The Palaeontological Association

49th Annual Meeting

18th–21st December 2005

University of Oxford

ABSTRACTS

The Palaeontological Association

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18th–21st December 2005

University Museum of Natural History and Department of Earth Sciences, University of Oxford

The programme and abstracts for the 49th Annual Meeting of the Palaeontological Association are outlined after the following summary of the meeting.

Confirmation of registration

Confirmation of registration bookings, and of oral and poster presentations, will be sent out by early November. The deadline for registration and for booking accommodation is Friday 25th November.

Venue

Information about Oxford city can be obtained on <**http://www.oxfordcity.co.uk/**>, and about the university and University Museum of Natural History on <**http://www.ox.ac.uk/**>.

Accommodation

All delegates, except those making their own arrangements, will stay in St Anne's College, some five minutes walk from the University Museum of Natural History.

Travel

Full details regarding maps of the university area in north Oxford, and details and timetables of air, rail, road/coach and park and ride connections, can be found on <**http://www.ox.ac.uk/**>. Oxford is easily reached from London airports, as well those of Birmingham, Bristol and many other regional centres. It has frequent transport services from central London, from where it is reached in about an hour by train, and about one and a half hours by coach.

Parking in the centre of Oxford is expensive and those travelling by car are advised to use the 'Park and Ride' facilities. There are no parking facilities for delegates at the Oxford University Museum of Natural History, or at St Anne's College, except for an extremely limited number of spaces at St Anne's that will be allocated, on request, to disabled delegates.

Registration

Registration will commence at 12 noon on Sunday 18th in the University Museum of Natural History, where it will continue throughout the meeting.

Seminar

A seminar on 'Ediacaran biotas' will take place in the Oxford University Museum of Natural History, beginning at 2.00 pm on Sunday 18th. This will be followed by a reception in the Museum starting at 6.30 pm.

Oral and poster Contributions

All oral and poster contributions will take place in the Oxford University Museum of Natural History, beginning at 8.45 am on Monday 19th December, and continuing on Tuesday 20th. Details regarding the presentation of these will be sent to all contributors.

Annual Address

The Annual Address will be given at 5:15pm on Monday 19th by Jim Kennedy on *William Buckland and the dawning of palaeoecology*.

Annual Dinner

The annual dinner will take place in Christ Church College at 8.00 pm on Monday 19th, and will be preceded by a reception at 6.30 pm in Blackwell's Bookshop.

Field Excursion

This will be to the Mesozoic of Oxfordshire, on Wednesday 21st (8.00 am to approx. 5.00 pm).

Derek Siveter
On behalf of the organising committee:

Martin Brasier

Stephen Hesselbo

Jim Kennedy

Philip Powell

Eric Seiffert

Derek Siveter (chair)

Schedule of events and timetable for presentations

SUNDAY 18th December

Registration will begin at 12 noon in the Oxford University Museum of Natural History (upper gallery), and will continue there during the afternoon seminar and evening reception until 8.00 pm.

14.00 – 17.30 pm Seminar: Ediacaran biotas

Oral presentations, University Museum of Natural History

14.00 A high-resolution temporal framework for the Ediacaran Period
Dan Condon

14.30 Invention and innovation in the early evolution of animals
Douglas Erwin

15.00 Earth's earliest Ediacarans
Guy Narbonne

15.30 Tea

16.00 The palaeobiology of the Doushantuo Formation: the first 80 million years of the Ediacaran Period
Shuhai Xiao

16.30 Decoding the Ediacara enigma
Martin Brasier

17.00 The palaeoecology of the Ediacara biota: evidence from successionally excavated beds, South Australia
Mary Droser

18.30 – 20.00 pm Reception, University Museum of Natural History

MONDAY 19th December

Registration from 8.00 am in the Oxford University Museum of Natural History (upper gallery).

Oral and poster presentations in the Oxford University Museum of Natural History (upper gallery).

In the programme and abstracts a star (*) indicates the speaker, and a dagger (†) indicates a candidate for either the President's Prize or the Council's Prize (respectively for the best oral and the best poster presentation by an Association member under the age of thirty).

MONDAY 19th December, continued

8.45 Welcome

9.00 Evolution and functional morphology: the importance of the fossil record
G. E. Budd

9.15 Exceptional preservation of *in situ* spores in the Rhynie chert plants
Charles Wellman, Hans Kerp and Hagen Hass*

9.30 Salebrids – Palaeozoic microfossils looking for a home
*F.-X. Devuyst and George Sevastopulo**

9.45 Is the conodont fossil record too biased to make multielemental reconstructions? Evidence from the Devonian of Russia
C. Giles Miller and Philip C. J. Donoghue*

10.00 Evolution of herbivory in basal sauropodomorph dinosaurs
Paul M. Barrett and Paul Upchurch*

10.15 The evolutionary history of calcification in planktic foraminifers and its influence on the global carbon cycle
Daniela N. Schmidt

10.30 Coffee and posters

11.00 Three-dimensional non-biomineralised arthropods from Upper Triassic shoreface clays, Somerset, England
A. K. Braiden†, P. J. Orr and S. L. Kearns

11.15 Skeletal microstructure, palaeoanatomy and biological affinities of the oldest stylophoran echinoderm from the earliest Middle Cambrian, High Atlas, Morocco
Sébastien Clausen† and Andrew B. Smith

11.30 Ichnology, palaeoecology and taphonomy of an early vertebrate habitat: the Ordovician Anzaldo Formation, central Bolivia
Neil S. Davies†, Ivan J. Sansom and Guillermo L. Albanesi

11.45 Micropalaeontological and ichnological analysis of Triassic/Jurassic boundary sections of SW Britain
Elisabeth C. A. C. MacDonald †

12.00 Evolution of soft-tissue attachment from Orthocerida via Bactritida to early Ammonoidea
Christian Klug and Björn Kröger*

12.15 Genome duplication, extinction and vertebrate evolution
Philip C. J. Donoghue and Mark Purnell*

12.30 Ammonoids across the Permian–Triassic boundary: a cladistic perspective
Alistair J. McGowan and Andrew B. Smith*

MONDAY 19th December, continued

12.45 **Lunch (buffet, St Anne's) and posters**

14.00 **A 125 million year record of body size changes**
Richard J. Twitchett

14.15 **Neogene planktonic foraminifera:**
remote sensors of the ancient ocean surface or a taphonomic conundrum?
Mark Williams, Alan M. Haywood, Claus Dieter Hillenbrand, Ian P. Wilkinson and C. Giles Miller*

14.30 **Gastropod diversity at the early Toarcian mass extinction event – turnover in South Germany**
Alexander Nützel and Christian Schulbert*

14.45 **On the edge of Laurentia: Late Ordovician (Upper Ardmillan) brachiopod associations in the unstable shelf and slope environments of Girvan, SW Scotland**
David A. T. Harper

15.00 **Competing groups of fishes: tests for asymmetry in the fossil record**
Matthew A. Wills and Rebecca Carter-Hitchin*

15.15 **How congruent are molecular and palaeontological estimates of divergence times?**
Andrew B. Smith, Davide Pisani, Jaqueline A. MacKenzie Dodds, Bruce Stockley, Bonnie Webster and Tim Littlewood*

15.30 **Tea and posters**

16.00 **Evenness and diversity of Lower Palaeozoic trilobite faunas of Laurentia**
Jonathan M. Adrain and Stephen R. Westrop*

16.15 **Upper Ordovician GSSPs and the British historical type area: a chitinozoan point of view**
Thijs R. A. Vandenbrouck

16.30 **The use of computational fluid dynamics in reconstructing the hydrodynamic properties of graptolites**
Susan Rigby and Gavin Tabor*

16.45 **Annual General Meeting**

17.15 **Annual Address: William Buckland and the dawning of palaeoecology**
Jim Kennedy

18.30 **Members' Reception**
(sponsored by Blackwell Publishing), Blackwell's Bookshop, 48-51 Broad Street, Oxford

20.00 **Annual Dinner, Christ Church College, St Aldgates, Oxford**

Following the annual dinner there will be a bar extension for delegates in St Anne's College until 1.00 am.

TUESDAY 20th December

Oral and poster presentations in the Oxford University Museum of Natural History (upper gallery).

9.00 **Bored echinoids: predation patterns on *Echinocyamus* from the Oligo–Miocene of Europe**
James Nebelsick and Andreas Kroh*

9.15 **A study on life strategies and environmental changes through the Middle Ordovician Elnes Formation, southern Norway**
Thomas Hansen

9.30 **The discovery pattern of dinosaurs and how many more species are to be found?**
Michael J. Benton

9.45 **New late Ordovician brachiopod assemblages from Kazakhstan**
Christian Baars and Leonid Popov*

10.00 **Elucidating possible developmental processes of Lower Devonian spore clusters by comparison with extant analogues and spore mimics**
Susannah E. M. Moore, Dianne Edwards and Alan R. Hemsley*

10.15 **How the chiton got its tegmentum**
Jakob Vinther

10.30 **Coffee and posters**

11.00 **Spinosaurid theropod dinosaurs are mechanical analogues of fish-eating crocodilians, not large alligatorids or typical theropods**
Emily J. Rayfield and Angela C. Milner*

11.15 **Tooth microwear analysis of dietary shifts during the evolution of Miocene sticklebacks**
Mark A. Purnell, David C. Baines, Paul J. B. Hart and Michael A. Bell*

11.30 **A new eigenshape-based morphometric method for analyzing 3D patterns of shape variation for surfaces and discrete objects**
Norman MacLeod and P. David Polly*

11.45 **Whale of a time in the deep sea**
Crispin T. S. Little and Kazutaka Amano*

12.00 ***Vetulicola cuneata* from the Lower Cambrian Mural Formation, Jasper National Park, Canada**
N. J. Butterfield

12.15 **Acritarchs, calcispheres, and the origin of the dinoflagellates**
Thomas Servais, Axel Munnecke and Daniel Vachard*

TUESDAY 20th December, continued

12.30 **Swiss light shed on the nature of embryos from the Ediacaran and Cambrian**
Neil J. Gostling, Philip C. J. Donoghue, Stefan Bengtson, Dong Xiping, John Cunningham and Marco Stampanoni*

12.45 **Lunch (buffet, St Anne's) and posters**

14.00 **A pyritized polychaete from the Middle Devonian Arkona Shale, Ontario**
Una C. Farrell and Derek E. G. Briggs*

14.15 **High-fidelity preservation of bone marrow in *c.* 10 million year old frogs**
Maria E. McNamara†, Patrick J. Orr, Stuart L. Kearns, Luis Alcalá, Pere Anadón and Enrique Peñalver-Mollá

14.30 **The taphonomy of Lower and Middle Cambrian arthropods from the Pioche Shale of Nevada, USA**
Rachel A. Moore† and Bruce S. Lieberman

14.45 **The oldest known complete holothurian (early Llandeilian, Ordovician), and the origin of the calcareous ring**
Lucy A. Muir† and Joseph P. Botting

15.00 **Ground truth: searching for the earliest signs of life on Earth**
Nicola McLoughlin†, Martin Brasier, David Wacey and Owen Green

15.15 **Obolellids and the origin of calcitic-shelled brachiopods**
Uwe Balthasar

15.30 **Tea and posters**

16.00 **Early embryonic development of the priapulid worm *Priapulus caudatus* and its palaeobiological significance**
Soffia Wennberg

16.15 **The evolution of ecospace utilisation in early Palaeozoic deep-marine environments**
Seán Burke† and Patrick J. Orr

16.30 **Neutron tomography of Eocene fossil conifers from Antarctica**
Rosemary S. Stephens†, Jane E. Francis, J. Alistair Crame and Alan M. Haywood

16.45 **Taphonomic clues to Paleogene mammal behaviour and interactions**
Katerina Vasileiadou†, Jerry Hooker and Margaret Collinson

17.00 **Asymmetry and the protective function of coccoliths**
Jeremy R. Young, Karen Henriksen and Markus Geisen*

TUESDAY 20th December, continued

17.15 **Volcanism, environment and new species; fresh evidence on lacustrine fish faunas from the Scottish Lower Devonian**
R. G. Davidson and N. H. Trewin*

17.30 **The problem of Palaeozoic tubeworms and the origin of calcification in annelids**
Olev Vinn and Paul D. Taylor*

17.45 **Announcement of prize winners and close of indoor sessions**

WEDNESDAY 20th December

Field Excursion – the Mesozoic of Oxfordshire
8.00 am Depart. Return at approximately 5.00 pm.
Leaders: Stephen Hesselbo and Philip Powell

Abstracts of seminar presentations

Decoding the Ediacaran enigma

Martin Brasier[1*], Jonathan Antcliffe[1], Richard Callow[1], Owen Green[1], Alistair Carty[2] and Duncan McIlroy[3]

[1]Department of Earth Sciences, Parks Road, University of Oxford, UK

[2]Archaeoptics Ltd, PO Box 3738, Glasgow, UK

[3]Department of Earth Sciences, Memorial University of Newfoundland, St. John's, Canada

The last decade has seen an open season on decoding the Ediacara biota, with suggested affinities for their biology ranging from lichens to underwater fungi, giant deep-sea protists to stem group metazoans. We report new findings on the palaeobiology of this biota, arising from the efforts of the East Avalonia project. High-resolution laser scanning in collaboration with the Bradgate Trust forms part of an initiative to conserve the evolutionary information at highly vulnerable but key Ediacara sites in Leicestershire, UK. New 3D reconstructions of the type specimens of *Charnia*, *Charniodiscus*, *Bradgatia* and *Ivesheadia* raise questions about the currently mooted taxonomy, palaeobiology and ecology of these early Ediacaran fossils. The ontogenies of these forms are compared with those for extant cnidarians and protozoans, from which they are found to differ. Further, the forms *Ivesheadia* to *Bradgatia* to *Charnia* resemble a heterochronic morphocline with repeated manipulation of generative zones. We use our new data set to test the hypothesis that evolution of the Ediacara biota ran through a predictable morphological trajectory in which each innovation in body architecture was a variation within an understandable growth mode.

A high-resolution temporal framework for the Ediacaran Period

Dan Condon[*] and Samuel Bowring

Earth, Atmospheric and Planetary Sciences, Massachusetts Institute of Technology, USA

Considerable progress has been made in the temporal calibration of the Ediacaran Period; this is crucial for the integration of geochemical and climatic proxies, determining rates of biological change, and causes and consequences of environmental perturbations and relationship to metazoan evolution. From high-precision U-Pb geochronology from which the base of the Ediacaran is constrained at two localities (China, Namibia) to be *c*.635 Ma; the Gaskiers glaciation is *c*.582 Ma and short lived; the oldest megascopic fauna (*Charnia wardi*) post-dates the Gaskiers deposits by < 5 Ma; a major perturbation in the global carbon cycle (Shuram anomaly) at *c*.560-551 Ma is unrelated to glaciation but is consistent with progressive oxidation and re-mineralization of the organic carbon reservoir; the first complex trace fossils, the probable stem group mollusc *Kimberella* and macroscopic algae (Miaohe biota) approximately coincide with this perturbation, suggestive of a link; and the first weakly calicified metazoans (*Cloudina*, *Namacalathus*, and *Namapoikia*) are at least 548 Ma but disappear at the Ediacaran/Cambrian boundary *c*.542 Ma, coincident with a short-lived negative isotopic excursion in carbonate carbon.

The palaeoecology of the Ediacara biota: evidence from sucessionally excavated beds, South Australia

Mary Droser[1*], James Gehling[2] and Sören Jensen[3]

[1]Department of Earth Sciences, University of California, Riverside, USA

[2]South Australian Museum, Adelaide, Australia

[3]Area de Paleontologia, Facultad de Ciencias, Universidad de Extremadura, 06071 Badajoz, Spain

Fossils of the Ediacara biota offer our earliest insight into diverse macroscopic life on this planet. In particular, given the diversity and range of exquisite soft-bodied preservation, the potential for unravelling aspects of the palaeobiology and palaeoecology is great. However, most studies of the Ediacara biota have typically focussed on individual specimens. Excavation of successive bedding planes of Ediacaran strata east of the Flinders Ranges (South Australia) allows an opportunity for detailed comparative palaeoecological analyses otherwise unavailable. These strata reveal organic assemblages dominated by textured organic surfaces (TOS) and simple tubular body fossils. The abundance and diversity of these structures has not previously been recognized. Typical complex Ediacaran body fossils, while striking and dominating some of the beds, are but relatively minor components of the combined overall surface area. Trace fossils are confined to a single morphotype that indicates the presence of Bilateria. Marked variability in all components of the fauna between successive surfaces suggests that Ediacara ecologies fluctuated at short intervals despite an apparently consistent sedimentary regime. Both TOS and tubular organisms share some patterning elements with more complex Ediacara body fossils, and may represent a simpler grade of organisms constructed in a similar manner.

Invention and innovation in the early evolution of animals

Douglas H. Erwin

Department of Paleobiology, MRC-121, National Museum of Natural History, Washington DC, USA

Economic historians make a useful distinction between inventions and innovations (inventions that succeed within an economy). Applying this distinction to the evolutionary novelties of the Cambrian metazoan radiation suggests many developmental inventions were necessary but not sufficient causes for the breadth of the diversification. Comparative developmental studies of modern animals are providing a detailed window into these developmental inventions, with the protostome-deuterostome ancestor, or urbilateria, occupying a critical node at the origin of the bilaterian clades. Highly conserved developmental elements between vertebrates and arthropods indicate that there was considerable developmental complexity at this node, but the level of morphological complexity remains disputed. Such inventions do not, however, seem sufficient to generate the morphological breadth of the radiation of bodyplans. Here the primary factor was likely the construction of new ecospace through positive ecological feedback and the construction of new niches.

Earth's earliest Ediacarans

Guy M. Narbonne

Geological Sciences and Geological Engineering, Queen's University, Kingston, Ontario, Canada

Modern molecular clocks imply that animals originated 600–900 million yeas ago, a time interval that includes the most extreme glaciations to have affected our planet. The oldest fossil evidence for animals is the Ediacaran-type fossil impressions of the Mistaken Point biota (575–560 Ma) in eastern Newfoundland, which pre-date the classic Ediacaran biotas of the White Sea and Namibia by 5–30 million years. The oldest Mistaken Point fossils post-date the glacial diamictites and cap carbonate of the Gaskiers Formation (580 Ma) by less than 5 million years, implying a causal relationship between the termination of Neoproterozoic glaciation and the proliferation of animal life. Even the oldest fossils of the Drook Formation (575 Ma) comprise four species of discoid, triangular, and frondose fossils, the longest almost 2 m in length, implying that the true origin of large animals must considerably pre-date even this early occurrence.

Mistaken Point organisms lived in a deep slope environment below both storm wave base and the photic zone. Fossils in the Conception Group were preserved as census populations beneath beds of volcanic ash, leading to tennis court-sized bedding surfaces strewn with hundreds to thousands of fossils. Analyses of these surfaces using modern methods in spatial ecology show that Mistaken Point assemblages exhibited community structures similar to those of Phanerozoic and modern filter-feeding animals.

With a few exceptions such as the widespread frond *Charnia*, the Mistaken Point biota contains few taxa in common with later Ediacaran assemblages. Bilaterian body fossils and trace fossils are conspicuously absent from Mistaken Point assemblages. Probable or even possible representatives of modern radial phyla are restricted to the cosmopolitan Ediacaran frond *Charniodiscus*, commonly but not universally regarded as a stem-group cnidarian, and a recently named triangular form. More than 75% of all Mistaken Point fossils are rangeomorphs, an extinct group of complexly branching colonial organisms. Exquisitely preserved specimens near Spaniard's Bay show that each rangeomorph specimen consisted of highly fractal elements. These elements were combined as modules to construct frond-, spindle-, comb-, or bush-shaped colonies. Rangeomorphs appear to represent an extinct high-level clade of early radial animals, perhaps intermediate between the poriferans and the cnidarians. They characterized the first 15 million years of Ediacaran evolution as represented by the Mistaken Point biota, perhaps because their fractal growth and modular construction required less genetic complexity than was required by other animal phyla. Rangeomorphs were unable to compete with later, more highly evolved animals, and occur only rarely in younger Ediacaran assemblages and are not known from any Cambrian or younger assemblages.

The palaeobiology of the Doushantou Formation: the first 80 million years of the Ediacaran Period

Shuhai Xiao

Department of Geosciences, Virginia Tech, Blacksburg, Virginia, USA

The Doushantuo Formation in the Yangtze Gorges area represents the first 80 million years and roughly 90% of the Ediacaran Period. Furthermore, this formation in South China contains extraordinarily preserved acritarchs, algae, fungi, and metazoans in its shales, cherts, and phosphorites; and each taphonomic mode, that is carbonaceous compression in shales, silicification in cherts, and phosphatization in phosphorites, has been documented at multiple localities. Thus the Doushantuo Formation offers an unusual opportunity to further our understanding of Ediacaran evolution in the wake of the Marinoan glaciation and on the eve of the Cambrian radiation. Available fossil evidence from the Doushantuo Formation to bear on the antiquity of eumetazoans, their possible ecological consequences, and alternative taphonomic pathways for the preservation of Ediacara organisms will be reviewed. In addition, a critical review of acritarch data from the formation will be presented, to test hypotheses about possible environmental control on biological evolution, for example that the evolution of large acanthomorphic acritarchs may be related to the 580 Ma Acraman impact or to the 635 Ma conclusion of the Marinoan glaciation.

Abstracts of oral presentations

Evenness and diversity of Lower Palaeozoic trilobite faunas of Laurentia

Jonathan M. Adrain[1*] and Stephen R. Westrop[2]
[1]Department of Geoscience, University of Iowa, USA
[2]Oklahoma Museum of Natural History and School of Geology and Geophysics, University of Oklahoma, USA

Evenness is attracting increasing attention as a parameter in palaeoecological studies of diversity. We examined trends in evenness in shelf trilobite faunas of Laurentia through the Lower Palaeozoic. This interval includes the Ordovician Radiation, which saw a profound reorganization of marine palaeocommunities. The data set comprises more than 130 collections with a total sample size of more than 35,000 individuals, spanning an interval from the Late Cambrian to the Late Silurian. There is no significant difference between Late Cambrian and Ordovician shallow subtidal (between fair-weather and storm wave bases) collections in either evenness or richness. A small but significant decline occurs in the Silurian. In contrast, deep subtidal (below storm wave base) settings show significant increases in both evenness and richness between the Late Cambrian and Silurian. Cambrian stage ("biomere") boundary extinctions of trilobites are marked by sharp declines in both evenness and richness that persist into initial phases of recovery. Strongly uneven trilobite assemblages with low species richness also characterize some stressed environments, including peritidal carbonates and deep, dysoxic basinal settings. Overall, trends in evenness parallel those for species richness and provide no support for a major decline in trilobite diversity as a consequence of the Ordovician Radiation.

New late Ordovician brachiopod assemblages from Kazakhstan

Christian Baars[*] and Leonid Popov
Department of Geology, National Museum of Wales, Cardiff, UK

An Upper Ordovician (Caradoc) section near Lidievka in northern central Kazakhstan is of biogeographic significance and demonstrates a transition from a basinal environment to the middle parts of an accretionary fan. This complex formed as alternating patches of siliciclastic mud and silt along a prograding slope of a narrow shelf of the early Palaeozoic Stepniak-Betpakdala terrane. Some sandstone units derived from mass flow deposits contain a taxonomically diverse brachiopod fauna, possibly derived from the shallow shelf. This high diversity allochthonous assemblage closely resembles the *Acculina–Dulankarella* Association previously reported from the early to mid-Caradoc Anderken Formation of the Chu-Ili terrane, where it is associated with carbonate build-ups. A second – autochthonous, low diversity – brachiopod assemblage from hemipelagic background deposits preserved as fine clastics is dominated by the minute plectambonitoids *Durranella* and *Kassinella*, which occur in association with some trilobites. Despite the different tectonic setting, possibly representing a separate volcanic arc in the late Ordovician, the brachiopod assemblage shows distinct affinity with the contemporaneous fauna of the Chu-Ili terrane. The two brachiopod assemblages and associated trilobites indicate close links with contemporaneous faunas of the low latitude Australian part of Gondwana and related terranes (*e.g.* Tarim and South China).

Obolellids and the origin of calcitic-shelled brachiopods

Uwe Balthasar
Department of Earth Sciences, Cambridge University, UK

The relationships of the three brachiopod subphyla Linguliformea, Craniiformea, and Rhynchonelliformea are currently poorly resolved and thus hamper the identification of the original state of the last common ancestor. In particular, the plesiomorphic state of the brachiopod pedicle and the shell composition are controversial and can only be resolved by study of the stem-groups of the respective sub-phyla. Unfortunately, the study of calcitic-shelled putative stem-group brachiopods is usually hampered by their preservation and the difficulties of isolating them from a limestone matrix. Here I report partially phosphatised obolellids from the Early Cambrian Mural Formation (Jasper National Park, Canadian Rocky Mountains) that exhibit unexpected linguliform characters. The calcitic shell of the Mural obolellids is penetrated by abundant sub-micron canals which are otherwise only known from the shells of organo-phosphatic groups. Also, the posterior margin is intriguing as it suggests that a single nerve entered the pedicle and that the base of the pedicle protruded into the body cavity, which is unknown from crown-group rhynchonelliforms. The occurrence of these linguliformean characters in obolellids suggests that they are derived from the linguliform stem-group.

Evolution of herbivory in basal sauropodomorph dinosaurs

Paul M. Barrett[1*] and Paul Upchurch[2]
[1]Department of Palaeontology, The Natural History Museum, London, UK
[2]Department of Earth Sciences, University College London, UK

Sauropodomorph dinosaurs (sauropods and 'prosauropods') were the dominant vertebrate herbivores of the Late Triassic to Late Jurassic, and remained important constituents of dinosaur faunas until the end of the Cretaceous. Recent work on sauropods has shown them to possess surprisingly diverse feeding mechanisms, most of which were in place by the Middle Jurassic. However, little is known regarding: i) feeding in basal sauropods and ii) the early evolution of feeding mechanisms within the group. In particular it has been difficult to reconstruct the sequence of character acquisition in the evolution of the various functional complexes associated with sauropodomorph feeding (*e.g.*, changes to craniodental and postcranial morphology, body size and gait). Discoveries of new Late Triassic taxa, re-identification of some 'prosauropods' as early sauropods, new information on early sauropodomorph morphology, and combination of this information with robust phylogenetic hypotheses is now shedding light on the evolution of feeding in this clade. It appears that many features known to be characteristic of later sauropods (*e.g.* reticulate tooth enamel, U-shaped mandibles) appeared early in the group's history and that some features not previously recorded in sauropods (*e.g.* fleshy cheeks) may have been plesiomorphic for Sauropodomorpha as a whole.

The discovery pattern of dinosaurs and how many more species are to be found?

Michael J. Benton
Department of Earth Sciences, University of Bristol, UK

Dinosaurs have been named since 1824, and the rate of naming of new taxa followed a sigmoid curve until 1980. After that point there has been an explosive growth in new

names. Synonymy rates, however, are enormous. Compared to normal assumptions of a synonymy rate of about 20%, the rate for dinosaur genera as a whole is 40% (and for European dinosaur genera, 60% – *i.e.* more than half the dinosaur genera named from Europe are synonymous). Further, there is no sign that this high rate of erroneous (= over-enthusiastic) naming has slowed. Comparisons of the numbers of named taxa suggest that valid new dinosaurs are best sought in new territories and new geological formations. The total number of named species is more related to the number of dinosaur workers, so there is statistical evidence that too many enthusiasts leads to high levels of synonymy, not strictly to high levels of recovery of new taxa. A new modelling approach uses such historical data to estimate the total number of valid dinosaurian species preserved in the rocks (which may or may not correspond to the total number that ever lived).

Three-dimensional non-biomineralized arthropods from Upper Triassic shoreface clays, Somerset, England

A. K. Braiden[1†], P. J. Orr[1] and S. L. Kearns[2]

[1]School of Geological Sciences, University College Dublin, Dublin, Ireland

[2]Department of Earth Sciences, University of Bristol, UK

Upper Triassic shallow-marine strata near Frome preserve three-dimensional non-biomineralized arthropods. There are specimens of the crustacean *Aeger*, rare isopods, and putative crustacean larvae from green and black clays, inter-bedded with thinly-bedded carbonates. Labile tissues preserved in *Aeger* include musculature and the gut *in situ*; the remainder of the carapace is infilled by framboidal pyrite, recrystallized micritic and sparry calcite. Muscle fibres are replicated in calcium phosphate; the enveloping sarcolemmas are not preserved. Three-dimensional preservation of fossils in clay (other than examples in early-diagenetic concretions) is rare. The alternatives are that the arthropods were reworked from the carbonates into the clays either at the time of deposition or later as a result of Recent weathering of the section. Although rare specimens are found with carbonate identical to the interbedded lithologies adhering to their exterior, careful sampling and processing of *in situ* unweathered clays has also yielded specimens. The issue is as yet unresolved.

Evolution and functional morphology: the importance of the fossil record

G. E. Budd

Department of Earth Sciences, Palaeobiology, University of Uppsala, Sweden

The evolution of complex morphological features, despite being a principal feature of the contribution of palaeobiology to evolutionary theory, remains poorly understood. Here, a model based on the constraining effects of functional morphology is elaborated, which attempts to tie in the large-scale evolution of novelty with the insights of population dynamics. The most important feature is that constraint is an evolutionary, not a static feature, and can be critically analysed in terms of functional morphology. Here I discuss how different types of redundancy (at least four) and preadaptation can be employed to overcome constraint, and show how this could have a predictive value. By far the most important source of data for this endeavour is the fossil record, which therefore must play a critical role in any understanding of the origin and evolution of novelty. It may be possible on this sort of basis to establish a genuine science of adaptive innovation that at least partly subsumes the highly fragmented topics currently passing for 'macroevolution'.

The evolution of ecospace utilisation in early Palaeozoic deep-marine environments

Seán Burke[†] and Patrick J. Orr

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A rapid increase in the diversity of trace fossils in shallow-marine environments is one of the defining characteristics of the Cambrian Radiation. The initiation of vertically orientated bioturbation allowed the exploitation of novel ecospace and the development of more complex and diverse communities. By the Early Ordovician complex (laterally- and vertically-partitioned) infaunal communities had evolved in shallow-marine environments, but the ecological evolution of deep-marine environments remains poorly understood. Precambrian infaunal activity was restricted to the uppermost few millimetres of sediment and was strongly influenced by the widespread presence of microbial mats. Cambrian deep-marine outcrops in SE Ireland and W Newfoundland are characterised by primarily horizontally orientated burrows and limited vertical bioturbation. Shallow horizontal open burrow networks are preserved as pre-depositional casts on the bases of event beds indicative of relatively stiff muddy substrates. Cambrian deep-marine ecosystems include incipient vertically oriented bioturbation but retain features typical of Precambrian environments such as stiff substrates. In contrast, Early Ordovician deep-marine sediments in SE Ireland and Portugal show more extensive sediment mixing, and thus ecospace utilisation, by vertically bioturbating organisms.

Vetulicola cuneata from the Lower Cambrian Mural Formation, Jasper National Park, Canada

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Vetulicola is an enigmatic Early Cambrian metazoan identifiable on the basis of its anterior, apparently bivalved carapace, a series of paired structures or openings within that carapace, and a posterior series of seven arthropod-like segments. Although originally described as an arthropod, more recent analyses noted a marked similarity to a number of more problematic forms, including *Didazoon*, *Xidazoon* and *Banffia*, none obviously arthropodan. The debate over the affinities of *Vetulicola* is centred largely on the histological interpretation of various structures, some of which can be inferred from their fossil expression in the Chengjiang biota; unfortunately, the extreme weathering of the Chengjiang precludes more detailed analysis. Here I describe an unweathered population of *Vetulicola cuneata* from the Lower Cambrian Mural Formation which allows substantially greater histological resolution. Preliminary observations suggest that the anterior 'carapace' and posterior segments may have been lightly mineralized, whereas the paired anterior structures appear associated with an internal organically-preserved 'cuticle'. Elemental mapping will further resolve the composition and arrangement of the various 'tissues' in *Vetulicola*, and contribute to its correct taxonomic placement. As the only reported occurrence of *Vetulicola* outside the Chengjiang biota, this (apparently correlative) Mural population also conspicuously expands its known geographic range.

Skeletal microstructure, palaeoanatomy and biological affinities of the oldest stylophoran echinoderm from the earliest Middle Cambrian, High Atlas, Morocco

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One of the most enduring problems in deuterostome phylogeny has been the position of a peculiar group of asymmetric fossils: the Stylophora. Disarticulated skeletal elements of the stylophoran ?*Ceratocystis* have been recovered from the Early–Middle Cambrian transitional beds of Morocco (the "Micmacca Breccia" of the Lemdad Valley, High Atlas). This finding not only represents the oldest stylophoran occurrence in the fossil record, but their exceptional preservation provides unique data on the microstructure of the stylophoran skeleton. Stylophoran plates are constructed of a three-dimensional mesh, identical to the stereom of living echinoderms, which provides a reliable guide to the nature of the investing soft tissues. Therefore, by comparison with modern echinoderm anatomy, the stereom microstructure of stylophoran elements demonstrates that (i) the large proximal lumen of their appendage was filled with muscle, leaving little space for a postulated mouth; (ii) ligamentary tissues bounded distal elements firmly together; (iii) covering plates of the appendage were most probably not articulated. Thus, although skeletal structure suggests that stylophorans are echinoderms, their appendage was not a feeding arm but a muscular locomotory organ. Taken together with their complete lack of radial symmetry, this supports interpretation of stylophorans as basal stem-group echinoderms.

Volcanism, environment and new species; fresh evidence on lacustrine fish faunas from the Scottish Lower Devonian

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New evidence continues to emerge from the Lower Old Red Sandstone fish beds of the Scottish Midland Valley. In all the lacustrine fish beds examined the lake environment was created rapidly, the transition from fluvial conditions occurring over a few millimetres of sediment; all the fish beds contain clay bands interpreted as altered volcanic ash (bentonites) from local eruptions. Analysis of the vertical distribution of the faunas within the fish beds suggests that the ash falls exerted control on fish mortality. At Balruddery Den near Dundee a laminated lacustrine fish bed rests on volcaniclastic fluvial sandstones with large (>10 cm) rounded vesicular volcanic clasts. The volcanic association supports the hypothesis that tectonic and volcanic activity was responsible for the rapid creation of lakes within the fluvial system. An enigmatic tiny (40 mm) cephalaspid, and a new species with elongated cornual processes, have been found at Balruddery. Further information has been collected on acanthodian fish distribution within the fish beds, indicating a range of habitats from fluvial to lacustrine.

Ichnology, palaeoecology and taphonomy of an early vertebrate habitat: the Ordovician Anzaldo Formation, central Bolivia

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Sacabambaspis janvieri is the oldest known fish from Gondwana, and complete articulated specimens are found within the mid-late Ordovician Anzaldo Formation of central Bolivia. The Anzaldo Formation was deposited in a number of shallow marine environments that can be divided into four ichnofacies containing thirteen ichnospecies of *Arenicolites, Cruziana, Curvolithus, Monocraterion, Palaeophycus, Phycodes, Planolites, Rusophycus, Skolithos,* and *Teichichnus*. Two of the ichnofacies (the *Cruziana* and *Skolithos* ichnofacies) are bathymetrically controlled, and two (a mixed *Skolithos-Cruziana* and restricted *Skolithos* ichnofacies) are controlled by localised depositional and salinity conditions. The complete vertebrate fossils are confined to the restricted *Skolithos* ichnofacies where they are found in association with concentrations of lingulid brachiopods. Data is presented that suggests that both the fish and the brachiopods were killed by a combination of freshwater inundations and influxes of terrigenous sediment that buried and preserved the organisms within nearshore obrution deposits. Subsequent colonization of these obrution deposits was then initially limited to opportunistic *Skolithos* tracemakers.

Salebrids – Palaeozoic microfossils looking for a home

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Salebrids are common but enigmatic Palaeozoic microfossils. They have been attributed variously to cyanobacteria, dascyclad algae, fungi, foraminiferans and brachiopods. Most salebrids appear to have been encrusters. They grew from an initial tubular chamber, divided by a longitudinal septum, by accretion of bubble-like or tubular chambers around the central tube, producing a variety of morphologies. The wall is made of laminated calcite, which is pierced by minute pores. Newly discovered salebrids increase the range of architecture recognized within the group and provide insights into its biology. Salebrids are common in shallow marine, photic palaeoenvironments, but are also found in deep water, aphotic facies and, therefore, are unlikely to be algae. They are superficially similar to Tertiary acervulinid foraminiferans but their wall structure differs from that of any Palaeozoic foraminiferan. The wall structure is, however, similar to that of fenestellid bryozoans, but salebrids lack zooecial apertures. Their morphology implies a mode of growth involving an external tissue layer. It is probable that they represent the basal skeletons of animals whose food gathering and other organs were not reflected in the calcite skeleton.

Genome duplication, extinction and vertebrate evolution

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Vertebrate evolution has been punctuated by three episodes of widespread gene or genome duplication, which have been linked with the origin of vertebrates, gnathostomes and

teleosts, respectively. These three events coincide with bursts of character acquisition and increases in phenotypic complexity, and many researchers have suggested a causal relationship between the two. However, this pattern is derived from data for living taxa only; when extinct taxa are taken into account, bursts of character acquisition disappear and genome duplication in vertebrate phylogeny can no longer be correlated with the origin of body plans. If patterns of character acquisition or morphological gaps between higher taxa are a reflection of phenotypic complexity, then more inclusive data sets incorporating fossil taxa provide no support for hypotheses linking genome duplications and the evolution of complexity in vertebrates.

Pyritized polychaete from the Middle Devonian Arkona Shale, Ontario

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The Middle Devonian Arkona Shale of Hungry Hollow, Ontario yields a diverse fauna of echinoderms, brachiopods, corals and trilobites. The discovery of a large three-dimensionally pyritized polychaete shows that rare local conditions favoured the preservation of soft-tissues. The polychaete, which is 43 mm long, is homonomous and has at least three pairs of head appendages, a finely annulated trunk with a minimum of 21 segments, and stout parapodia, some preserving chaetae. At least one of the head appendages has a distinctive tentacle-like form. There is no evidence of jaws, but this may be an artefact of preservation. A three-dimensional reconstruction, made using high-resolution CT-scanning, shows additional details including the bifid nature of the parapodia. A preliminary analysis of the affinities of the polychaete places it within the Aciculata (of Rouse and Fauchald, 1997). This discovery highlights similarities between the Arkona Shale and the Lower Devonian Hunsrück Slate of Germany.

Swiss light shed on the nature of embryos from the Ediacaran and Cambrian

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Fossilised embryos from the Ediacaran and Cambrian provide a unique insight into the development of metazoans contemporaneous with the establishment of phyla and body plans. However, study has been limited to superficial analysis of the surface, or destructive processes that allow only a single two-dimensional section revealing the interior of the specimen. In order to overcome these limitations we have employed Synchrotron Radiation microfocus Computed Tomography (SRmCT) to study the internal structure of the embryos at a resolution comparable to SEM analysis of surface morphology. The results of our experiments shed new light on their mode of preservation, anatomy, and phylogenetic affinity. SRmCT and associated CT technologies remove traditional limitations on the analysis of palaeontological materials and are likely to be as revolutionary within our science as was the development of the scanning electron microscope in the 1960s.

A study on life strategies and environmental changes through the Middle Ordovician Elnes Formation, southern Norway

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Biostratigraphic data have been analysed and compared to their associated lithology in order to clarify the environmental influence on the fossil associations found in the Middle Ordovician Elnes Formation of southern Norway. Four to five main types of sedimentary facies have been recognized, ranging from dark siliclastic mudstones over fine-grained turbidites to marls and limestones deposited in an outer shelf environment. Although the sea-level changes may be unclear, we have a good picture of the gradual changes in the depositional environment found throughout the formation. A multivariate analysis of the depositional environment and life strategies among the fossil groups reveals only a clear separation of the black shales and its hemipelagic and phosphatic shelled benthic fauna reflecting a maximum flooding; the other environments have too large an overlap. On the other hand three more biofacies are distinguishable in the biostratigraphic log. One is dominated by mobile benthos (trilobites) found in the marls and limestone, one is characterized by around 25% of sessile benthos found in intervals with dark grey mudstone, and finally one contains a large amount of hemipelagic and mobile benthic animals and a few sessile benthic ones. This last community is associated with intervals dominated by turbidites, but shows transitions to the ones above.

On the edge of Laurentia: Late Ordovician (Upper Ardmillan) brachiopod associations in the unstable shelf and slope environments of Girvan, SW Scotland

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Over 170 brachiopod species occur throughout the Upper Ardmillan Group of the Girvan District. A full inventory shows that near autochthonous background assemblages are dominated by variants of the deep-water *Foliomena* fauna, in fine-grained sediments, supplemented by diverse shallow-water assemblages periodically transported downslope. Diversity peaked in the Rawtheyan, associated with deposition of the highly fossiliferous Lady Burn Starfish Beds. Measures of taxonomic distinctiveness suggest, however, that although communities in the deep sea were diverse, they were characterized by fewer higher-taxonomic groups than those on the shelf. About 15 different assemblages, many partly contaminated by downslope sediment transport, are present in the Upper Ardmillan Group; these provide a useful overview of many of the potential brachiopod-dominated palaeocommunities along this part of the Laurentian margin. Statistical analysis suggests these faunas are similar to upper Ordovician assemblages from Pomeroy, Northern Ireland and some from the northern parts of the Appalachians. However, they contrast markedly with those of the North American Mid-Continent, although a few of the taxa from the latter area migrated onto the Laurentian margins during the Hirnantian, appearing for the first time in the widespread *Hirnantia* fauna of the High Mains Formation.

Evolution of soft-tissue attachment from Orthocerida via Bactritida to early Ammonoidea

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In Early to Middle Devonian claystone sequences of Morocco and Germany, pyritised and often secondarily limonitised cephalopod remains are common. Delicate details of soft-tissue attachment structures are occasionally preserved on internal moulds of cephalopods. Some orthocerids show faint imprints of the annular elevation and the dorsal furrow. A few bactritids display a distinctive annular elevation with two circular bands forming a paired or threefold, dorsal lobe. Among Devonian ammonoids, the muscle scars are further differentiated. In Early Emsian forms, a dorsal parabolic muscle scar is discernible. Among Famennian taxa, the large scars of the cephalic retractors have a more lateral position and are lengthened in a spiral direction. Morphological differences of these scars between these groups suggest different soft part morphologies. A comparison of these attachment scars shows that those of the bactritids are morphologically intermediate between the orthocerids and ammonoids. Shape and position of the muscle scars are interpreted as indication for a planktonic lifestyle in the orthocerids, a more active, nektonic mode of life in ammonoids and an intermediate mode of life among bactritids.

Whale of a time in the deep sea

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Some whales are very large animals, and sunken dead whales (whale falls) represent considerable, but sporadic, food enrichment sources to the seafloor. Sunken whales pass through three ecological successional stages: a mobile-scavenger stage, an enrichment opportunist stage and a sulphophilic stage during which considerable quantities of sulphide are released into the local environment. This last stage is characterized by the presence of animals that contain sulphide oxidizing bacterial symbionts (vesicomyid and mytilid bivalves and vestimentiferan tube worms). Based on shared species between whale falls, hydrothermal vents and methane seeps, it has been hypothesized that whale fall communities could act as evolutionary stepping stones between vent and seep communities. In the presentation we review the limited fossil record of whale fall communities, comprising eight examples from Oligocene rocks of Washington State, USA and three examples from the Miocene of Japan, and, using this data, examine the stepping stone hypothesis.

Micropalaeontological and ichnological analysis of Triassic/Jurassic boundary sections of SW Britain

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At present, the micropalaeontology of the Triassic/Jurassic boundary interval in SW Britain is poorly understood, despite a number of comparatively complete and fossiliferous sections crossing the boundary. Although there has been extensive study of the macrofauna and lithostratigraphy of the classic Triassic/Jurassic boundary sections, including St. Audrie's Bay, Somerset, little work has been done to integrate microfossil, ichnological and sedimentological data in order to enhance understanding of the boundary interval and the impact of the mass extinction event at the close of the Triassic. Traditionally, the first appearance datum of the ammonite *Psiloceras planorbis* has been used as the boundary marker for the base of the Jurassic, despite recent suggestions that this event may be diachronous in Britain and relates to an ecological rather than evolutionary control. Preliminary data presented here appear to demonstrate that the microfauna show little variation over this interval, suggesting that the FAD of *P. planorbis* is a truly evolutionary event. Furthermore, the distribution of microfossils (primarily foraminifera and ostracods), together with ichnological and lithological data, indicate a general increase in oxygenation and stability of the bottom water environment in the Lower Jurassic.

A new eigenshape-based morphometric method for analyzing 3D patterns of shape variation for surfaces and discrete objects

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Most morphometric methods available for characterizing shape variation in fossils are restricted to the consideration of small numbers of landmarks marking major structural features (*e.g.*, tooth cusps) and/or the outlines (*e.g.*, shape of tooth periphery) of objects or structures in two or three dimensions. While these data are sufficient for resolving a large number of palaeontological questions, taxonomic, functional analyses, evolutionary studies, *etc.* routinely make use of other sorts of morphological information. In particular no method has been available to facilitate the characterization and analysis of generalized 3D surface shape variation. We have developed a set of simple 3D surface digitization and sampling protocols that, when combined with the coordinate-point eigenshape morphometric method, enable any fossil morphology (regardless of complexity) to be characterized precisely and compared to the morphology of any other object sampled in a comparable manner. Moreover, this method can be used to summarize patterns of shape variation in a sample of objects so characterized within a linear theoretical shape space that supports a full range of ordination and 3D modelling procedures. Examples of the use of this technique in vertebrate and micropalaeontological contexts, suggests it can be extraordinarily valuable in a wide range of palaeontological applications.

Ammonoids across the Permian–Triassic boundary: a cladistic perspective

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The rapid diversification of ceratitid ammonoids during the earliest Mesozoic has been taken at face value as an example of explosive radiation following the Permian–Triassic mass extinction. However, the validity of this interpretation has never been tested within a phylogenetic framework. A total evidence cladistic analysis of Mid-Late Permian and Induan (earliest Triassic) ammonoids confirmed the monophyly of the Ceratitida. However, when the cladogram is calibrated against the observed fossil record, the resultant tree implies that the divergence of a number of early Triassic lineages actually occurred

talks

during the latest Permian. If these range extensions are taken into account then per-genus extinction rate across the Permian–Triassic boundary in ammonoids drops from *c*.85% to *c*.60%. Previous morphological studies can be placed into a phylogenetic context and demonstrate a general shift across lineages towards compressed unornamented morphologies in diverse clades. Partitioned phylogenetic analysis of suture line characters versus shell shape and ornament characters confirms the importance of suture-line characters for resolving the higher taxonomy of ammonoids.

Ground truth: searching for the earliest signs of life on Earth

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This talk will report the findings of the Oxford Geobiology Group's search for the earliest signs of life in *c*.3500 Ma Archean rocks from the Warrawoona group of Western Australia. We will critically analyse the geological setting, morphology and geochemistry of the putative microbial remains to assess their biogenicity. The latest field and petrographic data is presented and explains the environment of deposition of the diverse chert units, focussing on the Strelley Pool and Apex Cherts. This is used to assess the 'warm little ponds' versus 'hydrothermal cradle for life' paradigms that have been applied to these rocks. Detailed petrographic examination of the carbonaceous remains within these cherts is presented, using the latest imaging techniques to illustrate how the morphology and petrography of the artefacts can be distinguished from true microfossils. Finally, microtubular structures preserved in silicified sandstones from the Warrawoona Group are described. This case study illustrates how field mapping and petrographic data is combined with high resolution elemental and isotopic measurements, made using a state of the art nanoSIMS (secondary ion mass spectrometer that operates on a nano-meter scale) to test a possible microbial component in their formation.

High-fidelity organic preservation of bone marrow in c.10 million year old frogs

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The Miocene Libros and Ribesalbes lacustrine basins in NE Spain each host an exceptional fauna (including insects, frogs, salamanders, snakes and larval amphibians) and flora within deep-water, organic-rich, finely laminated facies. Frogs and salamanders are particularly abundant and occur as articulated skeletons enclosed in a thin, dark-brown coloured, carbonaceous bacterial biofilm that defines part, or the entire outline, of their soft tissues. Musculature and the first documented occurrence of fossilised bone marrow are preserved in the frogs and salamanders; both tissues occur as three-dimensional insoluble organic residues. The fossilised bone marrow retains the original texture and red and yellow colour of haematopoietic and fatty marrow, respectively; osteoclasts, their associated

extracellular matrix, and vascular structures are also preserved. Initial biogeochemical analyses demonstrate the presence of amide groups (important constituents of proteins) in the marrow, suggesting that preservation extends to the molecular level. The protective microenvironments of the bones inhibited microbial degradation of the marrow ('cryptic preservation'); *in situ* condensation and polymerisation of the original carbon compounds followed.

Is the conodont fossil record too biased to make multielemental reconstructions? Evidence from the Devonian of Russia

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Most published conodont illustrations are of P_1 elements, as they appear more variable and are often the most common element in discrete collections due to preservational biases. The other elements in the apparatus are generally less common and ignored. However, multielemental rather than single element studies are needed to uncover the phylogenetic relationships of conodonts and allow a meaningful interpretation of their fossil record. Three samples from the Givetian-Frasnian Vorota Formation from the Kozhym River section, Sub-Polar Urals, Russia provide well-preserved conodont elements suitable for reconstructing conodont apparatuses, a rarity for the Devonian. The elements are almost all complete and show a range of sizes suggesting that little or no sorting of element types has taken place. Percentages of the M and S elements in the collection are also consistent, suggesting that the collection reflects the life-frequency of the element types rather than biases caused by palaeobiological differences between taxa, post mortem sorting, field sampling or laboratory preparation. As a result, a new reconstruction for the conodont *Mesotaxis* can be made including a *Palmatolepis*-like element in the S_1 position and an M element that is very similar to M elements of *Polygnathus*.

The taphonomy of Lower and Middle Cambrian arthropods from the Pioche Shale of Nevada, USA

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The Pioche Shale of Nevada, USA, preserves remains of soft-bodied ecdysozoans spanning the Lower-Middle Cambrian boundary and it has been suggested that the difference in preservational style across the boundary reflects the spread of ocean anoxia at the end of the Lower Cambrian. The occurrence of similar taxa in the late Lower and early Middle Cambrian horizons allows a comparison of preservation style across the boundary. Element maps of anomalocaridid appendages and *Tuzoia* from both the Lower and Middle Cambrian strata show that iron oxide preservation is dominant across the boundary but that the diagenetic pathway differs. Only Middle Cambrian specimens are also preserved as thin carbon films. An understanding of the taphonomic history of the Pioche Shale fossils also allows a comparison with other late Early Cambrian soft-bodied faunas such as the Kinzers Formation of Pennsylvania, Latham Shale of California and Eager Formation of Canada.

Elucidating possible developmental processes of Lower Devonian spore clusters by comparison with extant analogues and spore mimics

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Comparisons of Lower Devonian spore clusters and extant, immature *Osmunda regalis* spores and spore wall mimics have provided insights into the development and formation of certain fossil spores. The fossil specimen containing *in situ* spore clusters is, as yet, unidentified but is considered 'rhyniophytoid'. The clusters contain spherical, finely granulate spores. Immature extant *O. regalis* spores also form clusters and exhibit a similar sculptural pattern to that of the fossil but are also surrounded by a discrete layer of unknown composition. In recent years self-assembly experiments have provided different perspectives on the processes involved in pollen and spore wall pattern formation. The spore mimics obtained from the latest experiments closely resemble the living organism and permit comparison with both the fossil and the extant spores.

The oldest known complete holothurian (early Llandeilian, Ordovician), and the origin of the calcareous ring

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Articulated holothurians are extremely rare as fossils. Isolated sclerites have been recorded from the Middle-Upper Ordovician, but definite body fossils are unknown before the Late Silurian. Consequently, although the Holothuroidea are almost certainly the sister-group of Echinoidea, there are significant uncertainties over how the separation occurred, and at what stage. In particular, the calcareous ring could be derived either from the ambulacral series, or from the Aristotle's Lantern, and the timing of dermal ossicle reduction is unclear. Articulated holothurians have been found in the lower Llanfawr Mudstone Formation of the Builth Inlier, central Wales. The specimens show iron-stained preservation suggestive of very early pyritisation. The holothurian possessed a multi-plated ring, and shows traces of a uniserial skeletal ambulacral system. This fits neatly into a previously published hypothetical series deriving the calcareous ring from the ambulacral series. Although the ring structure resembles that of Apodida, regarded by most workers as the earliest extant holothurian clade, it also possessed cruciform dermal sclerites, suggesting affinity with the Elasipodida. The suite of observable features suggests a phylogenetic position of the new specimens near the base of 'true' holothurians, and indicates a complex early history of Holothuroidea.

Bored echinoids: predation patterns on *Echinocyamus* from the Oligo–Miocene of Europe

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Predation on echinoids, though common in Recent environments, has rarely been used as a palaeobiological tool. Many predators on echinoids leave distinctive marks

especially those made by cassid gastropods. These can be recognized in fossil echinoid assemblages and are a useful comparison to predation patterns on molluscs with respect to evolutionary studies concerning predation patterns and pressures. In this study, fossil *Echinocyamus* assemblages from the Oligo–Miocene of Europe were investigated. These minute clypeasteroid echinoids are common members of Caenozoic and Recent echinoid assemblages. Numerous fossil specimens show holes passing through the test that are interpreted as boreholes. The large number of predated specimens allows for detailed statistic analysis within populations and among localities. The study encompasses the morphology of boreholes, predation frequencies, site selectivity patterns and the prevalence of multi-predatory attacks. Predation patterns are also analysed with respect to general population structures, depositional environments and stratigraphic age. The results are compared to predation data on echinoid predation through time and substantiate an increasing rate of predation rates on sea-urchins from the Cretaceous to the Recent.

Gastropod diversity at the early Toarcian mass extinction event – turnover in South Germany

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Except for the early Toarcian Posidonienschiefer (*Posidonia*-Shale), lower to early Middle Jurassic (Pliensbachian to Aalenian) marine grey shales of the Franconian Alb of South Germany yield abundant benthic gastropod faunas. Commonly, gastropods form the most diverse benthic group. Typically, these gastropod faunas have a similar structure. That is, they do not exceed a species richness of 30 and are strongly dominated by a few (mostly three) species while others are rare, species and specimens are usually small and do not exceed an adult size of 10 mm. These gastropod faunas are interpreted as soft bottom assemblages with the muddy substrate as the major controlling factor, whereas oxygen depletion was probably not an important limiting factor. The early Toarcian anoxic event terminated the rich Pliensbachian gastropod assemblages. A complete late Toarcian to early Aalenian section shows that gastropod faunas with similar characteristics became re-established, gradually increasing in diversity. However, these faunas completely differ taxonomically from the Pliensbachian pre-extinction assemblages. This suggests true extinction and subsequent immigration of new faunas, whereas evasion and re-immigration are unlikely.

Tooth microwear analysis of dietary shifts during the evolution of Miocene sticklebacks

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The three-spine stickleback, *Gasterosteus*, is an important model organism in studies of genomic and phenotypic evolution, adaptation and speciation. Most of this work is based on extant representatives of the genus, but Bell's detailed study of closely sampled stickleback populations in the Miocene of Nevada is a classic, text-book study of microevolution in the fossil record. What is clear from living sticklebacks is that

competition for food plays an important role in speciation, causing divergence in food gathering traits and ecological character displacement, leading to morphological change. Was the evolution of Miocene sticklebacks also driven by shifts in feeding? Until now this question has been unanswerable because determining the diet of fossil fishes (and most other organisms) has relied on functional inferences derived from morphology, a method which assumes that shifts in feeding are correlated with morphological change and cannot, therefore, be used to investigate the relationship between the two. We have developed a new method based on quantitative analysis of tooth microwear patterns in fishes. We are now able to determine the dietary preferences of fossil fishes. For the first time, this allows ecological models of competition and trophically driven speciation to be tested over real evolutionary timescales.

Spinosaurid theropod dinosaurs are mechanical analogues of fish-eating crocodilians, not large alligatorids or typical theropods

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The Spinosauridae are a clade of dinosaurs whose cranial morphology has diverged from the ancestral theropod condition to converge on a more crocodilian-like construction. This has implications for the feeding behaviour of the group and for wider issues of convergence and constraint in archosaur evolution. Previous morphological and taphonomic evidence has suggested that spinosaurs fed at least partly on fish. Described here are new data from CT scans and an assessment of mechanical performance of the biting spinosaur snout as compared to a typical theropod, an American alligator and an Indian gavial, performed to determine which structural morph spinosaurids most represent. Results reveal that in all respects, the skull of the spinosaur *Baryonyx walkeri* is mechanically very similar to that of the fish-eating gavial: there is no significant difference in bending versus torsional stress in gavial and *Baryonyx*, whilst in the theropod and alligator torsional stresses are significantly greater. The secondary palate (a bony plate of bone separating the nasal passages from the buccal cavity) helps lower bending stress in the gavial and *Baryonyx*, whilst it acts to lower torsional stress in the alligator. The results strongly support the hypothesis that *Baryonyx* employed at least a facultatively piscivorous lifestyle.

The use of computational fluid dynamics in reconstructing the hydrodynamic properties of graptolites

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Graptolites are some of the most commonly preserved Silurian planktonic organisms. The interpretation of graptolite functional morphology is rendered problematic by their lack of close modern analogues or homologues. Physical modelling of graptolites has explained some aspects of their hydrodynamic behaviour, such as their orientation relative to currents and their rate of response to new directions of water flow. However, this technique is slow and laborious and the accuracy of the physical models limits the level of detail that can usefully be studied. Computational fluid dynamics (CFD) are routinely used in engineering

applications in order to overcome these limitations. CFD models of graptolites have been generated and the results tested against the known outcomes of physical models. Three-dimensional models of graptolites, generated to true scale, are exposed to computed fluid flow from a variety of orientations. Cross-checks with physical modelling show that these iterative computational solutions produce verifiable results. Virtual graptolites can be modified at will and exposed to a range of current velocities. Results suggest that major improvements in our understanding of graptolite functional morphology will result from further use of this novel technique.

The evolutionary history of calcification in planktic foraminifers and its influence on the global carbon cycle

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Deep-sea carbonate sediments cover about half of the total oceanic floor. Modern carbonate production is a snapshot of the evolutionary history of carbonate producers. Evolutionary changes in the abundance and size of these organisms have resulted in temporal and spatial changes in carbonate export to the deep sea and hence the locking away of atmospheric CO_2. Understanding the relative contribution of the carbonate producers and how and why these change over time may provide us with tools to predict future impacts on the global carbon cycle and, hence, the pelagic feedback on atmospheric CO_2. In the present study the pattern of size changes in foraminiferal assemblages during the last 110 Ma has been mapped. Planktic foraminiferal sizes in the Late Neogene are unprecedented in the geological record. These size changes are related to latitudinal (biogeographic) and vertical (stratification) temperature differences in the ocean, providing new niches that allow specific adaptation and growth to large size. Throughout the Cretaceous and Paleogene, planktic foraminiferal carbonate production is negligible in comparison with coccolith carbonate production, whereas in the Late Neogene planktic foraminifera became a vital part of the carbon cycle.

Acritarchs, calcispheres, and the origin of the dinoflagellates

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Dinoflagellates are single-celled protists that constitute a major part of primary producers in modern oceans. Some dinoflagellates produce fossilisable resting cysts; most of them are organic-walled and to a lesser extent calcareous and siliceous. Although comparative ultrastructure, molecular and biogeochemical studies indicate a Precambrian origin for dinoflagellates, organic-walled dinoflagellate cysts are largely only reported from Middle Triassic and younger strata, while calcareous dinoflagellates have only been reported from Upper Jurassic and younger strata. In the Palaeozoic, organic-walled microfossils without clear biological affinities are attributed to the acritarchs, while many spherical calcareous microfossils are classified within the artificial grouping of the calcispheres. Here we confirm the conclusion of previous workers that many Palaeozoic acritarchs should be considered as the cysts of dinoflagellates. In addition, we show that some calcispheres can be related to calcareous cysts of dinoflagellates following comparisons of their ultrastructure with modern and fossil species.

How congruent are molecular and palaeontological estimates of divergence times?

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The phylogenetic relationships of 46 echinoids, with representatives from 13 of the 14 ordinal-level clades and about 70% of extant families commonly recognized, are established from a dataset of three genes and 119 morphological characters. When analysed separately, morphological and molecular data give closely similar results that congruence tests suggest are estimates of the same underlying tree. The combined data provides a largely resolved and well-supported tree, with complementary levels of support derived from morphological and molecular datasets. This tree, when calibrated against the fossil record, provides estimates of divergence times and completeness of the fossil record. The order of branching on the cladogram agrees largely with the stratigraphic order of first occurrences, and implies that the fossil record is 85% complete at family level and a resolution of 5 Ma time intervals. Molecular estimates of divergence times derived from applying relaxed molecular clock models, implemented using Bayesian- and penalised likelihood-based methods, are concordant with estimates based on the fossil record in approximately 67% of cases. There are two areas in the cladogram where morphological and molecular estimates disagree, one of which probably stems from failure of the fossil record, the other a result of extensive, non-autocorrelated rate variation in the molecular data.

Neutron tomography of Eocene fossil conifers from Antarctica

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A new non-destructive 3D imaging technique (neutron tomography) has been used to image exceptionally well-preserved conifer fossils of Eocene age (~ 50 Ma) from Antarctica. The conifer fossils are preserved in carbonate concretions within mudstones and siltstones of the La Meseta Formation, sediments that formed in a tidally-influenced estuarine environment. The conifer assemblage comprises fossil leafy branches, isolated leaves and cone scales of *Araucaria*, and are similar to modern Monkey Puzzle trees. Calcite permineralisation of the fossil leaves has preserved fine cellular detail and stomata. Neutron Tomography works like a CT-scan but uses high-speed neutrons instead of X-rays and so can recognise hydrogen and organics as well as "heavy" elements. Small concretions were scanned in three planes through 360° rotation, and computer software generated a three-dimensional database for each of the slabs. Rendering software was used to identify the fossil from the raw dataset and to create 3D images and animations. These 3D images can be 'serially sectioned' by computer, without destroying the fossil itself, allowing internal structures to be studied. This technique has never before been applied to fossil material, but shows great potential as a non-destructive method for studying fossils in three-dimensions.

A 125 million year record of body size changes

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The Permian to Early Jurassic interval witnessed many changes in the Earth's geosphere and biosphere, including two of the major Phanerozoic extinction events. The body sizes of marine animals, readily assessed by examination of the trace and body fossil records, also show dramatic changes. Data collected from museum, literature and field studies show that most bivalve, gastropod, brachiopod and marine vertebrate taxa underwent parallel, statistically significant, size changes at this time. Following Carboniferous-Permian maxima, body size declined through the Permian, reaching a minimum in the Early Triassic (the post-extinction Lilliput effect). Size then increased through to the Late Triassic, reaching a maximum in the Carnian, declined in the latest Triassic and earliest Jurassic (the Lilliput effect again?) before rising once more from the late Hettangian. Although facies biases occurred during some intervals, the broad pattern is considered to reflect biological reality. The most likely controls were oxygenation, food supply (oceanic productivity) and temperature. As a first order approximation, the size trends parallel inferred changes in atmospheric oxygen. Maximum sizes are recorded during times of global cooling, high atmospheric oxygen and inferred high oceanic productivity; minimum sizes occur when global temperatures are high and oxygen and productivity levels are low.

Upper Ordovician GSSPs and the British historical type area: a chitinozoan point of view

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From a chitinozoan perspective, the new Upper Ordovician GSSPs are compared to the historical type areas of the equivalent British Caradoc and Ashgill Series. Concomitantly, the first Upper Ordovician chitinozoan biozonation for British Avalonia is established. It consists of fourteen chitinozoan bio(sub)zones and has a predominantly Baltoscandian signature, supplemented with endemic Avalonian and Gondwanan influences. Main features include: (1) The chitinozoans of the Caradoc type area are re-organised into biozones which are more readily applicable than those previously established (Jenkins 1967). (2) The Baltoscandian *Fungochitina spinifera* Biozone brackets the base of the Ashgill Series in its type area. The base of the Ashgill therefore corresponds to a level in the Baltoscandian upper Oandu or in the Rakavere Stage; previously the base of the Ashgill was thought to fall in the overlying Vormsi Stage. (3) Application of chitinozoan correlation places levels with graptolites of the *Dicellograptus morrisi* Subzone (*Dicranograptus clingani* Biozone) in the Onnian and Pusgillian. Consequently, the level of the *Pleurograptus linearis* Biozone is moved into the Cautleyan or even higher. The suggested changes result in a much better agreement with the recently revised graptolite biozonation of the Cautley district.

Taphonomic clues to Paleogene mammal behaviour and interactions

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Late Eocene micromammals from the Isle of Wight (UK) have been described in terms of postmortem modifications on enamel, dentine and bone and the taphonomic history of each taxon has been established. The mechanisms that produced the accumulation and the agents that influenced the assemblage have been established. Furthermore, this study has expanded our knowledge on interactions between co-existing Paleogene taxa, provided information about their behaviour, and aided the reconstruction of the food chain in a Paleogene palaeocommunity. The majority of theridomyid and marsupial and the minority of glirid and nyctithere remains have been digested; the theridomyids also present evidence of chewing by a small carnivore. The most probable theridomyid predator is *Cynodictis* cf. *lacustris*, while predation of the other micromammals by the same carnivore cannot be excluded. Differences between taxa regarding proportions of predated individuals possibly reflect differences in locomotor adaptation; the theridomyids and marsupials are semi-terrestrial, while the glirids and nyctitheres exhibit evidence of scansorial mode of life. Some of the material was exposed on the surface for a short time period before being incorporated into the sediments; glirids gnawed some theridomyid remains during that time. Some of the remains were trampled by animals that visited the water bodies in the vicinity. Specimens do not show evidence of transport. The micromammals and *Cynodictis* were interacting members of the local community.

The problem of Palaeozoic tubeworms and the origin of calcification in annelids

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Calcareous, spirally-coiled tubes of small worms – 'spirorbiforms' – first appeared in the Ordovician and are represented in every geological system from then until the present day. Ordovician–Jurassic spirorbiforms differ from *Spirorbis* in having lamellar tube microstructures, some penetrated by pores and/or with pseudopuncta-like deflections of the laminae, and hemispherical tube origins. These features suggest that they are lophophorates, possibly related to the extant phoronid worms, and can be assigned to the extinct Order Microconchida. Several other Palaeozoic tubeworm-like fossils such as cornulitids, *Trypanopora*, *Tymbochoos* and *Anticalyptraea* have also been commonly interpreted as serpulids or at least annelids. Like microconchids they too have microlamellar pseudopunctate shell structures and hemispherical tube origins which differ from any known modern calcifying annelid. All these Palaeozoic problematical tubeworm-like fossils may be phylogenetically closely related to tentaculitids. Indeed, microconchids and trypanoporids have already been assigned to the Order Tentaculitida. Now it is time to emend this Order Tentaculitida by adding cornulitids, *Thymbochoos* and *Anticalyptraea*. The preliminary conclusion is that Palaeozoic seas were populated with diverse calcifying tubeworms which were not annelids and may instead have been phoronids or phoronid-like. The oldest true serpulids seem to have appeared in the Early Triassic.

How the chiton got its tegmentum

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Chitons are molluscs characterized by their eight dorsal plates and the surrounding mantle termed the perinotum. The outermost shell-layer in chitons is unique among the molluscs in possessing a branching canal system that houses sensory and secretory cells termed the esthetes. The Early Cambrian *Halkieria* has recently been suggested to be closely related to chitons. However, the shell plates of *Halkieria* do not seem to possess this canal system. It is surprising that the perinotal spicules in *Halkieria* are hollow and have a complex branching canal system, and it could be suggested that this canal system actually housed esthetal sensory cells. A number of similarities are noticed between the canal systems in the halkieriid spicules and the chiton tegmentum, for example the shape and size. The chitons secrete massive spicules but the lately discovered *Polysacos* has got an esthetal canal system in both shells and spicules. It is therefore suggested that the esthetal system in the chiton shell evolved from the supposed sensory system seen in the hollow spicules of *Halkieria* and the related *Thambetolepis*.

Exceptional preservation of *in situ* spores in the Rhynie chert plants

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In situ spores have been characterized for all seven plants known from the Lower Devonian Rhynie chert. Preservation of the *in situ* spores is highly variable, presumably reflecting different taphonomic factors and preservational effects relating to the silicification process. Some specimens exhibit exceptional preservation of spore characters not normally fossilized. In some immature sporangia early stages of spore ontogeny are present, and remarkably the fossil tetrads preserve the callose wall that encloses the tetrad and surrounds the component spores during early stages of spore wall formation. This is the first report of a fossilized callose (spore special cell) wall in land plants. In other specimens cellular detail within the sporopollenin spore wall is preserved, with the plasma membrane, and possibly also the nucleus, clearly discernible. This presentation will focus on: 1) mode of preservation of the spores; 2) what the exceptional preservation reveals regarding spore wall formation and reproductive strategy in the early land plants of the Rhynie chert.

Early embryonic development of the priapulid worm *Priapulus caudatus* and its palaeobiological significance

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The relatively poorly known phylum Priapulida is now classified as a member of the group Cycloneuralia together with nematodes, kinorhynchs, loriciferans and nematomorphs. Up to this point the embryology of *Priapulus caudatus*, one of the approximately 15 recent priapulid species, is not well documented. Lang has briefly described the development of the priapulid embryo, although no details were presented. This project closely monitors the embryonic development of *Priapulus caudatus*. Cell lineage and cleavage pattern

from the first cleavage until the gastrulation are presented. Noticeable in the discussion concerning the early evolution of the Ecdsyoza (cycloneuralians + arthropods) is the segmental and ceolomatic features, seen in arthropods. Have these features been lost in the cycloneuralians or were they secondarily gained within the arthropod group? An answer to this will not only help us to resolve several questions seen in the early arthropod evolution, but would indirectly give us new insights concerning the early bilaterian animals and their fossil record.

Neogene planktonic foraminifera: remote sensors of the ancient ocean surface or a taphonomic conundrum?

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Fossil planktonic foraminifera are used to reconstruct the properties of the upper water masses of ancient oceans. They have been utilised to provide estimates of sea surface temperature, data that has been used to ground-truth computer-based general circulation models for past climate reconstruction. For palaeoceanographers, the most widely used Neogene to recent planktonic species from tropical and sub-tropical regions is *Globigerinoides sacculifer*. This near surface-dwelling form has a complex history of nomenclature, but is based on (fossil?) material from a 'chalk' block collected on the coast of Papua New Guinea. Fossil, core top, and plankton tow *G. sacculifer* show significant differences in test calcification. Tow specimens, collected *in vivo*, are lightly calcified with translucent tests, calcite formed during ontogenesis. Core top and fossil specimens are heavily calcified, white opaque in appearance, and show evidence for thick gametogenic calcite veneers that add substantially to the mass of the tests. Fossil material, particularly from Miocene horizons, is dissolved and recrystallized. We estimate by how much the original ontogenetic oxygen isotopic signature ($\delta^{18}O$) of specimens is offset by this post-ontogenetic calcite, and show that much of the published oxygen isotope data is unusable for ground-truthing computer-based general circulation models.

Competing groups of fishes: tests for asymmetry in the fossil record

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Do higher taxa go extinct because they are displaced by better-adapted ones? Competition is frequently invoked to explain instances of taxon replacement in the fossil record, but its role is difficult to test. The classic double wedge – where one group waxes as the other wanes in the absence of any rapid environmental change – is usually cited as the smoking gun. A few studies have found direct fossil evidence of competitive interactions between individuals, but these require exceptional circumstances. Here we introduce a census approach to the evolution of fish groups. Stratigraphic and ecological data are scored for the 699 families of fishes with a fossil record, and randomisation methods are used to test the asymmetry of potential interactions between major groups. Five examples from the literature are tested here. In three cases, there is significant asymmetry of potential competitive displacement. These are the possible displacements of Agnatha by Placodermi, Holostei by Teleostei, and Osteichthyes by Chondrichthyes.

Asymmetry and the protective function of coccoliths

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The functional morphology of protists and especially planktonic protists is notoriously difficult to elucidate. Coccolithophores are a fine example of this. They produce beautifully elaborate coccospheres, but which if any aspects of the morphology are genuinely functional as opposed to being accidental outcomes of the biomineralisation process? We have previously argued with some ingenuity that the basic function of coccoliths was probably defensive. This has, however, failed to convince our colleagues and does not address the question of which aspects of morphology are functional. We recently returned to this subject and have used a combination of modelling and experimental techniques to demonstrate that coccolith structure is optimised for mechanical strength and so can provide significant protection. Asymmetry provides a further line of evidence. The primitive state for coccoliths is to show radial symmetry and departure from this has to be a product of active cellular regulation of the biomineralisation process for a functional purpose. Re-examination of all extant coccolithophores showing asymmetric coccoliths shows that asymmetry is consistently used to improve interlocking of coccoliths and increase the strength of the coccosphere. This also suggests that coccolith shape is much more intimately controlled and functionally adaptive than we have assumed.

Abstracts of poster presentations

A complete database of Upper Devonian/Lower Carboniferous megaspores

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Heterospory, one of the major land plant reproductive strategies, first evolved towards the end of the Early Devonian. Megaspore diversity and disparity rapidly increased during the Mid-Devonian to Early Carboniferous interval. However, the evolution of early megaspores over this critical interval is relatively poorly understood due to a paucity of described assemblages, contrary to the later Carboniferous where reports of dispersed megaspores are numerous. This gap in knowledge masks an important change, with marked differences between the nature of megaspore assemblages from the Late Devonian and the Late Carboniferous. As data on Devonian and Lower Carboniferous megaspores are scattered, the relationships between many genera and species remain unclear. A complete database of Devonian and Early Carboniferous megaspores is presented, based on a detailed bibliographical review. This database will serve as a taxonomical review and complete catalogue of all megaspores of the time period investigated. Preliminary stratigraphical range-charts and the first palaeogeographical plots of Late Devonian–Lower Carboniferous megaspores are also presented.

A review of *Yochelcionella* (Mollusca, Helcionelloida) from the Lower Cambrian of Laurentia

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The helcionelloid mollusk genus *Yochelcionella* Runnegar and Pojeta (1974) was first recorded from Laurentia from the Lower Cambrian of Newfoundland by Walcott (1891). Further study has revealed a fauna comprising five different species from Laurentia: *Y. erecta* (Walcott, 1890); *Y. americana* Runnegar and Pojeta, 1980; *Y. greenlandica* Atkins and Peel, 2004 *Y. gracilis* Atkins and Peel, 2004; and *Y. chinensis* Pei,1985. *Y. chinensis* Pei, 1985 is redescribed from over four hundred specimens from the Forteau Formation, Labrador Group, western Newfoundland, allowing an examination of morphological variation of this highly variable species. *Y. erecta* is described for the first time. The presence of *Y. chinensis* suggests a connection from Laurentia to the North China platform.

Diversity and distribution in Ordovician (Llanvirn–Caradoc) echinoderms of the Builth Inlier: real patterns and biases

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The Builth Inlier preserves a range of siliciclastic sediments containing remarkably well-preserved echinoderms. Species are often recognisable from relatively poor fossils, and some from disarticulated elements. Intensive collecting shows that diversity has been greatly underestimated; detailed ecological patterns have been overlooked. The oldest

rocks contain only *Iocrinus* species and rare asteroids, from moderately shallow water. The Builth Volcanic Group coincided with immigration of a diverse echinoderm fauna, mostly preserved under exceptional circumstances in a very shallow siliciclastic setting. This fauna is absent from the succeeding fine sediments, which are dominated by cornutes and a widely distributed mitrate, with rare holothurians and cystoids. All these are small, mostly disarticulated, and easily overlooked. The uppermost beds show undescribed crinoids colonising this deeper facies. If the Builth Inlier was typical, echinoderm diversity from similar areas is likely to be underestimated, because of taphonomic and collecting biases. This is a critical problem in attempts to understand the Ordovician Radiation on a regional scale, and the recognition of other diverse faunas could fundamentally change our views of the diversification.

EARTHTIME: a community-based initiative for calibrating geological time

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Many fundamental problems in the geosciences rely on precise and accurate knowledge of geological time. Current geological timescales are based on interpolation between geochronological tie points based on data of variable quality, commonly averaging dates obtained by different techniques, with differing (though often ignored) absolute uncertainties. Consequently, the greatest uncertainty in most analyses of geological and evolutionary rates is the timescale itself. Recent advances in geochronology and correlation methods now allow us to reframe research into the timing and rates of geological and biological processes in deep time, producing a newly calibrated geological timescale with significantly improved accuracy and precision standards commensurate with new and emerging geochronological and chronostratigraphical methodologies. To address these issues the EARTHTIME initiative (<**http://earth-time.org/**>) has been proposed as a new community-based effort to focus attention on the calibration of at least the last 800 million years of earth history. This requires using a unified, multi-chronometer (radio-isotopic and cyclostratigraphic) approach integrated with palaeo-biological and -climatic proxy datasets, allowing earth scientists to address a whole new series of questions that rely on knowledge of precise rates of biological, geological, and climatic change.

A closer examination of biomineralization in the late Precambrian

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Biomineralization has often been considered synonymous with the Cambrian explosion. However, abundant calcareous tubular and goblet shaped fossils (*Cloudina* and *Namacalathus*) in latest Neoproterozoic carbonates of the Nama Group, Namibia, are thought to be the first biomineralized metazoans and are found at a time when the Ediacara biota dominated marine communities. The existence of a low diversity, high abundance hard-bodied fossil assemblage, several million years prior to the Cambrian explosion has significant implications for the origins of biomineralization. Other examples (*e.g.* tufas) have raised the possibility that unusual preservation of a soft-bodied organism can give the appearance of a truly biomineralized organism. A taphonomic, petrographic and geochemical examination of material from the Nama Group, has confirmed *Cloudina* as the

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oldest biomineralized metazoan, which controlled the production of a lightly mineralized aragonite skeleton. In contrast to previous studies, *Namacalathus* is shown to be an organic-walled metazoan, which under certain conditions can become abiogenically permineralized.

New material of the sauropod *Rebbachisaurus* from the Cretaceous (Cenomanian) of Patagonia

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During a 2005 fieldtrip to Aguada Pichanas, a new fossiliferous area in Neuquén province, Argentina, a new specimen of the sauropod *Rebbachisaurus* was collected. It came from the middle part of the Huincul Formation (Middle Cenomanian), Neuquén Subgroup, Neuquén Group. The material includes an almost complete scapulo-coracoid, tibia and fibula. The scapula has a paddle-like scapular blade and a V-shape angle between this and the acromion, characters that diagnose *Rebbachisaurus* both from Patagonia and from North Africa. The tibia and fibula are also similar to those described as *Rebbachisaurus tessonei* from the Candeleros and lower Huincul formations at El Chocón. The new material improves our knowledge of *R. tessonei* because it is better preserved. *R. tessonei* from Aguad Pichanas, which is some 90 km northwest of El Chocón, is stratigraphically younger than the holotype from the latter locality. Therefore *R. tessonei* survived in South America after separation from Africa.

The significance of fossils in phylogenetic inference

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Fossils record extinct morphologies and unique combinations of character states, but their significance for phylogenetic studies has been controversial. Here, we investigate empirically the impact of fossil taxa compared with living taxa when used to reconstruct the most parsimonious cladograms. Two classes of metric are used to quantify their behaviour. The first class assesses the effects of omitting individual taxa prior to analysis, measuring the impact on tree topology and length. The second class uses a bootstrapping approach to quantify the effect of data perturbation on the mobility of individual taxa (leaf stability). In a data set of 50 matrices collected from the literature, there was no significant difference in the behaviour of fossil or extant taxa. We conclude that the fossils included in our sample of published studies are as influential as the living forms.

Ostracoderm swimming

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Stem gnathostomes, traditionally referred to as agnathans or ostracoderms, represent a crucial phase of vertebrate evolution during which many of the characters that are now

taken as typical vertebrate features appeared for the first time. While recent work has gone a long way to clarifying relationships and patterns of character acquisition, understanding of the ecology and biomechanics of these early fishes has lagged behind. Very little is known, for example, about how they swam. Examination of dermal plates from the post-cranial region of the heterostracan *Loricopteraspis dairydinglensis* has allowed us to determine the possible range of articulation between scales and, by extension, the maximum range of movement of the tail during an undulatory swimming cycle. In addition, re-examination of the original material of another heterostracan, *Errivaspis waynensi*, suggests that current reconstructions of the caudal fin need to be revised. Trace fossils of *Undichnia trisculata*, attributed to the cephalaspid *Zenaspis*, have also allowed us to infer the mode of movement of the trace maker across the substrate and the nature of its undulatory cycle. This work will lead to better understanding of the locomotion of early fishes.

A new whip spider (Arachnida: Amblypygi) from the Early Cretaceous Crato Formation of Brazil

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Whip spiders (Amblypygi) are distinctive arachnids with raptorial, prey-catching pedipalps and long, slender legs. Fossils are very rare and are restricted to the Carboniferous Coal Measures of Europe and North America, the Early Cretaceous Crato Formation of Brazil and New World ambers. We describe the second example of a whip spider from the Crato Formation; a relatively large animal with a body of at least 20 mm length and elongate pedipalps, each up to 80 mm long. It represents a new species that differs greatly from the one previously described Crato whip spider, which is much smaller and has only short pedipalps. Although incomplete and preserved ventrally, the new fossil preserves a number of significant details relating to the morphology of the pedipalp and its spination. These strongly suggest we have the oldest record of the extant whip spider family Phrynidae, a group recorded as fossils thus far only from Dominican (Oligocene) and Mexican (Oligocene–Miocene) amber, and which still occurs widely across South and Central America today.

Micro-organisms in the Neoproterozic banded iron formation and their roll in the precipitation of silica and iron: an example from Um Ghames, Egypt

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The Um Ghames area is a part of the basement complex of the Eastern Desert of Egypt. Slightly metamorphosed banded iron formation of Proterozic age is located in this area. From this, several forms of stromatolitic micro-organism remains and biogenic structures, including blue green algae, filamentous micro-organisms such as fungal hyphae and fossilised microbial bacteria, in addition to unidentified carbonaceous matter, are described for the first time. The stromatolites are composed of calcite and quartz with variable amounts of magnetite and stilpnomelane. They include coccoidal and laminated forms. A biotic origin is suggested for the deposition of this banded iron formation. The fine-grained magnetite is considered to be primarily the product of Fe-oxidizing bacteria.

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It is also suggested that iron may adsorb to bacterial cell walls as in modern microbial communities. Several lines of evidence indicate that the chert alternating with Fe-rich bands are produced biogenically through silica secreting micro-organisms, and they are then modified by diagenetic processes. A Neoproterozoic age is suggested for this biota. The role of these micro-organisms in the Precambrian atmosphere and hydrosphere is discussed.

New and 'forgotten' crinoids from the Llandovery (early Silurian) of the British Isles

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The crinoids of the Llandovery (early Silurian) remain poorly known. They are best known from North America (*e.g.* Brassfield Formation, Midwest U.S.A.; Anticosti Island, Canada) and the British Isles. The only comprehensive account of the British Llandovery Crinoidea formed part of the (unpublished) Ph.D. thesis of W.H.C. Ramsbottom. In over 50 years since Ramsbottom's work, many of his thesis taxa have been published and revised, and new species have been described from the Llandovery of the British Isles. However, three of Ramsbottom's species still await formal description. The monobathrid camerate *Hapalocrinus* sp. nov. from the Damery Beds (Telychian Stage, *griestoniensis* Biozone, Tortworth Inlier, Welsh Borderland) is a good species of a genus better known from the Devonian. Another diplobathrid, *Dimerocrinites* sp. nov. (Newlands Formation, Aeronian Stage, *triangulatus* Biozone, Craighead Inlier, southwest Scotland), represents a well known genus from the Much Wenlock Limestone Formation of England. The cladid *Petalocrinus* sp. nov. from the Petalocrinus Limestone (upper Telychian or lower Wenlock Series, Woolhope Inlier, Welsh Borderland) is so common that it forms a mappable horizon. Further, the first author of this report has collected a new, articulated species from the Gasworks Mudstone Formation (Rhuddanian Stage?, Haverfordwest, South Wales), indicating that the British Llandovery still contains new and exciting crinoids that await discovery.

Palaeoecology of a marine impact crater in the Ordovician sea

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The aftermath of marine impacts, in particular the patterns of faunal recovery in and around marine craters, are poorly understood. In the Ordovician Baltoscandian epicontinental sea a bolide impact resulted in the Tvären crater, which is now located in the Stockholm archipelago, Sweden, where two drill cores were recovered in 1991. The alteration of the seafloor topography caused by the impact offered new habitats within the crater and its sheltering rim. For a significant time interval the post-impact succession in the crater had a depth-controlled palaeoecology. Graptolites and chitinozoans are present throughout the succession. Asaphids, mostly *Neoasaphus ludibundus*, are one of the most frequent and persistent faunal members and they became established at an early stage. Small strophomenids and remopleuridiids enter at a later stage, after the crater became less restricted through sediment infilling and a consequent reduction of depth. The rim wall, acting as a reef-like environment, was occupied by a diverse fauna of echinoderms, ostracods, bryozoans, brachiopods and trilobites.

Growth patterns of the Ediacaran genera *Dickinsonia* and *Parvancorina*

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The taxonomic position of the Ediacara biota still remains controversial, even at the kingdom level. Various taxa have been referred to as fungi, lichen, microbes, extinct 'Vendobionta,' and a variety of crown-group animals. Morphometric studies on growth series of Ediacara taxa hold the promise both to refine the species-level taxonomy and to yield broad-scale phylogenetic inferences. Studies of *Dickinsonia* and *Parvancorina* from South Australia suggest that several of the named species are only taphonomic variants; species of both genera exhibit determinate growth and allometric trends. *D. costata*, for example, is not found with more than ~75 segments or longer than ~225 mm, and the rate of new segment addition drops rapidly with increasing length. These patterns support a metazoan rather than a fungal interpretation for these taxa, and also suggest strong differences between them and taxa abundant in the Newfoundland Ediacara biota, which seem to grow by inflation (*Charniodiscus*, *Aspidella*) or fractal addition (rangeomorphs).

Terminal Cretaceous ammonite evolution and extinction in the Tunisian Basin

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Relatively rich macrofaunas found in several Tunisian K/P boundary sections has led to the recognition of their importance in the macrofossil extinction debate. Outcrops in central Tunisia preserve an uninterrupted sequence from Upper Cretaceous to the Lower Paleogene. The present study focussed on ammonite records from the Campanian to Maastrichtian. Both Campanian and Maastrichtian ammonite faunas are dominated by heteromorphs: nostoceratids in the Campanian to Early Maastrichtian and scaphitids in the Late Maastrichtian. The latter time period has the most diverse faunas, with about 21 species. Ammonites continue to occur in the sections until close to the K/P boundary, with only a 1.9 Ma gap between the highest observed occurrence and the boundary. Interpretation of these records in respect of the timing, rate, pattern and causes of the extinction of the ammonites requires consideration of the role of collection failure, taphonomy, sedimentology, palaeoenvironment, and diagenesis, which may obscure the real patterns. The most plausible way of interpreting our data is to place the ammonite extinction level at the K/P boundary, in direct relation with the meteorite impact.

Taking the climate out of CLAMP: dealing with spatial autocorrelation under irregular geographical sampling of dicot leaf floras analysed under the Climate Leaf Analysis Multivariate Program

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The methodology associated with CLAMP (the Climate Leaf Analysis Multivariate Program), a standard method of inferring aspects of past climates from dicot leaf fossil

assemblages, assumes the absence of spatial autocorrelation in the relationship between leaf morphological variables and environmental parameters. In this presentation we provide a meta-analysis of the available CLAMP data, which shows that significant error in palaeoclimate estimation is introduced by irregular geographic sampling in the presence of spatial autocorrelation. This source of error is an instance of more general problems with CLAMP: if it is considered exclusively as a technique for estimation of palaeoclimatic variables, then the use of eigenvector-based exploratory statistical methods for model design is highly questionable, the error analysis insufficiently thorough, and the value of multivariate data unclear. On the other hand, multivariate data are needed to summarize and describe leaf architecture at the community scale for exploratory purposes. CLAMP is the only methodology that provides such data and would be of much greater utility in exploring biological questions like the phylogenetic or ecological distribution of leaf characters if its *a priori* emphasis on climate were eliminated.

Lower Cambrian arthropods from the Mount Cap Formation (Northwest Territories, Canada): what are they, what did they do and why does it matter?

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Exceptionally well-preserved but microscopic fragments of arthropod cuticle have been recovered through hydrofluoric acid maceration of Lower Cambrian shales of the Mount Cap Formation, Northwest Territories, Canada. Organic preservation to a sub-micrometer resolution reveals a diversity of setae and spines in association with fragments of appendages and body wall. New specimens significantly augment the diversity of known material and clarify relationships between disarticulated components. Among the more informative specimens are filter plates of up to 40 plumose setae with precisely interlocking setules, and lobes of delicate appendages bearing marginal ranks of diverse setae. These provide evidence for a complex food-handling apparatus adapted to exploit fine suspended particles, perhaps in the form of phytoplankton cells. Ecological, phylogenetic and taphonomic implications are considered.

Reinvestigation of the Insect Limestone flora

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The diverse fossil flora of the early Oligocene Insect Limestone of the Bembridge Marls Member (Solent Group) exposed on the Isle of Wight provides important evidence of the changing vegetation of Britain under a cooling climate. The first comprehensive review by Reid and Chandler in 1926 focused on the large collection of Joseph Edwin Ely A'Court Smith held at the Natural History Museum, London. The aquatic vegetation is dominated by angiosperms, especially bulrushes (*Typha latifolia*), with ferns such as the recently collected remarkable example of the leatherfern (*Acrostichum lanzaeanum*). Exceptionally fine preservation has also permitted the study of delicate structures, including winged seeds like the rare specimen of *Hooleya* from the walnut family collected earlier this year, and leaves from the surrounding forests. Despite a long history of research and the discovery of over 100 taxa, only about half the vascular plants have been fully described and named. In addition, some of the existing identifications are not currently accepted. Many previously

reported specimens are also preserved in a different lithology that probably came from higher in the sequence. Reinvestigation of museum collections and the collection of new material is leading to a revised floral list for the Insect Limestone.

Nitrogen and carbon isotopes in fossil fish from the Green River Formation, Wyoming

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Animals fractionate nitrogen and organic carbon isotopes during food digestion and preferentially excrete the lighter isotopes. Consequently their body tissues are approximately +3.4‰ more positive in $\delta^{15}N$ than their food and approximately +1‰ more enriched in $\delta^{13}C_{org}$. This simple relationship between consumer and food means that the trophic level of organisms within the same ecosystem can be distinguished on the basis of their isotopic signature. Various authors have successfully applied this technique to modelling trophic structure in present day and Neogene vertebrate ecosystems. However, in the present study nitrogen and organic carbon isotopic ratios are being used to investigate the community structure and palaeoenvironmental changes within a much older fossil ecosystem. The Early Eocene fish of Fossil Lake in the Green River Formation of SW Wyoming are part of an exceptionally well-preserved diverse aquatic community and preliminary analyses have yielded isotopic signatures comparable to those of modern fish. Throughout Fossil Lake, specimens have now been collected from a succession of mass mortality layers to enable further isotopic study of various fish assemblages as well as an investigation of the background chemostratigraphy. These isotopic ratios will then be used to infer relationships between organisms and changes in their habitat through time.

New somasteroids and ophiuroids from the Lower Ordovician of the Montagne Noire (southern France) and their significance to the early evolution of the asterozoans

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The Montagne Noire (Herault, Languedoc, France) yields one of the best assemblages of Lower Ordovician asterozoans, with numerous exceptionally preserved specimens. These were monographed by Spencer (1951) and recently described by Shackleton (2005) as part of a phylogeny of the earliest asterozoans. However, a definitive analysis of all the asterozoans from the Lower Ordovician of the Montagne Noire has yet to be carried out. The current study involves the description of all the early asterozoan communities of the Montagne Noire in the light of new specimens. This includes the re-analysis of material from the Saint-Chinian Formation (upper Tremadoc–Arenig) and importantly the introduction of previously unidentified specimens from the Landeyran Formation (middle Arenig). The study has considerably increased knowledge of the taxonomic diversity of the Asterozoa, allowing a greater understanding of their early morphological evolution. These new data have implications for the phylogeny of asteroids and ophiuroids in the Upper Ordovician of Great Britain, Ireland and Bohemia.

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The range of morphology in laboratory-simulated dinosaur tracks due to variation in sediment consistency

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Understanding the formation and preservation of a vertebrate track is fundamental to its correct interpretation. Laboratory-controlled simulations have been undertaken to investigate dinosaur footprint formation and preservation in medium-grained sands of several different moisture contents, ranging from dry to fully saturated. A reconstructed model foot of *Hypsilophodon foxii* was impacted into the substrates using a vertical trajectory with accurately controlled force of the foot's impact. Qualitative and quantitative analyses have shown that a range of footprint sizes and shapes have been produced using one particular indenter, depending upon the substrate consistency. The range of footprint forms produced shows that accurate identification of the trackmaker is complex and problematic. Therefore trackmaker assignments should not form part of ichnotaxonomic nomenclature. The apparent range of footprint dimensions also indicates that a footprint supplies misleading values of foot size, which could produce error in estimates of trackmaker body size (hip-height), and therefore gait and speed.

The cirripede *Pycnolepas* (Brachylepadomorpha) from the Albian of Amur, Russia

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Ten species of *Pycnolepas* of Late Jurassic to mid-Cenozoic age are now considered valid: *P. articulata* (Aptian, Antarctica), *P. bruennichi* (Paleocene, Denmark, Netherlands), *P. fimbriata* (Tithonian, Czech Republic), *P. ignabergensis* (Campanian, Sweden), *P. landenica* (Paleocene, Belgium), *P. paronai* (Miocene, Italy), *P. rigida* (Albian-Cenomanian, UK and France) and *P. tithonica* (Tithonian, Czech Republic). Two other species are here questionably referred to the genus: *Pycnolepas scalaris* (Cenomanian, UK) and *Pycnolepas orientalis* (Cretaceous, Russia). The genus thus is essentially European in distribution, with two notable exceptions, one of them being *P. articulata* from the ?lower Aptian of Antarctica. The other is represented by three isolated scuta from the Albian of Amur (Far East Russia), seemingly closely allied to *P. rigida*. In the absence of other valves, these are for now best left in open nomenclature. The distribution pattern of *Pycnolepas* suggests a rapid areal expansion of early members and a failure to radiate outside Europe subsequently.

Palaeoecology, biostratigraphy and taxonomy based on Ordovician trilobites from Russia

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In the St. Petersburg area (Russia), the middle Arenig to lower Llanvirn carbonate succession spans the upper part of the Billingen, Volkhov, and Kunda stages, of which the present study addresses the Volkhov and upper part of the Billingen stages. Bed-by-bed

sampling of two Russian sections has resulted in a large amount of trilobite material, thus facilitating a biofacies investigation and the recognition of biozones. The aim of the study is, additionally, to undertake a taxonomic revision of the stratigraphically important megistaspids, which are represented by several hundred specimens belonging to *Megistaspis (Megistaspis)*, *M.* (*Paramegistaspis)*, *M.* (*Rhinoferus)* and *M.* (*Megistaspidella)*. The chronostratigraphic zonation of the Billingen and Volkhov stages of Scandinavia is based on megistaspids, but the eastern Baltic faunas are rather different and provide only few ties for correlation across Baltoscandia. However, a very detailed correlation can be undertaken locally. Statistical investigations and variation in the abundance patterns of genera and subgenera indicate that the following four depth-dependent biofacies can be recognized: 1) *Megalaspides – M. (Paramegistaspis)*, *M. (Megistaspis)*; 2) *Niobella*, *M.(Rhinoferus)*; 3) *Ptychopyge – Onchometopus*; and 4) *Asaphus – M. (Megistaspidella)*.

Morphometric analysis of the conodont skeleton: investigating evolutionary trends during species transitions

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Conodonts possess an exceptionally good fossil record and so are ideally suited for detailed examination of evolutionary rates and trends. *Pterospathodus* has been observed to show gradual and directed morphological evolution through its temporal range and the genus has been divided into a series of species based on these changes. The ranges of these species have further been used to establish Silurian biozones. Particularly notable are trends in size increase and the development of lateral processes through time. Samples taken through the Viki borehole on the island of Saaremaa, Estonia are used to conduct the first quantitative analysis of morphological change within *Pterospathodus*. The analysis is carried out using new morphometric protocols developed for quantifying morphological change within conodonts. This has allowed rigorous examination of the qualitative observations of morphological change within *Pterospathodus*. The patterns of morphological variation revealed by the analysis have potential for refining Silurian biostratigraphy and species discrimination within *Pterospathodus*, whilst also providing a wider insight into the evolutionary patterns occurring during transitions between species.

The Santonian Stage in the Egyptian Cretaceous: macrofaunal, biostratigraphical and palaeobiogeographical analyses

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In Egypt, Santonian rocks are widely distributed, but definition of the Santonian Stage boundaries is a matter of controversy. The aim is to utilize macrofossil groups to provide a refined definition of the Santonian Stage. For this purpose the Cretaceous sections exposed at the Nile Valley, Eastern Desert, and Sinai were logged and their macrofossils collected. The measured successions are composed mainly of mixed carbonate and siliciclastic sediments, overlain by phosphatic and/or chalky beds of Campanian age and underlain by clastic beds of Coniacian age. Oysters, ammonites and echinoids occur in several horizons throughout, forming well defined and traceable biostratigraphic units. The Coniacian/Santonian boundary is delineated by the FOD of the basal Santonian *Texanites*

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texanus and/or *Tissotia semmamensis*, and the LOD of the Late Coniacian *Subtissotia africana* and other Coniacian ammonites. It coincides also with the FODs of *Pycnodonte proboscideum*, and both *Petalobrissus waltheri* and *Hemiaster fourneli*. The Santonian/Campanian boundary is located at the contact between the Santonian *Plicatula ferryi / Crassostrea roachensis* Zone and the Campanian *Plicatula pausicostata / Curvostrea heinzi* Zone. The litho- and biofacies framework indicates deposition in a shallow marine environment, on a littoral to infrasublittoral setting during a highly oscillating sea with several transgressive and regressive episodes. The Santonian succession in Egypt is bounded by two unconformity surfaces coeval with the Coniacian–Santonian transition and the Coniacian–Santonian–Campanian boundary. Palaeobiogeographic affinities and inter-regional correlation are also discussed.

Towards an integrated biostratigraphy for the Cretaceous of Greenland

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An integrated biostratigraphy is presented in chart format for the Cretaceous of Greenland, based on published data and supplemented by new material collected by CASP during 16 field seasons in eastern Greenland. About 45 successive ammonite faunas are recognised and are compared with the standard zonal successions for NW Europe and for the Western Interior of North America. Supporting macrofaunal zones and assemblages include those of belemnites and bivalves (especially inoceramids and buchiids). Palynological studies make particular use of the dinoflagellate succession, and micropalaeontological studies mainly the foraminifera and to a lesser extent the radiolarians. The different groups have varying potential through the Cretaceous and the use of an integrated biostratigraphy may allow several criteria to be used for dating individual horizons. Many improvements have been made to the time allocations in the individual columns. Thus the macrofauna, of prime use in the field, helps to recalibrate the microbiota successions, and conversely the microbiota improves the biostratigraphy of the ammonites and other macrofauna. The resulting revised biostratigraphy has important application to the hydrocarbon exploration of offshore Greenland and adjacent areas such as the northern North Atlantic.

An edrioasteroid-, machaeridian-, hyolithid-, and mollusc-bearing Early Emsian fossil lagerstätte in the Tafilalt (Devonian, Morocco)

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Early Emsian claystones and marls in the Tafilalt yielded two rich faunules comprising more than 1,100 specimens belonging to approximately 60 taxa. The older faunule is

remarkable because of the abundance of almost complete pyrgocystid edrioasteroids, complete asteropygid trilobites, paired acanthodian fin spines, hyoliths with opercula, and the presence of articulated machaeridians. Additionally, it yielded a diverse, largely infaunal bivalve assemblage. The younger faunule is marked by the appearance of the first ammonoids (represented by seven genera). These are accompanied predominantly by epibyssate bivalves, and by other cephalopods and gastropods. From the composition of both assemblages and the sedimentary environment it is concluded that normal oxic conditions in a moderate water depth prevailed and the sea floor was within the photic zone but below storm wave base. The rich benthic community indicates a soft bottom environment. The change in composition between the two faunules probably indicates a decrease in oxygen content in the sediment.

Quaternary nannofossil biostratigraphy and diachrony; correlation to oxygen isotope events

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Quaternary nannofossils have been carefully and intensively studied over the past thirty years resulting in a zonation scheme that is remarkable in at least three ways. First, it has very fine resolution, around 200,000 years. Second, the zonation appears to be very reliable throughout low latitudes. This is indicated both by consistency of sequence of events and by its correlation with oxygen isotopes and magnetostratigraphy. Third, it is based on rather subtle events; there is no great change in nannofloras during the Pleistocene. As part of a project on Quaternary nannofossils we have reviewed the literature to assess the degree of diachrony shown by the events, and we provide a new synthesis of correlations with marine isotope stages for biostratigraphers and Quaternary researchers. The objectives are first to provide an improved correlation of events with oxygen isotope stages and second to investigate patterns of diachrony in events and so constrain the possible causes of diachrony. Our analysis is based on all available good quality correlations of Quaternary nannofossil events with oxygen isotope stratigraphy.

Patterns of the phylogenetic taxonomy of Palaeozoic ammonoids

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More than 4,000 species, approximately 700 genera and more than 100 families of Palaeozoic ammonoids can be counted today; these taxonomic units are increasingly used for the investigation of taxonomic rates. The underlying assumption of this practice – that Linnean classification is an adequate representation of change of morphological units – has been tested in this study. A family of Palaeozoic ammonoids is estimated to comprise a mean of six genera and 32 species, and a genus a mean of six species. The variability between different orders is very low. Since the erection of the first genera in the 19th century this relationship of taxa to subtaxa has remained nearly the same. The differences of scaling diversity and its dimensions between the orders of Palaeozoic ammoinoids are small. As in the 10th edition of the *Systema Naturae* of Linneaus, an exponential frequency distribution of numbers of subtaxa within taxa is observed. The classification of taxa with roughly ten subtaxa and an exponential subtaxon frequency

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distribution is considered to be a consequence of the artificial principle of economic subdivision of taxa. The low variance of scaling diversity and the similar frequency pattern of subtaxa within taxa justify the comparison of taxonomic rates at each rank.

Comparative study of two marine arthropod telsons: *Burgessia* (510 Ma, Burgess Shale Biota, British Columbia) and *Limulus* (Recent, Atlantic Ocean)

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During an examination of the Burgess Shale collection at the National Museum of Natural History, Washington D.C., well-preserved specimens of *Burgessia* were noted to exhibit two modes of telson: 1) a straight, stiff caudal spine; and 2) a sinuous, flexible whip-like tail. Mode 1) is analogous to the telson of living *Limulus*. During an actualistic taphonomic experiment, the *Limulus* telson became slimy and flexible after detachment of the specimen's appendages. *Burgessia* does not follow the decay sequence of *Limulus*, because in *Burgessia*, stiff and flexible telson preservation both occur with appendages attached. Previous investigations suggested that the exceptional preservation of *Burgessia* and other taxa in the Burgess Shale Biota were largely due to rapid burial, and so these animals suffered minimal open-air necrolysis. *Burgessia* is mostly preserved with a curved telson, which suggests some degree of telson flexibility when the animal was alive, or before death. Living *Limulus* moves its telson in aid of swimming and righting activities. One possible function for *Burgessia* stiffening its telson could be to speed up the recovery motion from the overturned posture.

Rates of morphological evolution and 'living fossils'

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Our understanding of major evolutionary events – be they adaptive radiations or the origin of new clades – is underpinned by our knowledge of the rates involved. In a seminal study Westoll used a character-taxa matrix to show that during the Mid- to Late Devonian lungfish underwent rapid rates of change that tail off markedly post-Palaeozoic – this representing a text book example of evolution in a 'living fossil'. However, Westoll's analysis was non-cladistic (assuming a single stratigraphically ordered ancestor–descendent lineage), many additional taxa are now known, and dating has been refined. Here the cladistic method is applied to a 'total evidence' matrix of 88 dipnoan genera and 250 morphological characters. As evolution occurs along the branches (and not across the tips) of the tree, internal (rather than terminal) nodes were used. Although the results broadly support Westoll's original conclusions, the same pattern occurs in all additional groups tested (including vertebrates and invertebrates, both 'living fossil' and non 'living fossil'). This near-ubiquitous feature of evolution is consistent with Simpson's theory of 'quantum evolution' and explains why new groups typically appear abruptly in the fossil record and why adding ever younger taxa to cladistic matrices only increases homoplasy. Future research should concentrate on finding a biological explanation for this phenomenon.

New finds of Cambrian parasitic pentastomids and the remaining questions about their affinities and evolutionary fate

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The relationships of pentastomids (tongueworms) are still controversial. One hypothesis, based on molecular and sperm data, suggests affinities with branchiuran eucrustaceans. Another, based on morphology, palaeontology, ontogeny and neuro-anatomy, regards pentastomids as stem arthropods that deviated before the achievement of a well-sclerotized and jointed cuticle (Arthropoda *s.s.* level). A few specimens of late Middle Cambrian to early Ordovician larval pentastomids described between 1989 and 1994 from 'Orsten'-type lagerstätten in Sweden and Canada demonstrated (a) striking morphological conservatism with present-day forms, (b) already a high adaptation to parasitism, and c) high diversification, particularly in terms of attachment devices, already requiring by that time a similarly diversified host group. A single specimen of a new species from Västergötland, Sweden and 60 specimens of different sizes newly collected from the same area, form the basis of our current re-investigation. Major topics are the ontogeny, the taxonomic status of established taxa, and the affinities and possible co-evolution of pentastomids with the craniote/vertebrate clade. First results suggest at least three larval stages that elongate without adding segments. Our re-investigation also helps test our working hypothesis that pentastomids were ectoparasites initially and never became endoparasitic, thus, having retained many plesiomorphic morphological characteristics.

'*Ediacaria booleyi*': a Phanerozoic 'wolf' in Ediacaran clothing

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The report, over a decade ago, of Ediacaran-type fossils preserved as semi-discoidal external casts on the soles of siltstone beds in the Booley Bay Formation of County Wexford, Ireland, was unusual in several respects. Named *Ediacaria booleyi*, these were apparently transported and emplaced by turbidity currents. More significantly, the organism was reconstructed as a discoidal form with a rigid exterior, and was deemed Upper Cambrian in age. A reinvestigation of the site has produced information incompatible with the original reconstruction. The strata in which the fossils are found are better interpreted as contourites, with a microbially bound seafloor. Analogue experiments with density compensated replicas and the presence of cross-laminations infilling moulds of actual fossil specimens have also highlighted problems with the taphonomic reconstruction. An alternative suggestion is that the structures were generated by benthic (possibly sessile) organisms, and that what is preserved represents only a portion of the overall morphology. Some specimens resemble 'swing-marks'. Interestingly, creatures living attached to microbially bound substrates in contour-current environments are well known from the Ediacaran Mistaken Point and Trepassey formations of Newfoundland. Re-emergence of this early Upper Ediacaran style ecology in the Booley Bay Formation has important implications for early Palaeozoic evolution.

Palaeoclimatological significance of early Cretaceous palynoflora in NE Africa

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Early Cretaceous palynofloras from northeast Africa bear general resemblance to their North Gondwanan counterparts. There were characteristic palynofloral provinces that extended equatorially from South America to as far as Papua New Guinea. In northernmost areas (the north Egyptian coastal plains) the palynoflora reveals a dominance of humidity-loving spores (*e.g.* ferns) and rare xerophytes (ephedroids, Cheirolepidiaceae). Fern spores such as *Deltoidospora* and *Cyathidites* are produced by several families such as Cyatheaceae and Dicksoniaceae, which are today inhabitants of warm-humid climates. Hygrophilous plants thrived therefore at the expense of xerophytes; the latter occur rarely and are interpreted to have been adapted to humid conditions. In southern Egypt a warm-arid climate during, at least, the Aptian is inferred from the increasing percentages of xerophytes, associated with ferns. Therefore the northernmost areas of ancient Gondwana had experienced fairly humid palaeoclimates during the nearly Cretaceous, while the southern regions are less humid. These conclusions, which are based on closely-spaced borehole samples, in addition to published information, exclude the occurrence of dry periods in the northernmost areas of NE Africa. These interpretations are consistent with those documented from South America (Colombia).

Disarming dromaeosaurs

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The prominent recurved, hypertrophied claw on digit II of dromaeosaur dinosaur feet has often been interpreted as a weapon adapted to perform a disembowelling function. In order to test the effectiveness of the disembowelling hypotheses, a hydraulic dromaeosaurid hind limb was constructed and tested against the soft tissue of a slaughtered pig and crocodile (farmed). Experimental results indicate that the 'killing claw' did not function as a slashing or cutting device, but as a meat-hook-like 'crampon'. The geometry of dromaeosaur claws caused the claw to rotate as it was pushed into prey, resulting in a maximum depth of trauma equal to the radius of the inside arch of the claw. The recurved claws of dromaeosaur dinosaurs were able to create an instant, live, climbing wall from the flanks of prey, allowing their serrated recurved teeth to inflict killing bites. Whilst the claw attachment would have been painful to prey, it was unlikely to have been life-threatening. An understanding of the functional morphology of recurved claws provides new insight into the ecology of dromaeosaurs and assists in the interpretation of rare dinosaur predator-prey associations.

Piecing together Macbride's cycadeoid collection at the University of Iowa

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The collections of the University of Iowa Museum of Natural History contain some of the earliest collected petrified cycadeoids in North America, from the Early Cretaceous Dakota Sandstone of the Black Hills, South Dakota. The site was a famous locality during the pioneering era of North American palaeontology, important enough that it was designated Fossil Cycad National Monument in 1922. By 1930, however, poor stewardship had resulted in near complete denudation through unregulated collection. The Iowa collection was made by Thomas Huston Macbride in 1893. Two specimens were designated as holotypes: of *Cycadeoidea dacotensis* (Macbride), and *Cycadeoidea mcbridei* (both Ward 1899). Following the early descriptions (the last significant publication was by G. R. Wieland in 1916), the material was unavailable for research and the collection was partially dispersed. Specimens were sent as gifts to other museums and both holotypes were sectioned and the pieces loaned to several institutions. Over time, the status of the holotype material has largely been unrecognized. Efforts are in progress to document the collection, to locate and record the dispersed specimens, and to retrieve and piece together (literally) the holotype material. The result should facilitate modern study of an important but historically unavailable early palaeobotanical type collection.

Finite element modelling of the mandible of the South American dinosaur *Carnotaurus sastrei* (Theropoda: Abelisauridae)

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Computerised tomography scanning was used to generate the first three-dimensional mandible reconstruction of the South American carnivorous dinosaur *Carnotaurus sastrei*. This non-invasive technique provides a suitable foundation for finite element analysis of biological structures such as the mandible. The model of the mandible was loaded in order to simulate six different biting situations (ventrally directed static bite applied at the anterior, central, and posterior teeth; with and without axial traction of a hypothetical prey). The mechanical strength of the mandible was also studied through an estimation of the maximum bite force capable to withstand failure stress. The bilateral muscle-driven bite force of *Carnotaurus* (3341N; estimated at the posteriormost teeth) would have been relatively weak in comparison with the one corresponding to living carnivores. Principal stress magnitudes varied predictably for the studied loading conditions, with peak stresses found at the intramandibular joint. When the effects of adductor muscle forces and reaction condylar forces are removed from the model, the maximum force withstood by the mandible may be up to 6.1 times higher than the estimated muscle-driven bite force. This suggests a mandibular design in *Carnotaurus* that is not particularly strong.

Walking and jumping with apterygote insects

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Abundant arthropod walking and jumping traces from the Lower Permian Robledo Mountains Formation of southern New Mexico provide direct evidence of the locomotory techniques of monurans, an extinct group of archaeognathan apterygote insects. The jumping traces are referred to the ichnotaxon *Tonganoxichnus robledoensis*, and demonstrate that forward progression via a linear succession of jumps of several times body length was a common method of monuran locomotion. The jumping behaviour of monurans is compared to that of the extant machilid archaeognathan *Petrobius*, which generally employs an unusual jumping gait for normal, directed, locomotion, although these

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jumps are typically only one body length. *Petrobius* also employs an essentially random escape jump of several times its body length. All of the *T. robledoensis* specimens analysed occur in linear successions, and there is no evidence of random jumps. Trackways referred to *Stiaria* are found following on from landing traces and demonstrate very slow and stable gaits, whereas those preceding jumping traces demonstrate faster gaits. Archaeognathans are the most primitive group of true insects, and the presence of these similar types of jumping behaviours in monurans and machilids suggests that such behaviours were a primitive method of insect locomotion.

Angel sharks (Squatiniformes) in the Late Jurassic of Europe

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Two valid species of angel sharks, *Squatina acanthoderma* and *S. alifera*, are represented in the Late Jurassic Plattenkalks of Germany (Solnhofen and Nusplingen). Their teeth and scales were studied on articulated specimens and provide good arguments for the erection of a separate genus of Jurassic angel sharks. The Late Jurassic cliff section near Boulogne-sur-Mer (France) and the Coral Rag of Hirschkopf (Germany) yielded abundant microvertebrate assemblages that contained about 500 isolated teeth and scales of two types of angel sharks. These two morphotypes are considered to belong to *S. alifera* and *S.? frequens* described from the Kimmeridgian of Dorset. Angel sharks are living fossils. According to their morphology, the biology of Late Jurassic angel sharks was not strikingly different to that of extant species, though little is known about the latter. Their dorsoventrally flattened ray-shaped body is an adaptation to a life on the sandy sea floors of warm and temperate oceans where they hide, and seek prey. The morphology of their sharply cusped teeth with lateral cutting edges makes them fierce predators with a diet of small fish and invertebrates.

Eugeneodontoids (primitive elasmobranchs) from the Triassic Sulphur Mountain Formation of western Canada

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An assemblage of eugeneodontoids is reported from the Sulphur Mountain Formation of western Canada (Alberta and British Columbia). The 27 specimens come from the Vega-Phroso Siltstone Member and therefore represent the first sample of eugeneodontoids of (Early) Triassic age. The remains include an almost completely 3-dimensionally preserved skull with dentition, and several other cranial and dental remains of caseodontids. The majority of the cranial material is identifiable as *Caseodus* aff. *eatoni*, Caseodontidae gen. et sp. indet. and *Fadenia* sp., whereas two fragmentarily preserved tooth whorls are best placed in a new species of *Fadenia* and a new genus of caseodontid. Individual tooth variation in eugeneodontoids and its bearing on taxonomy are critically assessed. Postcranial material predominantly complements previous reports on the Permian genus *Fadenia*. Tooth histology of eugeneodontids is osteodont with a distinctly restricted apical band of orthodentine. The thick tooth enameloid is composed of cross-bundled bands of slender crystals in irregular but well-defined orientation.

The vertebrate biostratigraphy of the Middle Devonian of the Orcadian Basin, northern Scotland

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Detailed fieldwork over 15 years, the last two in collaboration with BGS Edinburgh, on the Middle Devonian fossil fish from the Caithness area of the lacustrine Orcadian Basin has produced a new biostratigraphy, refined from that first advocated by Traquair in the late 1800s. The osteolepids and tristichopterids provide the most useful biostratigraphical markers, supported by coccosteids and dipnoans. The first fish to appear after the barren Lower and lower Middle Devonian was the osteolepid *Thursius macrolepidotus*. In the osteolepid sequence, it was replaced by *Osteolepis macrolepidotus* and *Gyroptychius agassizi* in the famous Achanarras Fish Bed. Above this, these two forms were replaced by *Gyroptychius milleri*. In younger horizons, *Thursius pholidotus* first occurs just below the appearance, but then complete mass mortality, of *Osteolepis panderi*. More research is required to determine the end range of *G. milleri*, as it apparently continues after *T. pholidotus* first appears. In the final infilling phase of the lake, *T. pholidotus* is replaced by *Tristichopterus alatus*. Limited field studies elsewhere in the basin and re-examination of Museum collections shows that this fish biostratigraphy probably applies across the whole basin, and further work is in progress to confirm this.

Clay-organic interactions in graptolitic mudrocks

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Graptolites are commonly preserved as organic compressions or pyrite steinkerns encased by clay minerals of a different composition to those in the host rock. These were traditionally interpreted as forming due to tectonism in strain shadows. However, the present study is inconsistent with such a model, and we propose that such preservation is a consequence of temperature dependent clay-organic interactions, possibly due to volatile phases being driven off with maturation. The following observations are critical: 1) non-aligned clays encase graptolites and other organic compression fossils in facies where there is no evidence of strain; 2) in localities where graptolites co-exist with shelly fossils, clays encase only the graptolites; 3) there is negligible difference in the amount of clay encasing individual fossils where both pyritised and flattened graptolites coexist; 4) clays encase even the most membranous graptolite tissues; 5) graptolites preserved in diagenetic grade facies do not appear to be encased by clays, unlike those in epizone grade facies; 6) several phases of clays can be identified where graptolites are preserved in anchizone grade facies.

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Palaeobiogeographic analysis of Tropical Domain conodont faunas from the Lower Ordovician (Ibexian) of Laurentia

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Conodonts in the Late Cambrian are cosmopolitan, but provincialism characterises Tremadocian to early Wenlock faunas. The traditional view of this provincialism envisaged two provinces: the high latitude, cold water North Atlantic Province (NAP) and the low latitude, warm water North American Midcontinent Province (NAMP). Although more recent analyses have refined this model, it is still assumed that NAMP conodonts faunas are uniform across all but the deep-water fringes of Laurentia. To test this assumption, the present study targets a single biozone from the upper Ibexian (*communis* Biozone), which lies at or just above the maximum flooding surface of the late Early Ordovician (EO_2) megacycle. The dataset comprises taxonomically synoptic conodont faunas from a number of well-documented localities across North America, together with western Newfoundland, Greenland, and Scotland. The faunas are from similar shallow shelf carbonate lithofacies, although one deep-water assemblage is also included. The multivariate analysis reveals that faunas from Scotland, western Newfoundland and Greenland consistently cluster together, suggesting the existence of a subprovince with significant endemism in NE Laurentia. There is no known physical barrier that could have induced biogeographic differentiation across Laurentia at this time, and latitude is thus likely to be the primary control.

Ecostratigraphical interpretation of lower Middle Ordovician (Kundan) argillaceous limestones from the Eastern Baltic based on brachiopods

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Detailed bed-by-bed sampling of mainly rhynchonelliformean brachiopods from argillaceous limestone beds at various localities in northwest Russia and northern Estonia has yielded a diverse, though not particularly abundant fauna. All the localities are aligned along a 400 km profile with increasing palaeowater depth towards the east. The brachiopod distribution data were processed using detrended correspondence analysis in PAST to partition any depth-related biofacies. This statistical appraisal indicated at least four different associations; a shallow-water *Lycophoria* association, an intermediate depth *Gonambonites* association and two deeper-water associations which are substrate dependent: the soft substrate, deeper water *O. callactis* association and the hard bottom, deeper-water *Orthambonites* association. Furthermore, the marl beds at the main locality, Putilovo Quarry, revealed a unique soft bottom fauna. The biofacies associations were used to interpret bed-by-bed ecostratigraphical divisions along the profile. These interpretations clearly indicate repeated transgressions and regressions that are divided into system tracts up through the sampled sections. These in turn were used to develop a relative sea-level curve for the greater part of the Kundan Stage in the East Baltic area.

Cretaceous (Late Campanian) trace fossils from Nuussuaq, west Greenland: responses to clastic surges in a dysoxic basin

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The Itilli formation (Upper Campanian) at Annertuneq, northern Nuussuaq, is characterised by marine, dark grey to black, commonly dysoxoic, mudstones with thin, intercalated sandstone beds. The marine succession was deposited in a restricted basin developed along parts of the west Greenland margin, associated with steep submarine slopes. The background sediments are largely barren of invertebrate fossils, except for a few horizons containing diagenetic concretions. The sparse invertebrate fauna contains ammonites, bivalves, gastropods and echinoderms and is generally dispersed throughout the more fossiliferous parts of the succession. Marked, however, is the abundant and locally diverse trace fossil fauna associated with surges of siliciclastic material into the basin. The ichnofauna is characterised by both horizontal and subhorizontal burrows, some of which are related to *Planolites*, while subvertical escape traces (fugichnia) occur more sporadically. The trace fossil fauna is associated with the relatively sudden, but periodic, emplacement of coarser grained sediments, possibly surge deposits, onto the seafloor. The rhythmic occurrence of the sandstones and their ichnofauna, has helped develop an event stratigraphy for this part of the basin.

Palaeophotosymbiosis – the key to understanding the life habit of hippocardioid Rostroconchia (Mollusca)

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Previous research on hippocardioid rostroconchs has focussed mostly on the peculiar morphology of these animals as well as on their anatomical orientation. Concerning their life habits, most members of the group were thought to have been epibenthonic or semi-endobenthonic. Unfortunately, the very few attempts to unravel their former life position were either based on a quite restricted part of the known taxa or applied generally to all members of the class. Our current re-survey of conocardioid and hippocardioid rostroconchs and the classification of the superfamily Hippocardioidea have led to a more detailed knowledge of the taxonomic diversity of the group. This advance combined with conclusions drawn from recent research on shell microstructure reveal the errors published as traditional text-book theories. Our presentation highlights the weaknesses of previous ideas on hippocardioid life position and feeding strategies. We present an alternative life habit for hippocardioid rostroconchs and provide conclusive proof that palaeophotosymbiosis was vital for survival.

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Palaeoecological reconstruction of St. Bride's Island, based on the fossils from Pant 4 fissure

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After the Rheatic marine transgression, a small part of modern day Glamorgan, South Wales, was isolated by sea and formed a small island distant from the mainland. It lay at a palaeolatitude of about 15° north, and the climate would have been subtropical. It was composed of a Carboniferous Limestone plateau and has yielded numerous Lower Jurassic fissure fills, preserving the remains of animals and plants. Many of the fissures have a fauna consisting of only three members: the pleurodont lepidosaur *Gephyrosaurus bridensis* and the mammals *Morganucodon watsoni* and *Kuehneotherium praecursoris*. The range of vertebrates from Pant 4 fissure is more extensive, consisting of the sphenodontian *Clevosaurus convallis,* an *incertae sedis* sphenodontian, the cynodont *Oligokyphus* and new mammals, including a larger morganucodontid. Isolated teeth are provisionally assigned to theropod dinosaurs and/or a sphenosuchid crocodylomorph and some possibly belonged to rhamphorhynchid pterosaurs. The small mammals, *Gephyrosaurus* and the sphenodontians would have been insectivorous, while *Oligokyphus* was herbivorous. The larger morganucodontid, along with the largest theropods, might have been carnivorous. Club mosses, ferns and cycads were present, but the dominant plant was the conifer *Hirmeriella muensteri*, a medium-sized tree, growing in patches across the island.

The mutability of the earliest paired appendages

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The Osteostraci (cephalaspids) are a specialised and intriguing group of agnathan fishes, currently thought to be the sister taxon of the jawed vertebrates. Although lacking jaws, the Osteostraci possess a number of gnathostome apomorphies, including paired appendages, which some authors argue to be homologous to the paired appendages of gnathostomes. Phylogenetic analysis of the intra-relationships of this group can help us answer questions about this proposed homology. Whilst previous authors have investigated such intra-relationships, in-depth systematic studies utilising modern cladogram construction techniques have yet to be conducted on the group. Such studies will also shed light on the debate as to whether paired appendages evolved once and were subject to reversions or evolved many times within and outside of the group. The Thyestidiens are a key monophyletic group containing both forms with paired appendages and without. They have long courted controversy regarding their position as either the most derived or most basal osteostracans. Here, a new phylogeny of the thyestidiens is presented based on a study of European material. This phylogeny provides the basis for an analysis of the interrelationships of the group and to tracing the evolution of key vertebrate innovations, crucially including paired appendages.

Reinvestigating Halle's pteridosperms

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In the 101 years since the first pteridosperms (seed ferns) were recognised a large number of taxa have been assigned to the group. However only a handful show seeds in organic attachment to fern-like foliage – the essential basis on which the pteridosperm concept was established. Reinvestigation of Halle's Permian pteridosperms from China has focussed on validating Halle's observations and interpretations, determining mode of seed attachment, and undertaking systematic and taxonomic revisions of each species. *Emplectopteris triangularis*, *Sphenopteris tenuis* and *Alethopteris norinii* are confirmed as pteridosperms; the first two show seeds attached to the leaf lamina while the third has attachment to the rachis. *Pecopteris wongii* is considered of uncertain affinity and Halle's interpretation of seed attachment remains unsubstantiated. Results are also presented from exhaustive searches though the Halle Collection leading to the discovery of two additional pteridosperms. Collectively these show that pteridosperms remained important components of Permian as well as Carboniferous floras globally, and provide important information on the morphology and organisation of pteridospermalean plants.

A new investigation into the Carboniferous lungfish C*tenodus*

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Ctenodus is one of four genera of lungfishes from the Carboniferous of the UK; it was the subject of intense debate during the 19th century, both in its affiliation with other osteichthyan groups, and as to the numbers of valid species. Classically defined on having tooth plates with a large number of parallel ridges, most species of *Ctenodus* were described on the basis of these plates, and although the skull roof of *Ctenodus* is well defined, associations of skull roof and tooth plates are uncommon. The question of the validity of a number of the 20 available species is raised, and new ways sought to use tooth plates in species designation. The current study also investigates the distribution of *Ctenodus* throughout the Carboniferous and questions whether morphological variation is a result of taxonomic difference, or is correlated with stratigraphy and palaeoecology. Initial studies suggest that the latter could explain morphological variation within the Upper Carboniferous, but that there is a real separation between Upper and Lower Carboniferous species. An overview and systematic descriptions are presented of the currently valid species of *Ctenodus*, based on old and also some new material. The phylogenetic position of *Ctenodus* within the post-Carboniferous lungfishes is considered, and a review of localities and their possible significance discussed.

Phytoliths (plant opal) from the New Zealand Subantarctic

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Phytoliths are microscopic particles of opaline silica produced by many plants. When preserved they provide valuable palaeoecological information and record local plant growth. They survive oxidation and are generally robust, but have rarely been studied from the fossil record. This study tests how accurately dispersed phytoliths in soils from

subantarctic Campbell Island, south of New Zealand, reflect the overlying extant vegetation cover. The study is important for assessing the limitations of interpreting the past using modern analogues and makes a significant contribution to knowledge of high latitude modern phytolith production and preservation. Canopy surveys, plant collections and soil sampling were completed for six 16m^2 plots within different vegetation communities on Campbell Island. Twenty-five taxa were recorded of which eleven (all monocotyledons) produced phytoliths. Soil assemblages comprise predominantly monocotyledon forms, with dicotyledon forms rare or absent. In contrast, the Neogene assemblages from the subantarctic contain both monocotyledon and dicotyledon phytoliths indicating a wetland palaeoenvironment (similar to the modern) with a shrub/tree component, but rare grasses (dissimilar to the modern).

The braincase of *Gyroptychius milleri* Jarvik

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The osteolepidid fishes of the Middle Devonian of Scotland are some of the earliest known members of the tetrapod stem group. Much of the material of these fishes is highly dorso-ventrally compressed, providing information on the external dermal bones only. However, there are some well-preserved specimens that have been prepared in a way to show some of the internal structures of the head region. In this poster descriptions are given of specimens showing internal cranial structures of *Gyroptychius milleri*, and a reconstruction of the braincase and some palatal structures is also presented. These cranial structures are then compared with those of other osteolepiform fishes, and its phylogenetic position discussed. *Gyroptychius* shares a number of similarities with tristichopterids, such as the presence of a large upper lobe to the caudal fin, and body proportions. The braincase of *Gyroptychius* is of interest to see if it shares more similarities with other 'osteolepidids', such as *Osteolepis*, or tristichopterids, such as *Eusthenopteron*.

CORE – Center of 'Orsten' Research and Exploration

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Etching of late Cambrian limestone nodules (orstens) from Sweden has, in the 1970s, yielded an exceptional, 3D-preserved assemblage of phosphatized arthropod microfossils with preserved cuticular details ('soft parts'). Subsequently, the term 'Orsten' has been used for a specific type of 3D-fossil preservation, in which the surface of the animals became impregnated by calcium phosphate during early diagenesis. Lack of further deformation resulted in three-dimensional preservation of the fossils, and even of ontogenetic stages. Additional discoveries of 'Orsten'-type lagerstätten in Australia, Canada, Poland, Russia, Great Britain, and China have expanded our knowledge of these types of fossils, not least in terms of their preservation and taphonomy. Additional records of similarly preserved fossils have come to light from deposits ranging in age from the Precambrian/lower Cambrian to the lower Cretaceous. The taxa identified so far (*c.* 85, the majority still to be described) represent different arthropod clades and nemathelminths. Continued investigation of 'Orsten' material has recently been guaranteed by the formation of the *Center of Orsten Research and Exploration* (CORE). This is an informal research group

in 'Orsten'-related fields that includes, besides the working group in Ulm/Bonn, a growing number of international scientists together with young researchers and doctoral students.

Long legged South American birds and the first avian fossils from Venezuela

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With almost 1,400 endemic or migratory species of bird occurring in Venezuela today, it seems surprising that fossil birds have never been reported from this country. Here, the first avian remains to have been recovered from Venezuela are described. The material comprises an associated right tarsometatarsus and tibiotarsus from the early Pliocene of the Codore Formation of north western Venezuela. The fossil-bearing horizon represents a deltaic palaeoenvironment with marine vertebrates, including crocodiles and turtles. The skeletal elements are long and narrow, and the presence of a circular distal intercondylar fossa bordered proximally by a prominent and centrally-situated tubercle for the m. tibialis anticus, allows confident referral to the Ciconiidae (storks). Several characters support referral to the extant *Jabiru*, although the presence on the tibiotarsus of a well-defined caudal groove, a narrower extensor tendon groove and shallower angled shelf distal to the tendon groove bridge, indicate that this is a new species. *Jabiru mycteria*, the only living species, still occurs in Venezuela, where it is mostly found in grassy wetlands. These specimens represent the first fossil record of *Jabiru*.

Missing molluscs: prolific providers of carbonate cement?

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Many marine molluscs secrete aragonite shells. Although some bivalves are profuse carbonate producers, relatively low production – up to ~300 g m^{-2} a^{-1} – characterises benthic molluscs in modern non-reefal carbonate settings. Remobilised carbonate from large-scale early diagenetic dissolution of molluscan aragonite has been proposed as a benthic autochthonous source of carbonate for cementation of limestones of limestone-marl/shale alternations (LMA), and as an alternative to the paradigmatic allochthonous aragonite mud source. Were there sufficient molluscs entirely to source cements of LMA limestones of different settings and ages? Numerical modelling demonstrates the capability of molluscan aragonite to provide adequate carbonate for cements of LMA limestones across variable thicknesses, porosities, accumulation rates and the Phanerozoic. For a 15 cm thick Ordovician limestone bed, for example, accumulated at 4 mm/1000 years, with an original sediment porosity of ~60%, only ~6 g of aragonite per m^{-2} a^{-1} is required for cementation; an amount equivalent to a fraction of a nautiloid cephalopod shell. A molluscan cement source is parsimonious for most LMA limestones, especially where aragonitic mud production cannot be reconciled with 'calcite seas', cool-water and distal settings, and epeiric seas where shallow water carbonate factories can 'switch off'.

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New zooplankton from the Soom Shale Lagerstätte

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The discovery of a new species of *Caryocaris* has revealed evidence of a zooplanktonic constituent to the Soom Shale fauna. The fossils increase the number of arthropods found from the Soom Shale; others found previously include trilobites and eurypterids. These caryocaridids are the second described members of the Crustacea from the Soom Shale (the first being ostracodes), and the first described belonging to the Class Malacostraca. The occurrence of *Caryocaris* in the upper Ashgill of the Soom Shale is the youngest record of a group that was previously thought to range from the Tremadoc to the Llanvirn. It is also the only known caryocaridid from South Africa. The new fossils show remarkable preservation, where layers of the carapace are either composed of carbon or replaced by clay and alunite group minerals. The mode of preservation may reflect differences in original tissue composition and/or structure. The taphonomic history of these fossils enhances our understanding of the processes of exceptional preservation in the unique Soom Shale Lagerstätte.

Acritarchs in the Ediacaran seas

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The Neoproterozoic is characterised by severe environmental turbulence and biotic diversification of several major groups. Global glaciations might have acted as evolutionary bottlenecks leading to rapid diversification of several lineages of single-celled and, eventually, multicellular organisms. The appearance of more than 50 ornamented acritarchs in the Australian Ediacaran suggests a possible evolutionary explosion. Acritarchs, being primary producers, probably had a profound effect on metazoan evolution. Acritarch diversification offers an excellent opportunity for biostratigraphy. Palynomorph assemblages containing mainly eukaryotic acritarchs and prokaryotic bacteria have been recovered from numerous southern and central Australian boreholes. Extensive sampling has produced a fourfold biozone subdivision of the middle Ediacaran based on first appearances of index species and characteristic assemblages. New samples from Murnaroo 1 are consistent with previous results and allow a more accurate characterization of the biozones, by tightening constraints on the first appearance of acanthomorph species. Acanthomorphs appear much closer to the Acraman impact ejecta layer than previously recognized.

Taphonomy of mass accumulations of articulated ophiuroids from the Middle Triassic (Muschelkalk) of Poland

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Three Middle Triassic ophiuroid accumulations consisting of *Aspiduriella similes* from three regions of Poland (Holy Cross Mountains, Upper Silesia and the North-Sudetic Basin) have been taphonomically investigated. All 428 specimens were included into three taphonomic groups. The majority (88.5%) are slightly disarticulated (group 2). Very well preserved specimens with small traces of disarticulation (group 1), as well as incomplete ones possessing only the central disc or with only a few proximal stumps (group 3) are more rare (6.5% and 5% respectively). The majority of the specimens (76.4%) are preserved with their oral side upward. Only 19.2% of specimens are preserved in life position, and relatively few (4.4%) are preserved oblique to bedding. All ophiuroids studied are preserved within a thin, pelitic layer. Taking into account their taphonomy, as well as the characteristics of the host sediiment, it is clear that all assemblages were transported prior to their rapid burial. The dominance of articulated skeletons indicates that the obrution was not only rapid but also a single event, as the repeated occurrence of such events would have destroyed any ophiuroids previously buried. Storm-related processes that re-suspended fine-grained material from near-shore environments and covered the deposited ophiuroids are the most likely burial agent.

High diversity brachiopod associations from the Late Ordovician (early Caradoc) Gryazno Formation of the St. Petersburg region, Russia

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Abundant and diverse shelly faunas were reported for over seventy years from the Lower Caradoc Gryazno Formation cropping out in a number of small exposures and old quarries in the western part of the St. Petersburg region. Recently, after discovery of the stratigraphically informative chitinozoans *Eisenackitna rhenana* and *Lagenochitina dalbyensis* in the Klyasino quarry section, the stratigraphical position of the Gryazno Formation is now well established. The main source of fossils is a bed of calcareous clay in the middle of the formation. Brachiopods are the most abundant and represented by such genera as *Platystrophia*, *Bilobia*, *Clitambonites*, *Vellamo*, *Equirostra*, *Orthisocrania*, *Philhedra*, and *Pseudopholidops*. It is one of the most diverse brachiopods associations yet known from the Ordovician of Baltoscandia. Taphonomic study suggests a quiet-water environment below storm wave base and within the photic zone. The brachiopod assemblage shows similarity with contemporaneous assemblages from other parts of Baltoscandia and to some extent with those from Avalonia. The taxonomic diversity, abundance and excellent preservation of brachiopods from the Gryazno Formation of Klyasino quarry make them ideal for morphological, shell structure, and palaeoecological studies.

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