southern Australia. (Towards the base gypsum nodules, beds and veins are visible). Overlying this is the Tea Green Marl (=Blue Anchor Formation), which is still part of the Keuper succession, but is harder weathering with a sandstone band. Above this we move in to the interesting stuff (fossil-wise) from the Penarth Group (see Figure 2), which marks the shift to a marine setting.

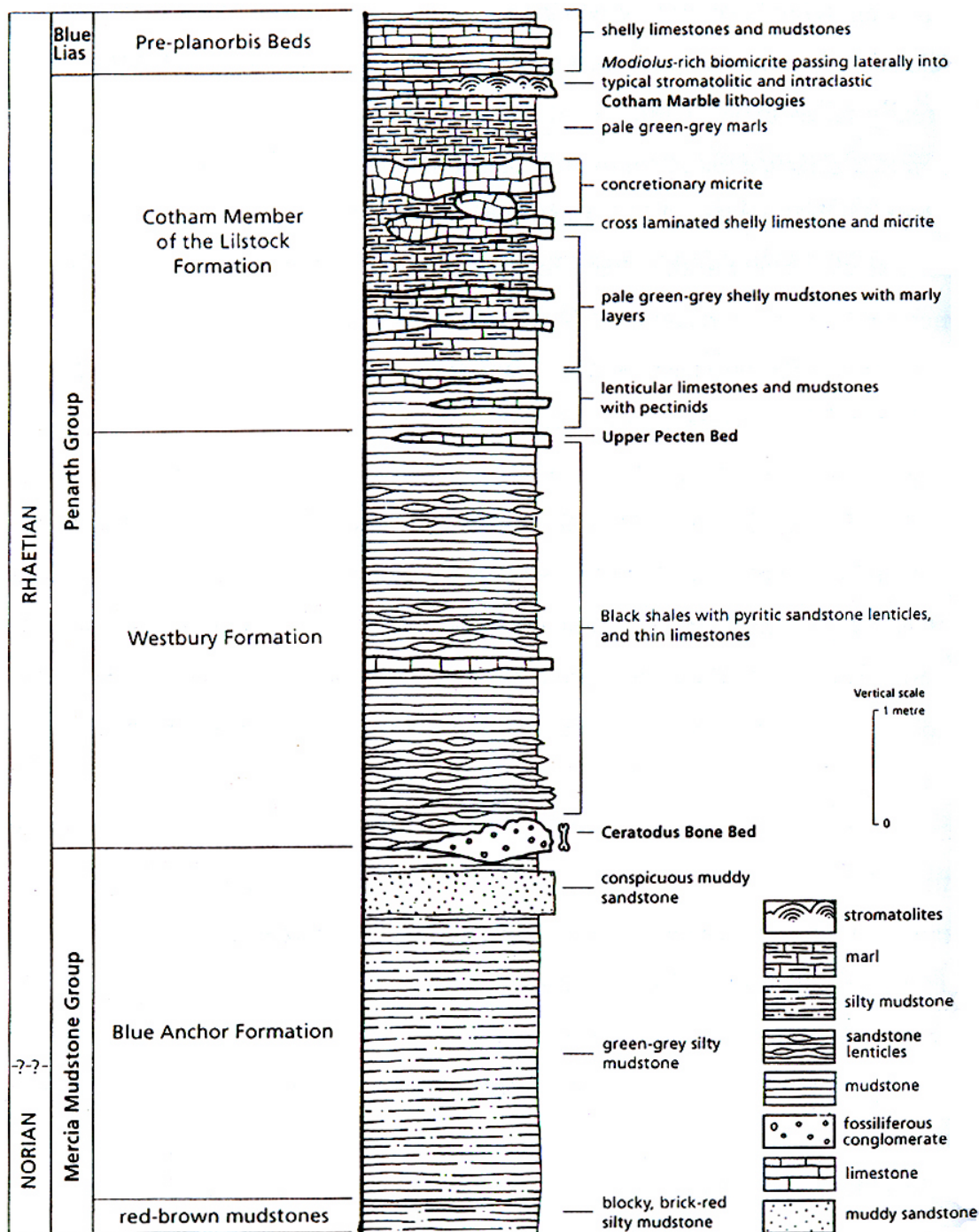


Figure 2 – Generalised stratigraphy at Manor Farm. (After Radley and Carpenter, 1998).

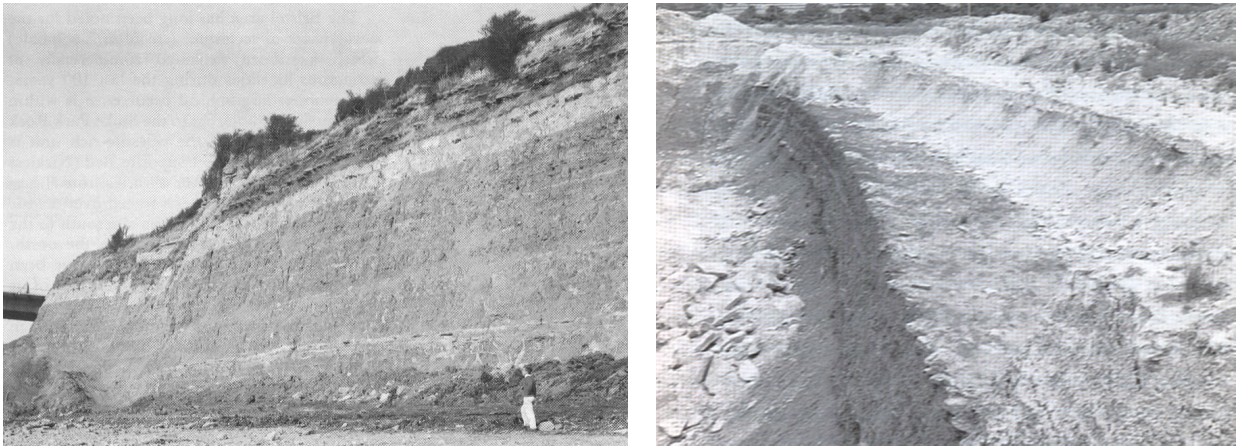


Figure 3 – The Aust Cliff (at left) and Manor Farm (at right) localities. (From Green, 1992 and Radley and Carpenter, 1998)

Fossils

The more famous material from the Aust section comes from the *Ceratodus* bone bed, which is only a few centimetres thick and lies at the base of the Westbury Formation (Penarth Group). Here the disarticulated remains of aquatic vertebrates (teeth, bones, scales and coprolites; see Table 1 and Figure 5) are found in great density. Similar material is also known from the overlying beds (Figure 4) where marine invertebrates are also common, although ammonites are conspicuously absent.

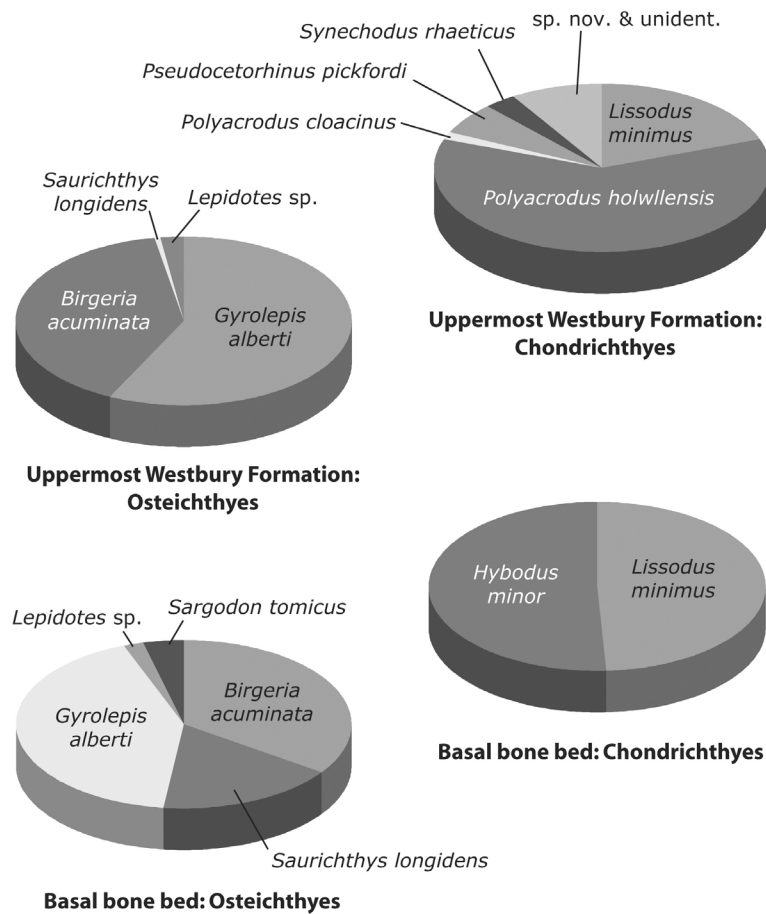


Figure 4 – Pie charts of shifting fish-diversity up through the Westbury Formation. (Figure by M. Sakamoto, based on unpublished microvertebrate data courtesy of Mike Curtis).

Aust Cliff

First described by Buckland and Conybeare in 1824, the Aust Cliff locality has been a popular site for fossil hunters (both professional and amateur) ever since. The abundance of good specimens is reliant on fresh cliff falls from the upper fossiliferous layers, but once you can identify the right beds you are likely to find something. Fossils from the bone bed are shiny in appearance and are darker than the surrounding matrix. Fish make up the bulk of the diversity (see Table 1 and Figure 5), but the vertebrae and other bones of aquatic reptiles are also common finds.

Manor Farm

Quarrying in the 1990's (for materials used in building the new Severn bridge) opened up a pit replicating the top (fossiliferous part) of the Aust section on nearby Manor Farm (Figure 3). Here you should be able to place *ex situ* fossil finds from Aust Cliff in their stratigraphic context (see Figure 2). You are also pretty much guaranteed to see fossils here, although collecting is limited to the slag pile.

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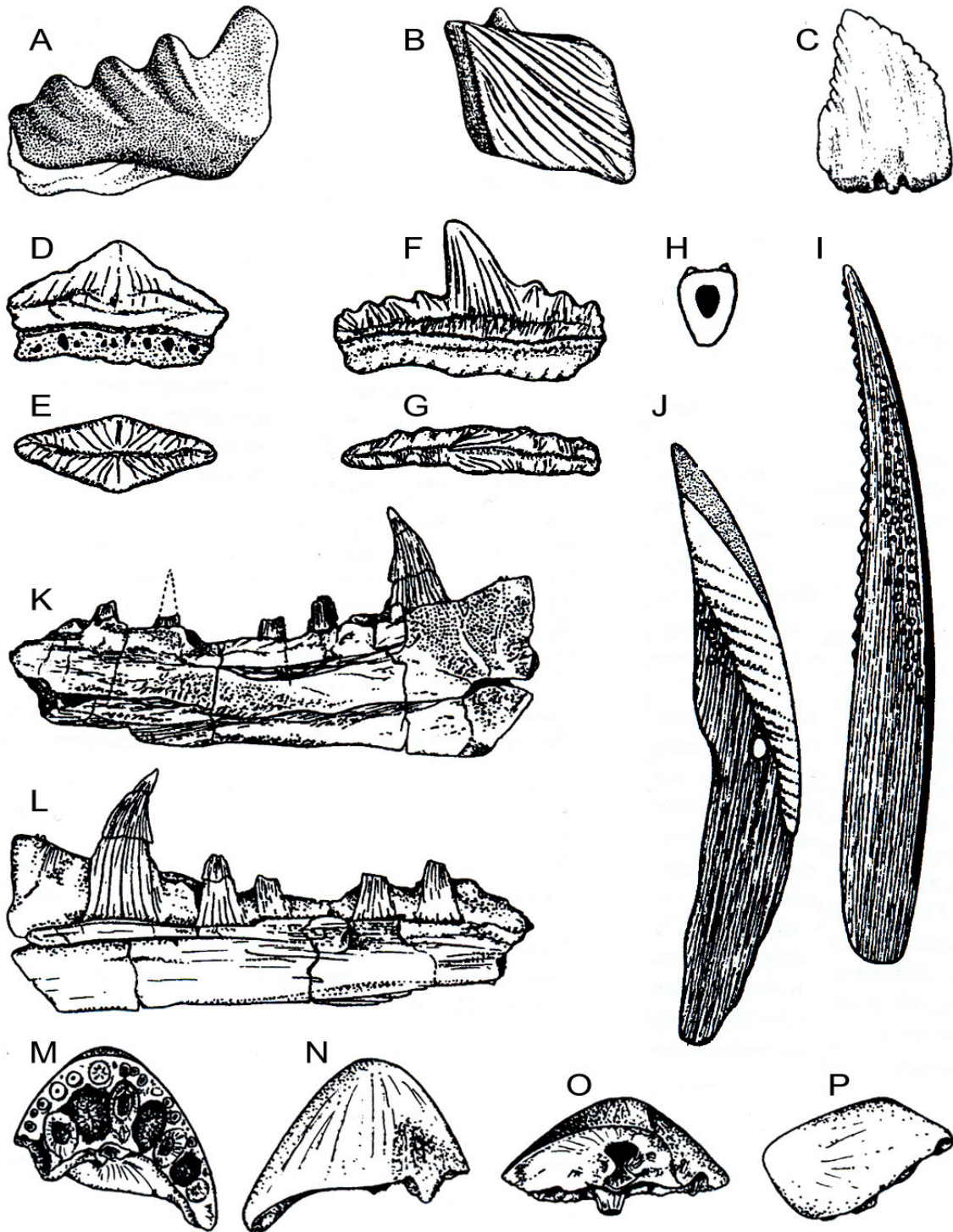


Figure 5 – Fish fossils from the *Ceratodus* bone beds. (A) idealised characteristic tooth plate of *Ceratodus latissimus* Agassiz (c. 6 cm long). (B) idealised scale of *Gyrolepis alberti* Agassiz (c. 0.5 cm long). (C) idealised tooth of *Pseudodalatius barnstonensis* Sykes (c. 0.3 cm long). (D), (E) typical *Lissodus minimus* Agassiz tooth (c. 0.3 cm in anteroposterior length) in lingual and apical aspects. (F), (G) idealised tooth of *Polyacrodus cloadcinus* Quenstedt (c. 2.5 cm in anteroposterior length). (H), (I) reconstructed fin spine of *Nemacanthus monilifer* Agassiz (c. 12 cm long) in transverse section and right lateral aspects. (J) fin spine of the rare *Palaeospinax rhaeticus* Duffin (c. 7 cm long). (K), (L) dentary of *Severnichthys acuminatus* Agassiz (c. 10.5 cm long). (M)–(P) rostromaxillary of *Severnichthys acuminatus* Agassiz (c. 3 cm long) in palatal, anterodorsal, and left lateral aspects. (Figure by S. Sahney, from Dineley and Metcalf, 1999; After Storrs, 1994).

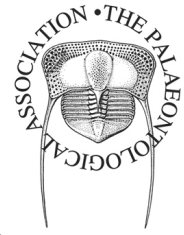
Table 1 – Vertebrate taxa known from the Westbury Formation (including the *Ceratodus* bone bed). (Compiled from Benton and Spencer, 1995, Dineley and Metcalf, 1999 and Swift and Martill, 1999).

Chondrichthyes (cartilaginous fishes)	
Elasmobranchii	
Euselachii	
Hybodontoidae	
<i>Polyacrodus (Hybodus) cloadcinus</i>	Figure 5F&G
<i>Polyacrodus holwellensis</i>	
<i>Lissodus (Acrodus) minimus</i>	Figure 5D&E
<i>Rhomphaiodon (Hybodus) minor</i>	
<i>Hybodus</i> sp.	
<i>Hybodontiformes incertae sedis</i>	
Neoselachii	
<i>Nemacanthus monilifer</i>	Figure 5H&I
<i>Palaeospinax rhaeticus</i>	Figure 5J
<i>Pseudodalatias barnstonensis</i>	Figure 5C
<i>Synechodus rhaeticus</i>	
<i>Pseudocetorhinus pickfordi</i>	
Shark coprolites	
Holocephalii	
Chimaeriformes	
<i>Myriacanthus paradoxus</i>	
Osteichthyes (bony fishes)	
Actinopterygii (ray-finned fishes)	
<i>Severnichthys acuminatus</i>	Figure 5K-P
<i>Gyrolepis alberti</i>	Figure 5B
Neopterygii	
Perleidiformes	
<i>Colobodus</i> sp.	
Holostei	
Halecostomi	
<i>Sargodon tomicus</i>	
<i>Legnonotus cothamensis</i>	
<i>Lepidotes</i> sp.	
Teleostei	
<i>Pholidophorus bigginsi</i>	
Sarcopterygii (lobe-finned fishes)	
Dipnoi (lungfishes)	
Ceratodontidae	
<i>Ceratodus latissimus</i>	Figure 5A
Ichthyopterygia	
Ichthyosauridae	
<i>Ichthyosaurus</i>	
Sauropterygia	
Plesiosauria	
?Plesiosauridae	
' <i>Plesiosaurus</i> '	
Archosauromorpha	
Choristodera	
Pachystropheidae	
<i>Pachystropheus rhaeticus (=Ryosteus)</i>	
Archosauria	
Dinosauria	
? <i>Camelotia</i>	
megalosaur	

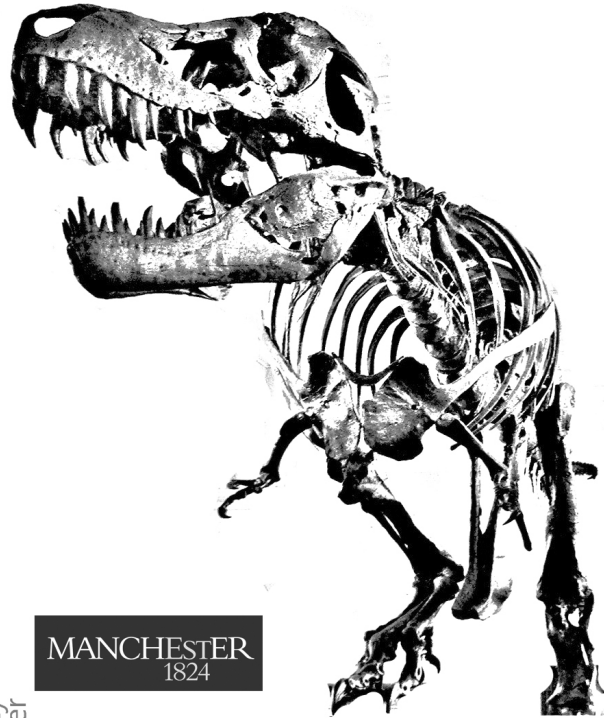
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More details coming soon...

Notes:

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