UNIVERSITY OF BIRMINGHAM

THE PALAEONTOLOGICAL ASSOCIATION

PROGRESSIVE PALAEONTOLOGY

2009

- BIRMINGHAM -

27th – 29th May 2009

School of Geography, Earth and Environmental Sciences, University of Birmingham

PROGRAMME AND ABSTRACTS

Supported by RCUK (via Roberts Funding), the Palaeontological Association, and the Lapworth Museum of Geology

Welcome and acknowledgements

It is with great pleasure that we welcome you to the School of Geography, Earth and Environmental Sciences at the University of Birmingham for this year's Progressive Palaeontology. The conference this year has more presentations than ever, with 24 talks and 12 posters being presented.

As always, Progressive Palaeontology consists of far more than just the presentations. The meeting will begin on Wednesday evening with an ice-breaker reception in the Lapworth Museum of Geology. The museum dates back to 1880, and its collections contain over 250 000 items, including rock, fossil and mineral specimens, and early geological maps, photographs, models and equipment. Thursday's presentation sessions will be followed by dinner at Celebrity Restaurant, where delegates can experience a traditional Birmingham balti. The conference will be rounded off on Friday with a field trip to the Silurian reefs of Wenlock Edge in Shropshire.

We would like to thank the following for their help in supporting, planning and running Progressive Palaeontology 2009:
RCUK (via Career Development and Transferable Skills Training (Roberts) Funding) and the Palaeontological Association for funding the conference. The staff of the Palaeobiology and Palaeoenvironments Research Group at the University of Birmingham for their advice and support. Mark Sutton and Jason Hilton for their help with designing and building the website. Karl Bates, Peter Falkingham (University of Manchester) and Graeme Lloyd (University of Bristol) for imparting their Prog Pal organising wisdom. June Morris, Vanessa Chesterton and Aruna Mistry for help with the financial and logistic side of things. Cynthia for doing the catering. Rob Raine for providing the original logo design and artwork.

And finally, we wish next year's organisers the best of luck!

Phil Jardine, Helen Hughes, Sarah King, Andy Rees, Lil Stevens and Andrew Storey
The Progressive Palaeontology 2009 organising committee

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Programme and timetable for presentations

WEDNESDAY 27TH MAY

19.30 - 21.00: Ice-breaker reception in the Lapworth Museum of Geology, University of Birmingham

THURSDAY 28TH MAY

Talks will take place in the Dome Lecture Theatre, Earth Sciences, University of Birmingham

8.30 – 9.00: Registration in the Lapworth Museum foyer

9.00 – 9.15: Welcome

9.15 – 10.45: Session one (chair: Helen Hughes)

9.15 – 9.30: Leila Battison, Jonathan B. Antcliffe, Martin D Brasier - *The earliest fossil evidence for life on land and the freshwater origin of algae?*

9.30 – 9.45: Karl T. Bates - *Sensitivity analysis in evolutionary robotic simulations of bipedal dinosaur running*

9.45 – 10.00: Aodhán D. Butler, Philip C.J. Donoghue, John A. Cunningham - *Experimental taphonomy: analysing the role of microbial activity*

10.00 – 10.15: Andrew Storey - *A deep-water Silurian trilobite association from the Lake District*

10.15 – 10.30: Kelly R. Richards, Pamela G. Gill and Emily J. Rayfield - Morganucodon watsoni*: Phylogenetics, biomechanics and variation*

10.30 – 10.45: Nicholas P. Edwards, Uwe Bergmann, Peter L. Larson, Roy A. Wogelius, Phillip L. Manning - *Elemental analysis of fossils via synchrotron x-ray fluorescence and environmental scanning electron microscopy*

10.45 – 11.15: Coffee and posters in the Lapworth Museum

11.15 – 12.45: Session two (chair: Phil Jardine)

11.15 – 11.30: Susan Beardmore and Patrick J. Orr - *Taphonomy of Triassic marine reptiles from Monte San Giorgio, Switzerland*

11.30 – 11.45: Sarah King – *Can plant communities travel? Tracing Late Palaeozoic wetland forests across the world*

11.45 – 12.00: Javier Ortega – Hernandez and Simon J. Braddy - *The phylogeny of aglaspidids: towards a better understanding of early arachnomorph relationships*

12.00 – 12.15: Ben J. Slater, Michael J. Benton and Matias Reolid - *Description and phylogenetic implications of a new Jurassic turtle from Spain*

12.15 – 12.30: James E. Jepson, Vladimir N. Makarkin and Edmund A. Jarzembowski - *Lacewings (Insecta: Neuroptera) from the Lower Cretaceous Wealden Supergroup*

12.30 – 12.45: Philip D. Mannion - *How diverse are my sauropodomorphs? Using residuals to elucidate diversity patterns from the biases of the rock record*

12.45 – 13.45: Lunch in the Lapworth Museum

13.45 – 15.15: Session three (chair: Andrew Storey)

13.45 – 14.00: David A. Legg, Simon J. Braddy and Jason A. Dunlop - *The supposed scorpion* Acanthoscorpio mucronatus *Kjellesvig-Waering, recognised as a juvenile eurypterid and its implications for scorpion systematics*

14.00 – 14.15: Peter L. Falkingham - *Ick! No Fossils! Advances in vertebrate palaeoichnology*

14.15 – 14.30: Alexander G. Liu, Duncan McIlroy and Martin D. Brasier - *Earliest evidence for macroscopic locomotion in the Ediacaran: trace fossils from the Mistaken Point Formation, Newfoundland*

14.30 – 14.45: Duncan J. E. Murdock, Philip C. J. Donoghue, Stefan Bengtson and Marco Stampanoni - *Tommotiid tomography: Using SRXTM to reveal the sclerite architecture of 'small shelly fossils'*

14.45 – 15.00: Mark R. Johnson, Zartasha Mustansar, Phillip L. Manning, Lee Margetts, and Paul M. Mummery - *Breathing new life into old fossils*

15.00 – 15.15: Nicholas J. Crumpton, Mark A. Purnell, Pamela G. Gill, Gareth Jones and Emily J. Rayfield - *Microwear and morphology: a quantitative analysis of diet in two of the earliest mammals*

15.15 – 15.45: Coffee and posters in the Lapworth Museum

15.45 – 17.15: Session four (chair: Sarah King)

15.45 – 16.00: Russell Garwood - *High-fidelity computer reconstruction of Carboniferous Coal Measures arachnids*

16.00 – 16.15: Muhammad Hanif - *Integrated high-resolution biostratigraphy and isotope stratigraphy of the Paleocene/Eocene Thermal Maximum (PETM) in N. W. Pakistan*

16.15 – 16.30: Zartasha Mustansar, Mark Johnson, Phillip L. Manning, Lee Margetts and W. Sellers - *Reverse engineering dinosaurs*

16.30 – 16.45: Peter D. Heintzman, James E. Tarver, Marcello Ruta and Michael J. Benton - *A supertree of Perissodactyla, with investigation into global diversity through time*

16.45 – 17.00: Alex De Jonghe, Malcolm Hart, Greg Price and Christopher Smart - *Microfossils for the Oxford Clay Formation adjacent to the Christian Malford Lägerstatte*

17.00 – 17.15: Matthew D. Larvan, Mark T. Young, Emily J. Rayfield and Paul Upchurch - *The craniofacial evolution of sauropodomorph dinosaurs: a quantitative approach using geometric morphometrics and finite element modelling*

19.30: Dinner at Celebrity Restaurant, Birmingham city centre

FRIDAY 29TH MAY

9.00 – 1700: Fieldtrip to Wenlock Edge

The minibus will depart from outside the Lapworth Museum at 9.00 am. We will visit two localities, Lea Quarry and Ippikin's Rock, before having lunch in the Wenlock Edge Inn. We will be back at the University by 5.00 pm. Delegates are advised to bring waterproof clothing and sturdy shoes.

Abstracts of oral presentations (A-Z)

Sensitivity analysis in evolutionary robotic simulations of bipedal dinosaur running

Karl. T. Bates
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Constructing musculoskeletal models of extinct vertebrates requires subjective assumptions about soft tissue parameters rarely preserved in the fossil record. Despite these necessary assumptions about fundamental input values, paleobiologists rarely perform objective tests of best estimate models before reaching conclusions based on predicted results. The extent to which lack of knowledge on soft tissue anatomy limits the accuracy of running speed estimates of extinct dinosaurs is therefore poorly understood. In this study a sensitivity analysis is performed on an evolutionary robotics model of the non-avian theropod dinosaur *Allosaurus*, used previously to estimate maximum running speed in this extinct animal. A range of muscle parameters were varied over the range observed in extant vertebrates, while mass related parameters were altered across the range of published estimates for *Allosaurus*. Muscle parameters have a linear relationship with maximum running speed, whilst surprisingly total body mass and torso centre of mass have little effect. Muscle force values produced the greatest range in predicted running speeds (4.5 - 10.7 m/s) and stride lengths (4 - 5.8 m) in the sensitivity analysis, equating to 65.9% and 30.7% variation about the original 'best estimate' prediction, a relatively high potential margin of error. These results highlight the importance of sensitivity analyses in biomechanical modelling of extinct taxa, particularly where values for soft tissues parameters are not tightly constrained. The current range in plausible values for soft tissue properties makes a robust quantitative assessment of behavioural ecology and species interactions in dinosaurian communities extremely difficult.

The Earliest Fossil Evidence for Life on Land and the Freshwater Origin of Algae?

Leila Battison, Jonathan B. Antcliffe and Martin D Brasier
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Fossil assemblages from terrestrial settings are rarely seen before the Devonian ~ 350 Ma ago. Evidence for freshwater and terrestrial life in the Precambrian has therefore been circumstantial rather than detailed and none has yet come from freshwater phosphate. We here demonstrate that phosphate from ~ 1200-1000 Ma

Mesoproterozoic lake sediments of the Torridon Group, NW Scotland preserve a remarkable suite of organisms forming a freshwater, terrestrial, phototrophic ecosystem. Ephemeral lakes and streams developed in intermontane basins within the interior of the supercontinent of Rodinia and periodically experienced prolonged desiccation allowing phosphate precipitation. These phosphates contain microbial remains comparable with modern eukaryote (chlorophyte) algae and cyanobacteria with delicate cellular and sub-cellular structures, desiccation-resistant cysts and aplanospores. Studying the phosphates by optical microscopy of biological thick sections enables observation of the spatial distribution of the cells, allowing reconstruction of the life cycles of these billion year old microbes. This suggests that Earth's terrestrial biota and its associated phosphorus cycle were well established on land by ~1000 Ma. It also suggests that many algal groups, many of which today are obligate freshwater denizens, may have originated in fresh water lakes over a billion years ago.

Taphonomy of Triassic marine reptiles from Monte San Giorgio, Switzerland

S. Beardmore and P.J. Orr
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The Besano Formation, or Grenzbitumenzone, from the Monte San Giorgio region in Southern Switzerland is transitional across the Anisian-Ladinian (Triassic) and well known for its exceptionally preserved marine reptile fauna. This formation is 18 metres thick and represents about four million years of time. The lithologies, alternations of black bituminous shale and laminated dolomites, were deposited into an intra-platform basin, and represent slow, hemipelagic sedimentation and more rapidly deposited event beds, respectively, the latter derived from the surrounding carbonate algal reefs; anoxic bottom water conditions prevailed.

The primary aim of this project is to model aspects of skeletal and soft tissue preservation in the marine reptiles of the Besano Formation; emphasis is on identifying what, if any, taphonomic trends recur between taxa. This is a test of how sensitive a taxon's taphonomy is to its biology. With the presence of two lithologies, representing different facies, taphonomic pathways could potentially be related to patterns of sedimentation and the environment. Initial observations presented herein suggest skeletons are consistently both more highly articulated and complete in the black shales; notably specimens of a taxon recur in the same skeletal posture. In the dolomites many skeletons occur as disarticulated, but associated, elements scattered across the surface of the matrix; individual bones more commonly retain more of their three-dimensionality. Ultimately, the models generated will be developed further by incorporating fossil assemblages from other localities of different geological ages that contain taxa not found in the Besano Formation.

Experimental taphonomy: analysing the role of microbial activity

Aodhán D. Butler, Philip C.J. Donoghue, John A. Cunningham.
Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol BS8 1RJ

Taphonomy, the study of decay and fossilization, has been transformed into an experimental science over the past two decades. This work has focussed most especially upon the process of mineral replication of labile organic remains, providing novel insights in the interpretation of fossil remains. However, the process of fossilization – the mineral replication of organic tissue – tells us nothing about the transformation of the organic substrate on which mineralization occurs. It is this step which is most crucial to correctly interpreting the anatomy of exceptionally preserved fossil organisms and thus fully realising their evolutionary significance.

Our aim is to determine the processes behind this initial stage of organic transformation through experimental simulations of decay, in particular we aim to examine the role of microbial activity. Replication of plant and animal tissues by microbes is well documented in the fossil record but has only recently become the subject of experimental investigation.

To achieve this we are investigating the development of microbial communities within decaying organisms using electron microscopy. In addition, controlled experiments testing inhibition of microbes and autolysis will allow further understanding of their role in the process of organic transformation, preliminary results of which will be discussed. We also hope to determine whether microbial activity and mineral precipitation are co-localised.

We have demonstrated that in situ cryo-sectioning of decayed organisms is feasible for animals of a variety of sizes and allows fine scale analysis of tissue ultrastructure, microbial infiltration and biofilm formation. EDX analysis of decay experiments has also indicated the replication of both biofilms and soft tissue in calcium phosphate.

Microwear and morphology: a quantitative analysis of diet in two of the earliest mammals

Nicholas J. Crumpton[1], Mark A. Purnell[2], Pamela G. Gill[1], Gareth Jones[3] and Emily J. Rayfield[1]
[1]*Department of Earth Sciences, University of Bristol, Bristol*
[2]*Department of Geology, University of Leicester, Leicester*
[3]*School of Biological Sciences, University of Bristol, Bristol*

Morganucodon and *Kuehneotherium* are iconic and historically controversial basal mammals found in Early Jurassic fissure-fill sites within Carboniferous Limestone in Glamorganshire, South Wales. Previous workers have noted differences in tooth and jaw morphology between these taxa, leading to the assertion that each utilized a distinct food source. Differences in molar microwear supports this hypothesis. Here I describe a study exploring possible dietary causes of microwear patterns, in the hope of revealing the trophic ecology of these early mammals. This validation will be based on a comparative analysis of microwear in extant faunivorous bats. Surface roughness is quantified through microtextural analysis, a novel and highly repeatable method of microwear analysis that limits the operator error of traditional approaches. Four UK bat genera were chosen, from 'hard-object' feeding beetle-specialists to 'soft-object' fly-specialists allowing microwear indicative of a continuum of dietary preference to be recorded. Comparison between bat microwear textural parameters and those on the molars of *Morganucodon* and *Kuehneotherium* will shed light on the dietary preferences of these extinct mammals. Additional support for the interpreted trophic ecology of the two extinct taxa will be gained through finite element analysis (FEA) of gross tooth morphology gleaned from microCT fossil scans. The hypothesis is that *Morganucodon* molars were able to withstand greater loading forces than *Kuehneotherium*, whereas *Kuehneotherium* was specialized to consume more tractable foodstuff. This study is of importance, as it will be one of the first attempts to apply such a repeatable, quantitative technique to discriminate between the trophic ecology of two extinct animals.

Microfossils for the Oxford Clay Formation adjacent to the Christian Malford Lägerstatte

Alex De Jonghe, Malcolm Hart, Greg Price and Christopher Smart
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In the 1840s, during the construction of the Great Western Railway west of Swindon, a number of beautifully preserved coleoids (belemnites and squid-like cephalopods) were found. These famous specimens of *Belemnoteuthis* and *Mastigophora*, as well as a

number of fish, were eventually described as a *Fossil Lägerstatte* under the name of the "Christian Malford Squid Bed". Many of these specimens, which come from the Phaeinum Zone (Callovian) of the Oxford Clay Formation, contain soft tissue, muscle fibres and the contents of their ink sacs.

In October 2007 the British Geological Survey funded an excavation of the site some ~100 m from the original borrow pits along the railway. Our work on borehole core No 10 has recovered exceptionally large numbers of statoliths, otoliths (fish 'ear' bones), squid hooks and foraminifera. Statoliths are the small, paired, aragonitic stones found in the heads of coleoids. Jurassic statoliths have yet to be described in any detail as there is only one reference to them in the literature (Clarke, 2003).

The exceptional abundance of statoliths and squid hooks recorded in the samples from the core is thought to represent a Jurassic squid-breeding ground which existed for a long interval of Callovian time. The annual spawning of female squids massively enlarges their ovaries and this breaks down the body wall leaving spent individuals to die.

The occurrence of abundant, though low diversity, foraminiferal assemblages in the same samples point to an oxic, though possibly stressed, environment. The significant proportion of deformed foraminifera in the assemblages appears to confirm that the environment was less than optimum.

Elemental analysis of fossils via synchrotron x-ray fluorescence and environmental scanning electron microscopy

Nicholas P. Edwards[1], Uwe Bergmann[2], Peter L. Larson[1], Roy A. Wogelius[1], Phillip L. Manning[1]
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Many geochemical and biological analytical techniques have been employed in the identification and quantification of soft-tissues in the fossil record, such as mass spectrometry, the polymerase chain reaction, immunological and geochemical techniques such as scanning electron microscopy and X-ray diffraction analysis.

In this study, elemental analysis using rapid-scan Synchrotron X-Ray Fluorescence (SXRF) and Environmental Scanning Electron Microscopy (ESEM) of an exceptionally well-preserved vertebra from *Iguanodon* sp. (Wessex Formation, Isle of Wight) has been undertaken on a sectioned specimen that reveals detailed internal microstructure. Analyses have been undertaken to investigate the possibility that the

exceptional preservation might retain some original distribution and concentrations of trace elements within soft-tissue structures, allowing the review of the relationship between mineral (bioapatite) and non-mineral (collagen) phases of fossil bone. Also ESEM analysis of an exceptionally well preserved beetle (Coleoptera, Crato Formation, Brazil) reveals detailed microstructure of the exoskeleton and eyes. The results of this program of research help to elucidate information on the composition, elemental distribution and structure, as well as provide valuable insight to the depositional environment, taphonomy and biology of the organisms.

It is suggested that this and subsequent work will support the value of these techniques in studying fossil remains, not only providing information on the taphonomy and biology of extinct organisms but using this information as a tool for prospecting for similar fossil localities with comparable taphonomic regimes. These techniques could also be used to aid fossil preparation to prevent seemingly invisible but valuable chemical information from being lost or masked by the preparation and consolidation processes.

Ick! No Fossils! Advances in Vertebrate Palaeoichnology

Peter L. Falkingham
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The uses of vertebrate trace fossils in expanding our understanding of past life are many. Created through the interaction of an animal with a substrate, the morphology of the resulting deformation can be linked with a multitude of factors such as gait, speed, soft tissue morphology and so on. Why is it then that this vast wealth of information created by living animals is mired in a misleading taxonomic system? The pitfalls and difficulties of vertebrate ichnotaxonomy are discussed, and the case is made for more research on what can be learnt about the animals from tracks. Research is presented to elucidate the sources of the geometric and morphological variation in tracks. By applying advanced computational methods to reconstruct conditions at the time of track formation, stresses and strains within the substrate beneath an animal's foot can be examined in real time. The production of specific morphological features, such as displacement rims, radial cracks etc, can then be constrained according to specifics of substrate consistency, pedal morphology, palaeoenvironment, and locomotor mechanics.

High-fidelity computer reconstruction of Carboniferous Coal Measures arachnids

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Trigonotarbid arachnids were one of Earth's earliest predators, present in nascent Late Silurian terrestrial ecosystems. By the Carboniferous, shortly before their extinction in the Permian, they were amongst the most abundant arachnid groups. Their fossils from this period are typically hosted within Siderite nodules, and have traditionally been studied by splitting the concretion and inspecting the surface thus revealed. Most of these fossils are three-dimensionally preserved, resulting in incomplete data recovery with this method, as portions of the anatomy often remain hidden in the matrix. This work employs high-resolution X-ray microtomography (CT) and computer-aided visualisation to overcome such limitations. Presented are computer models of trigonotarbid fossils from the Coseley Lagerstätte (Midlands, UK). Two species are reconstructed; a heavily ornamented representative of the genus *Eophrynus*, and a larger member of the genus *Anthracomartus*. The scans provide new morphological information for both species – such as coxal-endites on the limbs of *Anthracomartus hindi*, and marginal spination on *Eophrynus prestivicii* – and highlight similarities between the family Anthracomartidae and the primitive Devonian Palaeocharinidae, suggesting an early branching and persistent trigonotarbid clade. The models also indicate a changing mode of life within this clade, a possible response to increasing ecological strain. This study is the first application of 'virtual palaeontology' to the trigonotarbids, and the findings demonstrate the potential of X-ray microtomography to revolutionise the study of siderite-hosted Coal Measures fossils.

Integrated high-resolution biostratigraphy and isotope stratigraphy of the Paleocene/Eocene Thermal Maximum (PETM) in N. W. Pakistan

Muhammad Hanif
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A continuous marine sedimentary section across the Paleocene/Eocene boundary interval is preserved in the Dungan Formation of middle Indus Basin, Pakistan. This formation is composed mainly of black-colored shale with mudstone interbeds. Warraich *et al*. (2000) measured a ~5m thick *Morozovella velascoensis* planktonic foraminifera zone (P5) from the Dungan Formation. Based on high resolution sampling this zone yielded ~170cm strongly laminated interval, which is barren of foraminifera. Abundant and well preserved planktonic foraminifera can be found prior to and after this barren interval. Based on planktonic foraminiferal high resolution biostratigraphy three zones of Molina *et al*. (1999) can be identified; *Morozovella aequa* Zone prior to

barren interval, *Pseudohastigerina wilcoxensis* and *Morozovella edgari* zones respectively after the barren interval. Two zones of Berggren and Pearson (2005) (E2 and E3 equivalent to *P. wilcozensis* and *M. edgari* zones respectively) after the barren interval can also be identified and the boundary between their E2 and E1 can be placed just after the barren interval. Based on dinoflagellate stratigraphy the barren interval is assigned to the *Apectodinium homomorphum* Zone.

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Warraich, M. Y., Ogasawara, K. & Nishi, H. (2000), 'Late Paleocene to early Eocene planktic foraminiferal biostratigraphy of the Dungan Formation, Sulaiman Range, central Pakistan', *Paleontological Research, Palaeontological Society of Japan* **4**, 275-301.

A Supertree of Perissodactyla, with Investigation into Global Diversity through Time

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A global species level supertree of the extant and fossil Perissodactyla (Mammalia) was constructed using the Matrix Representation with Parsimony (MRP) method, with phylogenies derived from both morphological and molecular data; a first for any mammalian group. The supertree comprises of over a third of the nearly 1000 perissodactyl species presently regarded as valid and contains representatives from all families and over two thirds of genera. Preliminary analyses have revealed a basal Titanotheriomorpha (Brontotherioidea), which is sister to a Hippomorpha (Equoidea) - Moropomorpha (Chalicotherioidea, Tapiroidea, Rhinocerotoidea) clade. The Moropomorpha consists of a Tapiroidea - Rhinocerotoidea clade, sister to the Chalicotherioidea. Division of the supertree into separately analysed subsets, and subsequent merging into a composite, decreased both resolution and clade support compared to the global analysis. Subset supertrees, one comprising solely molecular and the other morphological source phylogenies, were highly congruent in areas represented by numerous source trees. Phylogenetic study effort has generally been even across the entire order, although the Amynodontinae, Hyracodontidae and Deperetellidae are relatively underrepresented compared to the relatively 'overrepresented' Brontotheriidae. The supertree was superimposed onto known temporal ranges to infer ghost ranges, which were then used to infer total

perissodactyl diversity, as well as originations and extinctions throughout the Caenozoic; using both observed (only known ranges) and inferred (known and ghost ranges) data. Furthermore, subsets of perissodactyl diversity through time were inferred at the superfamilial level.

Lacewings (Insecta: Neuroptera) from the Lower Cretaceous Wealden Supergroup

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Neuroptera is a small order of holometabolous insects, readily identifiable from their many veined 'lace-like' wings. They are first recorded in the Permian, but their 'Golden-Age' was in the Cretaceous. Prior to this study only three families of Neuroptera had been recorded from the Wealden Supergroup; Brongniartiellidae, Psychopsidae and Kalligrammatidae, and one species described, the kalligrammatid *Kalligramma roycrowsoni*. This study has shown the presence of two additional families Osmylidae and Ithonidae, and thirteen new species. The presence of the family Brongniartiellidae has not been confirmed by this study, with the previously assigned specimens being transferred to Psychopsidae. The Osmylidae represents the first record of the family in Britain, and the ithonid is the oldest record of its family. A second specimen of kalligrammatid has also been recorded, extending the presence of this family in Britain from the mid-Valanginian to early Barremian. All specimens are from the Weald Clay collected from various Brickworks, with the exception of *K. roycrowsoni* from the older Wadhurst Clay. Using modern analogues it can be interpreted that these neuropterans would have lived in an arboreal environment, with some species, e.g. the osmylids living near water. The insects, before deposition would have undergone disarticulation and possible fluvial sorting with wings more commonly preserved, than body parts.

Breathing new life into old fossils

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X-ray micro-computed tomography (micro-CT) and 3D image-based modelling software has unlocked the ability to digitally repair distorted or broken fossil specimens, thus opening the way for interpretation of previously unusable finds.

A fossilised terminal ungual phalanx from the manus of the dromaeosaur *Velociraptor mongoliensis* (Manchester Museum, University of Manchester, specimen LL.12392) was micro-CT scanned at the Henry Moseley X-ray Imaging Facility. Inspection of low-resolution fast-scans, revealed the *Velociraptor* manual ungual specimen was broken in several places, previously going unnoticed due to cement repair of the fossil. After conducting a longer high-resolution scan of the ungual the high sensitivity of the apparatus enabled separation of areas of differing density, in this case the fossilised bone and cement.

Image-based modelling software produced by Simpleware allowed slice-by-slice repair in three planes, resulting in a complete, fully stitched 3D digital model of the ungual, whilst maintaining internal cavities and the micrometer reconstruction of trabecular architecture.

3D dissections of geometrically precise reconstructions allows the interpretation of previously unusable specimens and reinterpretation of already described fossils. Further, use of Simpleware's software to convert repaired fossils into micron level finite element meshes will enable the biomechanical testing of these repaired structures. Testing of fossil structure and function is already underway at the University of Manchester and is adding to our knowledge of extinct animals.

Can plant communities travel? Tracing Late Palaeozoic wetland forests across the world

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Ancient wetland plant communities (coal forming forests) persisted from the mid Carboniferous in North America and Europe through to the end of the Permian in South China. Recent palaeobotanical findings have proposed significant taxonomic and systematic similarities between these two temporal and geographic end members, postulating a united Amerosinian phytogeographic realm which linked the North China block to Euramerica before the end of the Carboniferous, and a Euramerican origin for the wetland communities in China. This is in contrast to many accepted global palaeogeographic maps which show the North and South China blocks as islands until much later in the Permian. The validity of this hypothetical realm is being evaluated by comparing large floristic datasets from Europe, America and China. Initial, UK based results are equivocal, suggesting that the dynamic and heterogeneic nature of these communities may act, at least on a local scale, to conceal linking elements if they did indeed exist.

The craniofacial evolution of sauropodomorph dinosaurs: a quantitative approach using geometric morphometrics and finite element modelling

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Sauropodomorph dinosaurs include the largest terrestrial animals that have ever existed, reaching the biomechanical limits of terrestrial gigantism. As such, questions as to how these animals processed sufficient vegetation to fuel their multi-tonne bodies have been of key interest. Here, the macroevolutionary history of craniofacial form and function of thirteen sauropodomorph taxa was investigated using relative warps (RWA) and finite element analysis (FEA). For the RWA, landmarks for the cranium in dorsal and lateral aspect, and mandible in lateral aspect, were used to represent and explain variation in cranial morphology. To assess the mechanical behaviour of

sauropodomorph craniofacial shape, 2D FE-models were created and scaled to the same size (basicranial length of *Shunosaurus*), for each of the three views, for each taxon. A bite force of 500 N was applied to the tooth row at the premaxillary-maxillary suture to enable structural comparison between similarly loaded models. Both RWA and FEA demonstrate that sauropods became more divergent in terms of craniofacial form and function throughout the Mesozoic. In contrast, "prosauropods" show general craniofacial conservativeness. An evolutionary trend towards cranial and mandibular robustness in sauropods is documented by both analyses. Form more strongly correlates with function than phylogeny, especially for the mandible. This suggests that historical contingency has less impact than feeding behaviour on 'shaping' craniofacial form in sauropodomorphs. However, as these correlations are only moderately strong they support the theory that cranial biomechanical optimisation is a trade-off between multiple functions.

The supposed scorpion *Acanthoscorpio mucronatus* Kjellesvig-Waering, recognised as a juvenile eurypterid and its implications for scorpion systematics

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Acanthoscorpio mucronatus Kjellesvig-Waering was one of three species of fossil scorpion described from the Lower Devonian (Pragian?), Beartooth Butte Formation (Wyoming). A restudy of the only known specimen has revealed this taxon to be a juvenile eurypterid. Previously unrecogonised features supporting this placement include a *Dolichopterus*-type swimming paddle and a type-A genital appendage. The overall size of the individual, limb proportions and eye placement indicate this specimen is a juvenile. Only two species of eurypterid have previously been described from the Beartooth Butte Formation: *Strobilopterus princetonii* (Ruedemann) and *Jaekelopterus* (?) *howelli* (Kjellesvig-Waering and Størmer). *A. mucronatus* is considered an early instar of *S. princetonii* based on swimming paddle morphology and allometric growth estimates. *A. mucronatus* is a junior synonym of *S. princetonii* and is thus suppressed under Article 23.1 of the ICZN.

A. mucronatus has previously been assigned to Mesoscorpionina, a clade of terrestrial scorpions. Its reassignment thus has implications for the understanding of scorpion systematics and terrestrialisation. A reanalysis of Jeram's (1998) data matrix was undertaken with *A. mucronatus* removed. Greater levels of support were found and Mesoscorpionina became paraphyletic with regards to crown-group scorpions. Other problematic scorpion taxa are briefly discussed in this context.

Earliest evidence for macroscopic locomotion in the Ediacaran: trace fossils from the Mistaken Point Formation, Newfoundland

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Reliable evidence for locomotion in the Precambrian is scant, and confined to relatively simple horizontal burrows and trails from shallow-water marine settings, all dated at 560Ma or younger. In the absence of evidence for movement, a whole host of biological affinities have been suggested for the oldest Ediacara biota, which has hitherto lacked any trace fossils.

Conventional wisdom has suggested that the Avalonian ecosystems of Canada and the U.K. were populated by a community of sessile animals, incapable of escaping the ash falls and turbidity currents which frequently overwhelmed their ecosystems. We report evidence from a bed within the Mistaken Point Formation of Newfoundland which suggests that at least some members of the Ediacaran ecosystems, some 565Ma, were motile. This evidence takes the form of horizontal surface traces, up to 17cm in length, with marginal positive ridges and crescentic internal markings. Experimental evidence suggests that modern actinian cnidarians (sea anemones) provide a close analogue for the type of organism capable of producing such traces.

The presence of such structures in rocks of this age raises the possibility that at least some of the Ediacara biota were motile animals. It also pushes the global record of horizontal surface locomotory trace fossils back by ~5Myrs.

How diverse are my sauropodomorphs? Using residuals to elucidate diversity patterns from the biases of the rock record

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Deducing diversity patterns is an important element in understanding the macroevolutionary history of a group of organisms. However, there is increasing evidence suggesting observed diversity merely mirrors fluctuations in the rock record; thus, any patterns we see may purely reflect sampling biases. Sauropodomorph dinosaurs were an important component of Mesozoic terrestrial ecosystems and their evolutionary relationships are well understood; as such, they make an appropriate case study for attempting to elucidate genus-richness from the vagaries of the fossil

record. A taxic diversity curve has been produced for all valid sauropodomorph genera and has been compared statistically with several sampling proxies. Models that are perfect predictors of diversity have been created using these proxies, then subtracted from taxic diversity to leave a residual diversity signal that cannot be explained in terms of sampling biases. Numbers of dinosaur collections show a strong correlation with Mesozoic diversity, while Cretaceous genus-richness is also correlated with sea-level and dinosaur-bearing formations. After correcting for these biases, the residual sauropodomorph diversity appears to be genuinely high in the Pliensbachian-Toarcian, Bajocian-Callovian, Kimmeridgian-Tithonian and Aptian, while low diversity levels are recorded for the Oxfordian and Berriasian-Barremian, with the J/K boundary seemingly representing a real diversity crash. Diversity in the remaining Triassic-Jurassic Stages appears to be largely controlled by sampling biases. Late Cretaceous diversity is difficult to elucidate and it is possible that this Epoch remains relatively under-sampled. Although distorted by sampling biases, much of sauropodomorph diversity is a reflection of a genuine biological signal.

Tommotiid tomography: Using SRXTM to reveal the sclerite architecture of 'small shelly fossils'

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The earliest skeletal remains in the fossil record are represented by the so-called 'small shelly faunas (or fossils)' (SSFs) of the early Cambrian. Despite their clear importance in the understanding of the earliest diversification of metazoans and the evolution of biomineralisation, SSFs have been understudied, largely because traditional methods of light and scanning electron microscopy are laborious, technically difficult and ultimately destructive. By using synchrotron radiation X-ray computed tomography (SRXTM) a complete submicron resolution 3D model can be produced, and manipulated using tomographic software to reveal the microstructure, modes of growth, and skeletal assembly of these enigmatic fossils. One group of SSFs, the tommotiids, are characterised by multi-unit phosphatic skeletons composed of small basal-internal accreted sclerites with variable morphologies. Analysis of a number of sclerites from a range of tommotiid genera, including *Sunnaginia*, *Micrina*, *Lapworthella*, and *Eccentrotheca*, has shown a common architecture possessed by several members of the group. The three-dimensional characteristics of which implies a common model for the accretion of sclerites among tommotiids. However, not all taxa possess this characteristic architecture, which has implications for the validity of

tommotiid classification and the acquisition of skeletal characters in the lophophorate stem. Further investigation of a range of SSF taxa will elucidate the range of modes of biomineralisation present in these faunas, as well as further demonstrating the validity of SRXTM as a powerful and informative analytical technique for a wide range of fossil materials.

Reverse engineering dinosaurs

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This paper describes how computer based techniques originally developed for traditional engineering applications such as automobile design can be used together with biomedical imaging to reverse engineer dinosaurs. The broad aim is to create models to test hypotheses about the biomechanics of dinosaurs, thus relate form to function in a scientifically robust way.

The techniques used include computer aided X-ray tomography to digitize the external geometry and internal micro-structure of fossilized bone. Computer Aided Engineering (CAE) software is used to convert the digital images into finite element models for testing a range of hypothetical loading scenarios.

Compared with traditional CAE, there are two main issues to address. Firstly, whilst it is not unusual for the internal microstructure of fossilized bones to be preserved, the preservation of soft tissues is extremely rare. This has been addressed by the authors in a novel way. Computer Aided Design techniques can be used to create the geometry of the missing soft tissues and add them to the image based model of the fossilized bone. The result is a reconstructed model that comprises both real and virtual components.
The second issue is that, for extinct organisms, the mechanical properties of the biological materials are unknown. Here reasonable estimates of these properties can be obtained from laboratory tests on extant species.

The reconstruction of biologically realistic systems enables the distribution of stress in bone to be studied in relation to soft tissues such as muscles, ligaments and tendons. The quantification of stresses and strains generated within the biological structure facilitates the elimination of those scenarios where form could not match function. In this way, reverse engineering has the potential to give palaeontologists a new insight to the biomechanics of extinct species.

The phylogeny of aglaspidids: towards a better understanding of early arachnomorph relationships

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Aglaspidids are a group of poorly understood Lower Palaeozoic arachnomorph arthropods that remain phylogeneticaly problematic despite previous efforts to resolve their affinities as either chelicerates, stem-chelicerates, sister taxa to cheloniellids or trilobite-allied arachnomorphs. Consequently, they are regarded as a "bucket taxon" in which numerous taxa have been included based only on a general resemblance, usually characterized by a semicircular cephalon devoid of facial sutures, a faint glabellar region and a pair of anteriorly oriented oval eyes, although blind representatives occur. Despite the recognition of a labrum in Cambrian representatives and a hypostome in some Ordovician forms, no formal account of all aglaspidids and aglaspidid like arthropods has been undertaken. This study comprises an extensive re - evaluation of aglaspidid taxonomy and phylogenetic affinities.

Aglaspidid – like taxa comprise a polyphyletic aggregation of arthropods that share a superficially similar morphology and are frequently rather poorly preserved, commonly leading to misinterpretation and debate over their affinities. These include forms such as problematic Upper Ordovician arthropods from the Letná Formation (Czech Republic), which are now reinterpreted as representatives of the Trilobita and Xiphosura. In response to the absence of a detailed analysis of aglaspidid phylogeny, we performed the first cladistic analysis of these and other superficially similar arthropods, including a newly described genus from the Upper Cambrian of Tasmania. Preliminary results suggest the presence of a clade comprising the aglaspidids sensu stricto, which are more closely related to trilobitomorph arthropods than to chelicerates as previously suggested, putting aglaspidids in a near basal position of the euarthropod tree.

***Morganucodon watsoni*: Phylogenetics, biomechanics and variation**

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Morganucodon watsoni is a basal mammal from the Early Jurassic of South Wales, occurring within fissure fills in three quarries. Mosaic characters can be seen in the postcranial skeleton that disclose *Morganucodon*'s position at the point of emergence of true mammalian features. The fossil record of early mammals is notoriously

incomplete, phylogenetic studies are complicated by a lack of skeletal material and the evolution of characters such as upright stance is difficult to pinpoint. However, although knowledge of *Morganucodon* postcranial anatomy is based on limited material- unstudied skeletal remains are abundant and, although fragmentary, are unique amongst basal mammals in their completeness. In this research, previously unstudied material will be integrated into an existing phylogenetic analysis; preliminary examination suggests this material will provide at least seven of the characters missing from existing phylogenetic analyses. Landmark analysis of different elements within the postcranial skeleton will draw attention to ontogenetic, intra- and interspecific variations within the populations and their possible environmental and functional explanation. Previously figured long bone material will be micro-CT scanned and bending strain analysis will provide a quantitative analysis of the stresses likely to have affected the limb bones in life, and a large-scale rapid prototype model will provide information on the range of movement allowed by the limb articulations. These two techniques will allow the posture of *Morganucodon watsoni* to be inferred, whether sprawling or upright.

Description and phylogenetic implications of a new Jurassic turtle from Spain

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Turtles originated in the Triassic and began to diversify in the Late Jurassic. However, turtle fossils from the Jurassic are comparatively rare, making phylogenetic analysis of the relationships between groups at this important time in turtle evolution difficult. Any turtle remains from this period are therefore of high significance. This research focuses on preparing and describing a new specimen of Upper Oxfordian turtle from the Betic Cordillera in southern Spain. The specimen will be an important addition to our knowledge of early Testudines (crown-group turtles), as it comes from the time when the two major monophyletic infraorders of Testudines, the Pleurodira and Cryptodira, were diverging. The specimen is being chemically and mechanically prepared in order to fully expose diagnostic characters essential to conducting a cladistic analysis of its relationship to known taxa. Initial assessment of exposed characters places it at a basal position within the Eucryptodira, which would lend further support to the hypothesis that the basal cryptodiran lineages became established rapidly after the evolution of Testudines in the Late Jurassic.

A deep water Silurian trilobite association from the Lake District

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Rich shelly faunas, including trilobites, are common in British Silurian successions. The most abundant and diverse trilobite faunas occur in shelf and platform facies, with more basinal areas typified by graptolite- and cephalopod-bearing mudstones. Trilobites do occur locally in deeper water environments, however. The example described here occurs in the late Wenlock/early Ludlow Coldwell Formation of the Howgill Fells, which then formed part of the Lake District Basin. In the Howgill Fells the Coldwell Formation is represented by a 10 m thick interval of fossiliferous silty limestones and calcareous mudstones. The formation comprises a graptolitic mudstone separating two calcareous members, each containing a rich shelly fauna including disarticulated trilobites and brachiopods. The fragmentary nature of the assemblage along with the disparity between the number of cephala and pygidia suggests sorting. Transport, however, was probably local, as none of the taxa described are known from platform or shelf environments. The fauna of the Coldwell Formation appears to have inhabited deeper-water settings, below storm wave-base. The lower member occurs during a time of lowstand, but the upper member represents a local shallowing event and reflects the foreland basin setting of the Lake District Basin.

Although the fauna of the Coldwell Formation differs from the contemporaneous shelf faunas that occur in the UK, there are some localities with similar faunas. The Swedish Colonus Shale for example, occurs in a basinal setting also, and yields a fauna closely resembling that of the Lake District.

Abstracts of poster presentations (A-Z)

Digital imaging and public engagement in palaeontology

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Public engagement and the promotion of science to a wider non-academic audience form an integral role of the professional scientist in the 21st Century. The high level of public interest in palaeontology means that the earth's prehistoric past can provide an important medium through which to communicate information concerning contemporary scientific issues. With increased demands on research time and resources, a means to synchronize the communication of research to academic and non-academic audiences in an effective way would greatly enhance public awareness of palaeontology as a science. Digital imaging and documentation techniques offer one such means to achieve this feat, particularly as digital models of fossils can be effectively used to visually communicate what would otherwise be complex or technical information to a non-academic audience. Digital or 'virtual' fossils can also be used in stand-alone interactive educational displays for museum exhibits or websites, in addition to public engagement events. The electronic 'life' in these fossils is particularly attractive to the generation of computer literate students who start using computer-based learning packages from an early age. The raw material for such interactive packages is often restricted by access to accurate content, something the science could easily provide. Here we detail two case studies in which digital data taken from our own research that has contributed to public engagement programmes and the use of fossils as an educational resource. Although currently in use, these examples will continually be developed and updated as the research progresses, illustrating the ease with which digital research data can be modified to suit a wider audience.

New Terebratulid species from the Cretaceous of Farafra Oasis, Egypt

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Maestrichtian chalky limestone rocks of Khuman Formation Farafra Oasis have yielded several small capillate terebratulida, *(Terebratulina farajraensis* n. sp. and *T.* aff. *farafraensis)*. Specimens were recorded for the first time from Cretaceous rocks in Egypt and among these the first occurrences of *Terebratulina cf. terebratulina* Louisianae Stenzel are described in other work by the same authors. The specimens have affinity to genus *Terebratulina* d'Orbigny, which is characterized by a small shell, capillate ornamentation, circular outline of dorsal valve, and gently convex to inflated dorsal valve. The anterior commissure is incipiently to broadly uniplicate and deltidial plates are disjunct. The differences included in having small foramen, calcalifer type of crura, massive teeth inserted into wide socket floor and bilobed cardinal process in present materials. It is surprising that among these materials one specimen so called *Terebratulina* sp. has a larger shell size and strongly deflected anterior with tow costellae extending alone dorsal valve from anterior to umbonal region.

Excess Homoplasy and Deep Phylogenetic Constraint

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Often evolution repeats itself and distantly related species evolve to be more similar than their ancestors were. This is convergent evolution. When repeated evolution is inferred among cladistic characters, as surveyed here, we can label this homoplasy. What causes homoplasy? Similar environmental conditions may force different biological groups to adapt in the same way. But, there may be limits to what can evolve. Shared genetic, developmental or architectural constraints may limit evolution to a few repeated options.
Repeated evolutionary events allow us to test the constraints on evolution. The results of this study show patterns in the likelihood that evolution will repeat itself. Particular phylogenetic groups show characteristic amounts of novel and repeated evolution even when their ecologies vary. These patterns in evolutionary flexibility imply that what can evolve depends on the history of a lineage as well as on environmental conditions. The earliest evolutionary branching events have had permanent effects on later evolution.

Trilobite associations and taphonomy of the Silurian reefs of eastern north Greenland

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The Upper Llandovery reefs of Peary Land, North Greenland, yield abundant and well preserved trilobites belonging to the long-ranging Cheirurid-Illaenid Association, characteristic of white limestone facies. This study combines the results of lithofacies analysis with identification of trilobite associations, their taphonomy and spatial distribution. These techniques together provide a palaeoenvironmental and taphonomic context for the reef environments of North Greenland. Early lithification and stabilization in a moderately high energy environment within the photic zone is inferred from analysis of the reef limestones. Trilobites locally comprise the dominant faunal group within the reef, where they are commonly associated with brachiopods and subordinate cephalopods. The trilobites occur in taphonomically controlled associations, with low species-diversity accumulations dominated by scutelluids, more diverse illaenid-scutelluid accumulations, and encrinurid- dominated faunas. These associations have been strongly influenced by hydrodynamic sorting, reflected in the disparity of individual trilobite elements, size sorting of sclerites, and stacking patterns. Although a distinct group of communities occupied the reef, the present occurrence of taxa partly reflects energy gradients within the reef. This highlights the importance of sedimentological and taphonofacies analysis when interpreting the distribution of biotas in environments such as reefs.

Palaeoecological Change through the Permian-Triassic Mass Extinction Event: Comparison of Methods

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Different authors use different methods to assess Permian-Triassic palaeoecological changes, yet no comparative study of different methodologies has been published. We compared two methods of assessing palaeoecological parameters such as diversity, richness and skeletal abundance from limestone thin sections: point counting and an equal-area approach. Results demonstrated that there are significant differences between methodologies. Point counting is relatively 'quick and dirty'. It is somewhat biased with respect to organism size, by overemphasizing larger taxa/bioclasts, and underemphasizing smaller taxa/bioclasts. Some point counting 'palaeoecological' data are not considered useful for measuring biotic recovery, as

previously suggested by some authors, because they are affected by taphonomic processes. The presence of diagenetic veins may reduce apparent abundance; winnowing may increase it. Trends in abundance between locations and regions through time, however, tend to broadly agree between methods, although we recorded Early Triassic samples with much higher skeletal abundances (up to 75%) than in previous published studies. Data from locations in Italy, Oman, and USA were compared. The most diverse samples are Griesbachian in age from Oman, whilst the Dienerian-Smithian samples from western USA are less diverse. These data agree with previously published inferences of varying recovery rates based on analysis of tiering and trace fossils.

Late Paleocene floral diversity trends on the western U.S. Gulf Coast

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The interval of rapid global warming at the Paleocene-Eocene boundary (the Paleocene-Eocene Thermal Maximum) has received much attention as a past analogue for modern global warming. Of particular interest is the potential impact of rapid warming on tropical plant communities. The well-preserved pollen and spore record of the U.S. Gulf Coast provides a record of highly diverse paratropical plant communities throughout the Late Paleocene and Eocene. Most attention has focused on the eastern Gulf Coast (Mississippi and Alabama), but sections in Texas, which represent the western Gulf Coast, also preserve a record of Late Paleocene vegetational change. We use this record to assess floral diversity and compositional trends throughout the Late Paleocene Calvert Bluff Formation in east-central Texas. We additionally use the palynomorph assemblages to provide information on the position of the Paleocene-Eocene boundary on the western U.S. Gulf Coast.

Late Asturian – early Cantabrian macrofloras from the Llantwit Beds, South Wales, United Kingdom

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The Llantwit Beds are an interval of mainly coarse alluvial sandstones with some coals and mudrocks, found in the eastern part of the South Wales Coalfield. They yield well-preserved assemblages of plant compressions, of late Asturian and early Cantabrian

age. The flora is dominated by medullosalean pteridosperms, with subsidiary lycophytes, sphenophytes, sphenophylls, ferns, lyginopteridaleans, and cordaites. They are contemporaneous with the better known Radstock Flora from the neighbouring Somerset Coalfield, but are better preserved and should potentially yield cuticles. There are also well-documented palynofloras from the Llantwit Beds, that can be compared with the macrofloras and thus help improve our understanding of the taphonomic biases inherent in these two sources of information on vegetation of this age. This was a critical time in the evolution of the Coal Forests, just before they underwent a major contraction in Euramerica and an expansion into China. A more complete documentation of these Welsh floras will therefore help us understand more fully the dynamics of the vegetation change occurring in the tropics at this time.

Testing the potential monospecificity of the sabre-tooth cat genus *Homotherium* using comparative data from recent large cats

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Fossil remains of the sabre-tooth cat *Homotherium* (Pliocene-Pleistocene) have been found on multiple continents. Since the early 19th century, they have been attributed to many different species, which often seem to have similar stratigraphic occurrences and morphologies. This research tests whether the genus consisted of only one or a couple of species, in which' case observed variation could be due to broad geographic range, individual variation, sexual dimorphism, or age. Descriptions, figures, and measurements from literature were analysed and the results indicated that all species must likely be united into one single species, as the morphological differences are quite trivial. In order to better establish this unlikely conclusion of a single, widespread species existing unchanged for a long period of time, additional comparative data were required. For this, measurements of the dentition, mandible, and cranium of recent lions (*Panthera leo*) and tigers (*Panthera tigris*) from a variety of geographic regions were obtained. The results demonstrated convincing differences between lions and tigers, and also between the recent cats and *Homotherium*. However, the intraspecific variation found in lions and tigers is very similar to the variation in the sabre-tooth cats, supporting the previous hypothesis that the genus *Homotherium* is monospecific.

Competing sweep-feeding strategies in stylonurid eurypterids

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Stylonurid eurypterids comprise a monophyletic suborder of aquatic chelicerates known from marine, brackish and freshwater environments through the late Ordovician to end Permian. Stylonurids have traditionally been considered to be bottom-dwelling scavengers, however it is now known that two clades independently underwent an evolutionary trend towards a sweep-feeding mode of life. This trend is characterised by the modification of spines on the anterior prosomal appendages and a broadening of the metastoma, however the exact method of sweep-feeding is different in both clades. The Stylonuroidea bear multiple pairs of fixed spines on each podomere and could have used their appendages as dragnets, raking through the substrate surface in a broad arc and sweeping everything in reach towards the chelicerae and coxae for processing ('indiscriminate sweep-feeding'). Hibbertopteroidea have a single pair of flat, laterally expanded blades on each podomere, each of which was covered in sensory setae. These would have allowed hibbertopteroids to probe the substrate and snatch up any prey they encountered ('tactile sweep-feeding'). Plotted range data indicates that the two groups of sweep-feeders may have been in competition with one another, as the Hibbertopteroidea only fully diversify as the Stylonuroidea enter their decline. Sweep-feeding can also explain why the Stylonurina persisted through the decline of the Eurypterina during the Devonian; unable to compete for prey with the more manoeuvrable nektonic Eurypterina, stylonurids adapted to occupy a distinct sweep-feeding habit and so were unaffected by the competition from jawed vertebrate and other invertebrate predators that contributed to the eurypterine decline.

Aspidin – The Earliest Vertebrate Skeletal Tissue is Acellular Bone

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Aspidin, the hard tissue comprising the integument of the earliest skeletonising vertebrates, has been the subject of vigourous debate over its biology and homology for the last 60 years, having been identified as a form of dentine, cementum and cellular or acellular bone. Previous workers had failed to reach consensus on the nature of structures present in the tissue or resolve aspidin's homologies, in part hindered by the limited technology of the day. We have revisited this debate and used new techniques to elucidate the true function of these structures and use this to draw further conclusions about the placement of aspidin in the development of

skeletonisation in the vertebrates. Etched histological specimens were investigated using SEM to examine and characterise aspidin in the main groups of heterostracans, with SRXTM imaging used to create a 3D model revealing the architecture of the heterostracan dermoskeleton. This has allowed us to conclude that the structures that typify aspidin include: a linked osteonal network, individual or woven bundles of unmineralised intrinsic fibres and extrinsic fibres of attachment. This is consistent with aspidin being a form of acellular bone.

Jaw mechanics and feeding in the early tetrapod *Acanthostega gunnari*.

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Acanthostega gunnari, a limbed stem tetrapod from the Fammenian, Late Devonian of East Greenland, is one of the earliest examples of a vertebrate taxon that displays adaptations for a terrestrial lifestyle. While it retains many primitive features, such as internal gill arches, a lateral line system and a tail fin, it has evolved the more derived feature of limbs with digits, indicating the possibility of a semi-aquatic niche. Recent comparisons of cranial suture morphology between taxa utilising different feeding strategies and *Acanthostega* have indicated that its skull was most similar to taxa that fed in terrestrial, rather than aquatic environments. To test this conclusion, a combination of two-dimensional Finite Element Analysis and Geometric Morphometrics are currently being applied to the mandible of *Acanthostega* and twenty-two other closely related taxa that range from fully aquatic to fully terrestrial in their feeding strategies. Trends in the ability of mandibles to resist stresses and strains combined with differences in morphological adaptation will allow us to determine which end of the scale *Acanthostega* is closest to, and thus make a reliable determination of its feeding habits. We predict that *Acanthostega* will plot with taxa adapted for feeding on land that utilise a direct-biting mode of feeding rather than a suction-based method seen in most aquatic species.

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Field Trip Guide

Itinerary

08.45 - Meet outside the Lapworth Museum of Geology, University of Birmingham
09.00 - Depart the university
10.30 - Arrive at Wenlock Edge. Visit Lea Quarry and Ippikin's Rock
13.00 - Lunch at The Wenlock Edge Inn
14.30 - Visit the Much Wenlock Museum (if time)
15.30 - Depart Much Wenlock
17.00 - Arrive at the university

Introduction

This year's field excursion will focus on the Silurian reef facies of the Much Wenlock Limestone Formation at Wenlock Edge in Shropshire. Wenlock Edge is often described as an ancient analogue to the patch reef system of the present Bahamas. The edge forms a 17 mile long north-easterly striking limestone escarpment, and extends from the River Onny at Craven Arms to Gleedon Hill (one mile NNE of the village of Much Wenlock). The escarpment continues on to Tick Wood and curves eastwards to Ironbridge in the valley of the River Severn where it is known as Benthall Edge (figs. 1 & 2).

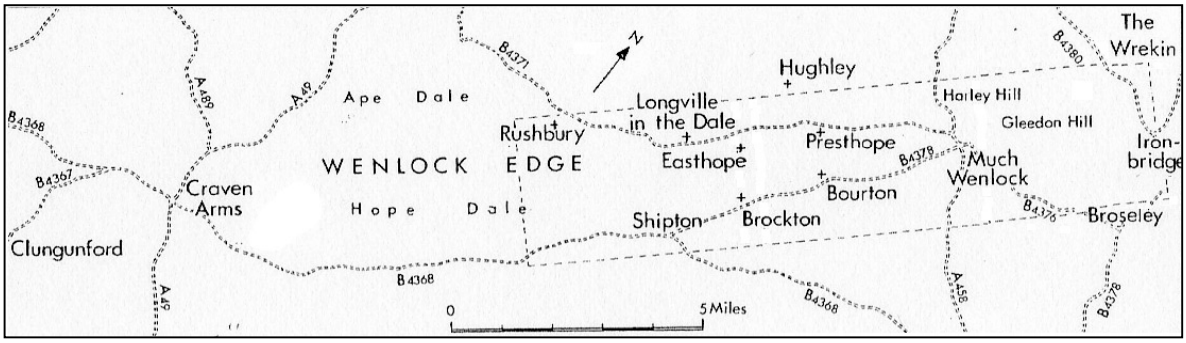

Fig. 1. Map of the Wenlock Edge and surrounding area. The dashed box represents fig. 2 (adapted from Shergold and Bassett, 1970, p. 115).

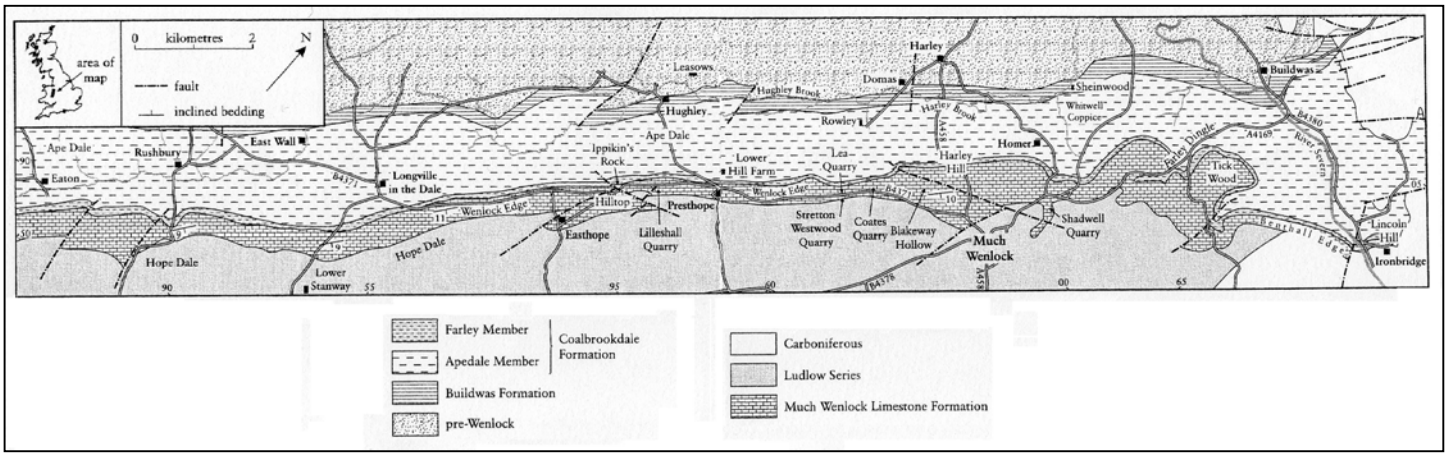

Fig. 2. Geology of the Wenlock Edge-Benthall Edge area between Eaton and Ironbridge (adapted from Aldridge, 2000, pp. 236- 237).

Along its strike the Much Wenlock Limestone can be divided into two main facies; reef and non-reef. The reef facies characterise the succession between Benthall Edge and Easthope, whereas between Easthope and the River Onny, reefs are absent (Shergold and Bassett, 1970).

Reef facies are best seen at Ippikins Rock, Lea (fig. 3) and Knowle Quarry, which will be visited on this field excursion. Coates Quarry, Blakeway Hollow, and Harley Hill are other good localities (fig. 2). As well as attracting geologists since the early 19th century, the pale limestone of Wenlock Edge has been heavily quarried; the origins of Knowle Quarry date to before 1770.

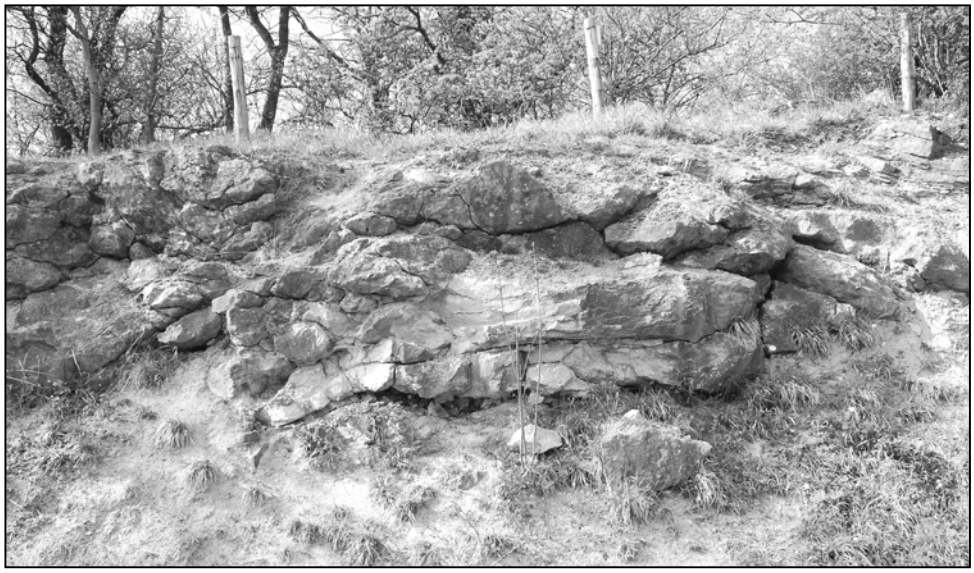

Fig. 3. Domal form of a patch reef at Lea Quarry

Geology of the Wenlock Edge area

The Wenlock Edge area is divided into several principle lithologies. Running from Easthope to Harley Hill, the limestone ridge (Much Wenlock Limestone Formation) dips at roughly 10º to the south-east and is offset along its length by faults. Stratigraphically below is a sequence of mudstones known as the Coalbrookdale Formation, and above, the siltstones and limestones of the Ludlow Elton Group.

Further Northwards at Hughley Brook, the Hughley Shales comprises a sequence of purple and green to blue grey mudstones (the Purple Shales and Buildwas Formations respectively). These occur stratigraphically below the Coalbrookdale Formation (fig. 4).

At Wenlock Edge, the Much Wenlock Limestone Formation reaches a maximum thickness of 29 m and shows a high degree of variability. At its base, in transition from the Coalbrookdale Formation, the blue limestone facies comprises a fossiliferous blue-grey crinoidal limestone with interbedded dark grey shales. Moving up the sequence into the Jack's Soap facies, the beds become more nodular and irregular, although the shale partings remain. This transition is well exposed at Coates and Farly Quarry. Overlying this, the Measures liothofacies comprises thickly bedded blue-grey argillaceous limestones with shale partings (Shergold and Bassett, 1970). The top of the formation, the Gingerbread lithofacies, consists of a series of coarse

grained limestones that are cream/white when fresh, and brown when weathered, with a honeycomb texture.

The Much Wenlock Limestone Formation is diachronous (Thomas, 1978) and at Dudley in the West Midlands, the formation spans the whole Homerian (*lundgreni* to *ludensis* graptolite biozones). At Wenlock Edge this formation belongs to the *ludensis* biozone only (~423 Ma), and occurs during a time of eustatic lowstand (Johnson, 2006). In the lower Ludlow a eustatic transgression ensues and a gradual deepening upwards sequence can be seen in the Elton Group.

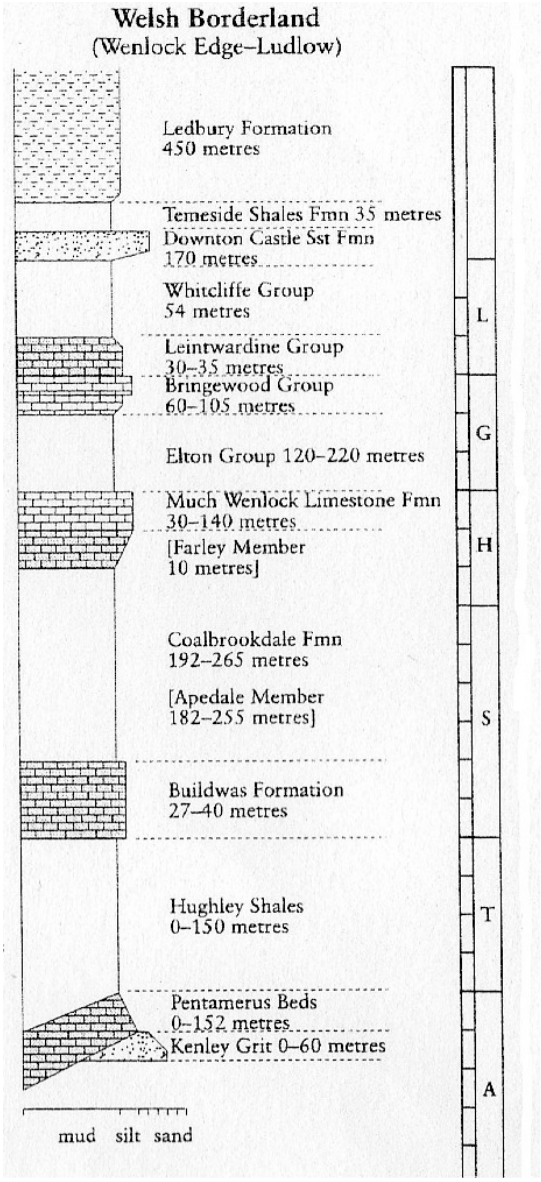

Fig. 4. Stratigraphy of the Welsh Borderland. Stages are represented by symbols: Aeronian, Telychian (Llandovery), Sheinwoodian, Homerian (Wenlock), Gorstian, Ludfordian (Ludlow) (after Aldridge *et al.* 2000, p. 9).

Fossils

The Much Wenlock Limestone Formation is a well-known lagerstätte and contains a diverse fossil assemblage, with some 600 species described. Crinioids, brachiopods and bryzoans dominate the assemblage, with trilobites representing a small element of the fauna. Tabulate corals are the dominant reef builders (e.g. *Favosites, Halysites, Heliolites*), but stromatoporoids (as seen at Ippikins Rock) and branching rugose corals are also common. These faunas can be collected from the Gingerbread and Measures liothofacies at Lea Quarry.

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