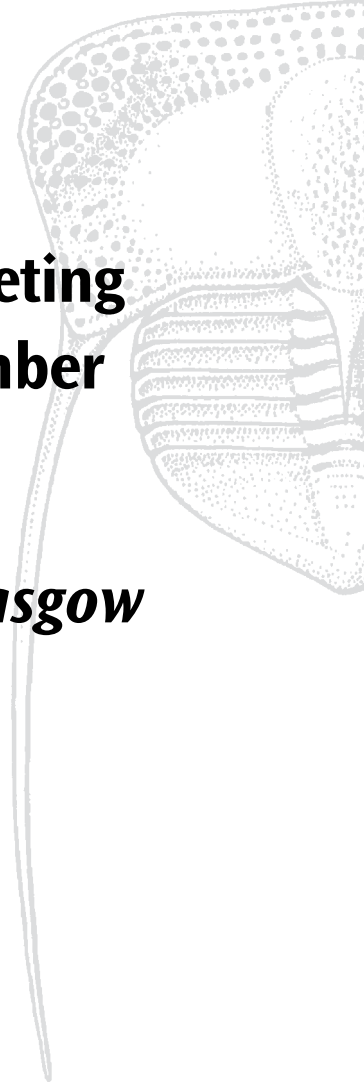


**The  
Palaeontological  
Association**

**52nd Annual Meeting  
18th–21st December  
2008**

***University of Glasgow***

**ABSTRACTS**







# The Palaeontological Association

## 52nd Annual Meeting

### 18th–21st December 2008

#### Department of Geographical and Earth Sciences and Hunterian Museum, University of Glasgow

The programme and abstracts for the 52nd Annual Meeting of the Palaeontological Association are outlined after the following summary of the meeting.

#### *Third Circular and late registration*

The third circular will be sent out to delegates in mid-November. The deadline for late registration is 21st November. Registration is via the Palaeontological Association website (<<http://www.palass.org>>).

#### *Venue*

The meeting will take place in the Sir Charles Wilson Building, 1 University Avenue on the main campus. Information on the University of Glasgow can be obtained from <http://www.gla.ac.uk/>>. The Sir Charles Wilson Building is building E15 on the map at <[http://www.gla.ac.uk/media/media\\_1887\\_en.pdf](http://www.gla.ac.uk/media/media_1887_en.pdf)>.

#### *Accommodation*

Delegates must make their own arrangements for accommodation. Rooms were reserved for the conference in a variety of hotels at a range of prices and within easy reach of the University up until 17th October. Some may still be available in these establishments, although this can no longer be guaranteed. Rooms there and elsewhere can be booked through the University via the Annual Meeting pages on the Pal. Ass. website (<<http://www.palass.org>>). Links providing information on cheaper, hostel-style accommodation are also provided on the website and there are many other hotels and Bed & Breakfast establishments in the West End of Glasgow, where the University is situated, and in the city centre.

#### *Travel*

The city has excellent rail and motorway links to the rest of the UK. The nearby international



airports are served by a wide range of carriers, including budget airlines. Glasgow Airport is seven miles (11 km) from the University and there is an airport bus to the city centre. Prestwick Airport is 22 miles (35 km) away and has a rail connection to the city centre. See the Glasgow University travel information page for more details, at

<<http://www.gla.ac.uk/about/locationmapsandtravel/mapsandtravel/>>.

Please note that parking in the University area is scarce and expensive.

### *Registration at the conference*

Registration will take place in the Sir Charles Wilson Building, 1 University Avenue. The registration desk will be open from 09.00 to 17.00 on 19 – 21 December. For those arriving on 17th December to attend the field trip on 18th December, a registration desk will be available in the Gregory Building of the University of Glasgow should you wish to collect your conference pack then. The Gregory Building is on Lilybank Gardens and is building D2 on the campus map at

<[http://www.gla.ac.uk/media/media\\_1887\\_en.pdf](http://www.gla.ac.uk/media/media_1887_en.pdf)>.

### *Symposium*

A special symposium entitled “Biomaterials – the hard part of palaeontology” will take place in the lecture theatre of the Sir Charles Wilson Building, beginning at 2pm on Friday 19th December. This will be followed by a Civic Reception at Glasgow City Chambers, George Square, Glasgow (close to Queen Street mainline station and Buchanan Underground station), commencing at 7pm.

### *Oral and poster contributions*

All oral and poster presentations will take place in the Sir Charles Wilson Building. At the conference, each poster will be assigned a number indicating the location of the poster board for each poster.

Posters will be available for viewing throughout the conference, and there will be a dedicated poster session from 9.00 to 10.30 am on Sunday 21st December.

### *Annual Address*

The Annual Address will be given at 17.15 on Saturday 20th December by Prof. Jenny Clack, on “The emergence of tetrapods: how far have we come in the last twenty years and where can we go in the next?”

### *Drinks Reception & Annual dinner*

There will be a drinks reception in the Hunterian Museum hosted by the Museum and the Geological Society of Glasgow, followed by the Annual Dinner in the Bute Hall, the main ceremonial hall of the University. The wine served with the meal is funded by Wiley-Blackwell. The drinks reception will commence at 19.00 and dinner at 20.00.



### *Field excursion*

There will be a field excursion on Thursday 18th December to explore some of the fossiliferous Carboniferous rocks of the Midland Valley of Scotland, departing at 09:00. Participants should assemble before then in the entrance hall of the Gregory Building on Lilybank Gardens, Building D2 on the campus map available at <[http://www.gla.ac.uk/media/media\\_1887\\_en.pdf](http://www.gla.ac.uk/media/media_1887_en.pdf)>.

### *Acknowledgements*

We would like to express our appreciation to the following who provided generous financial support: Wiley-Blackwell, The Geological Society of Glasgow, Department of Geographical & Earth Sciences and the Hunterian Museum of the University of Glasgow, EDAX, Oxford Instruments, Gatan, FEI Instruments, Scottish Natural Heritage, The Royal Society, The Geological Society, Informa UK Ltd, Dunedin Academic Press, Thomas Tunnocks Ltd and the Paleontological Institute at the University of Kansas.

**Maggie Cusack, Alan Owen & Neil Clark**



# Schedule of events and timetable for presentations

## Thursday 18th December

9:00 Departure for Field Excursion to examine fossiliferous sites in the Carboniferous of the Midland Valley. Participants should assemble before then in the entrance hall of the Gregory Building on Lilybank Gardens (Building D2 on the campus map available at <[http://www.gla.ac.uk/media/media\\_1887\\_en.pdf](http://www.gla.ac.uk/media/media_1887_en.pdf)>).

## Friday 19th December

### *Symposium*

The meeting will take place in the Sir Charles Wilson Building at the University of Glasgow (E15 on University map at <[http://www.gla.ac.uk/media/media\\_1887\\_en.pdf](http://www.gla.ac.uk/media/media_1887_en.pdf)>) where registration will also take place, 09:00–17:00.

The speakers and their topics at the half-day symposium “**Biominerals – the hard part of palaeontology**” on the afternoon of Friday 19th December will be:

- 14:00 **Common mechanisms of biomineralization and the implications for the evolution of hard tissues**  
Prof. Steve Weiner (Weizmann Institute of Science, Israel)
- 14:30 **The history of biocalcification in the sea: observations and experiments**  
Prof. Steven Stanley (University of Hawaii, USA)
- 15:00 **Multiple origins of animal skeletons and dynamic adaptive evolution documented by molluscan shell matrix proteins**  
Dr Kazuyoshi Endo (University of University of Tsukuba, Japan)
- 15:30 **Coffee**
- 16:00 **Isotope record of Phanerozoic seawater as recorded by fossil shells**  
Prof. Jan Veizer (University of Ottawa, Canada)
- 16:30 **Trend in limestone formation from the Archaean to the Present**  
Prof. Peter Westbroek (University of Leiden, The Netherlands)
- 19:00 **Civic reception in the Glasgow City Chambers**



## Saturday 20th December

### **Oral presentations**

\* Candidates for the President's Award are marked with an asterisk.

The meeting will take place in the Sir Charles Wilson Building at the University of Glasgow (E15 on University map at <[http://www.gla.ac.uk/media/media\\_1887\\_en.pdf](http://www.gla.ac.uk/media/media_1887_en.pdf)>) where registration will also take place, 09:00–17:00.

**8:45** Introductory remarks

### **Preservation and Taphonomy**

**9:00** Soft tissue preservation in Late Triassic lacustrine deposits from Solite Quarry, Virginia, USA

Patrick J. Orr, Stuart L. Kearns, Derek E. G. Briggs, Nicholas C. Fraser, Diane Johnson, Matt Kilburn and John Wade

**9:15** Experimental degradation of vertebrates: taphonomy of keratinous tissues and implications for the fossil record

Maria E. McNamara\* and Patrick J. Orr

**9:30** An experimental investigation of isotopic changes during early diagenesis: Implications for palaeontological studies

Jo Hellowell\*, Cris J. Nicholas and Robbie Goodhue

**9:45** Earliest Cretaceous 'firestorm amber' with spiders webs, from the ~140 Ma dinosaur trackway beds of Bexhill

Martin Brasier, Laura Cotton and Jamie Hiscocks

**10:00** Pyritized olenid trilobite faunas of upstate NY: Palaeoecology and taphonomy

Úna C. Farrell and Derek E. G. Briggs

**10:15** Modes and distribution of exceptional preservation in the Builth Inlier (central Wales): the volcanic connection

Joseph P. Botting and Lucy A. Muir

**10:30** Coffee and Posters

### **Biominerals**

**11:00** Spikey bivalves: intra-periostracal crystal growth in anomalodesmatans

Antonio G. Checa and Liz Harper

**11:15** Pachythecalids, the rugosan origin of the Scleractinia

Jean-Pierre Cuif

**11:30** Using skeletons of extinct and extant bryozoans to test the calcite–aragonite seas hypothesis

Marcus M. Key, Abigail M. Smith and Dennis P. Gordon



- 11:45 Determining the microstructure of the lenses in the schizochroal eyes of trilobites**  
Clare Torney\*, Martin R. Lee, Alan W. Owen, Robert W. Martin and Paul R. Edwards
- 12:00 Mineralogy of coleoid cephalopod shells: evolution or diagenesis?**  
Y. Dauphin
- 12:15 Isotopic analysis of the life history of the enigmatic squid *Spirula spirula*, with implications for studies of fossil cephalopods**  
G. D. Price, R. J. Twitchett, C. Smale and V. Marks
- 12:30 Lunch**

***Proterozoic – Early Cambrian life***

- 13:30 Taphomorphs and taxonomy of the Ediacara Biota in Avalonia**  
Alexander G. Liu\*, Duncan McIlroy, Jonathan B. Antcliffe and Martin D. Brasier
- 13:45 Making ‘census’ of Ediacaran communities in Charnwood Forest**  
Phil Wilby, John Carney, Mike Howe and Helen Boynton
- 14:00 Doushantuo fossils are not giant bacteria, but bacterial pseudomorphs of animal embryos**  
Elizabeth C. Raff, Kaila L. Schollaert, David E. Nelson, Philip C. J. Donoghue, Ceri-Wyn Thomas, F. Rudolf Turner, Barry D. Stein, John Cunningham, Xiping Dong, Stefan Bengtson, Therese Hultgren, Marco Stamparoni, Yin Chongyu and Rudolf A. Raff
- 14:15 A Lower Cambrian radiolarian from Australia with entactinarian affinities: Implications for the emergence of the Rhizaria**  
Taniel Danelian and Stefan Bengtson
- 14:30 Review of bradoriid and phosphatocopid arthropods from the Early Cambrian of South Australia**  
Timothy P. Topper, Christian B. Skovsted, Glenn A. Brock and John R. Paterson
- 14:45 New insights into early animal diversity, evolution and ecology from the Lower Cambrian fossil archive of South Australia**  
Glenn A. Brock, Christian B. Skovsted, John R. Paterson, Lars E. Holmer and Timothy P. Topper
- 15:00 Coffee and Posters**

***Functional Morphology***

- 15:30 Trilobite eyes and their visual systems**  
B. Schoenemann and E. N. K. Clarkson
- 15:45 The function of forks: The asaphid-type hypostome**  
Thomas A. Hegna
- 16:00 Fossil evidence for the origin of spider spinnerets, and a new arachnid order**  
Paul Selden



**16:15 3-dimensional analysis of dental complexity in high fibre plant feeders**

I. Corfe, S. Zohdy, A. Evans, P. C. Wright, G. Wilson and J. Jernvall

**16:45 Annual General Meeting****17:15 Annual Address:**

The emergence of tetrapods: how far have we come in the last twenty years and where can we go in the next?

Jennifer A. Clack

**19.00 Reception** at the Hunterian Museum**20.00 Annual Dinner** in the Bute Hall (opposite the Hunterian Museum)

(including post-dinner bar)

The Hunterian Museum and Bute Hall are located in the Gilbert Scott Building, University of Glasgow (A15 and A13 on University map at [http://www.gla.ac.uk/media/media\\_1887\\_en.pdf](http://www.gla.ac.uk/media/media_1887_en.pdf)).

## Sunday 21st December

### ***Oral\* and poster presentations***

\* Candidates for the President's Award are marked with an asterisk

Sir Charles Wilson Building at the University of Glasgow (E15 on University map at [http://www.gla.ac.uk/media/media\\_1887\\_en.pdf](http://www.gla.ac.uk/media/media_1887_en.pdf)).

### ***Poster Session***

*Coffee available from 10:00.*

**9:00 Delegates are requested to stand by their posters**

### ***Environment and Ecology***

**10:30 Patterns of shell damage and repair in Recent terebratulide and rhynchonellide brachiopods from Doubtful Sound (New Zealand)**

Liz Harper, Miles Lamare and Daphne Lee

**10:45 Bivalve sclerochronology and climate change: evidence of global warmth and fluctuating oceanic heat supply from the Pliocene of the southern North Sea Basin**

Andrew Johnson, Annemarie Bird, Jonathan Hickson, Bernd Schöne, Peter Balson, Tim Heaton and Mark Williams

**11:00 The Burning Question: New limits for combustion in low oxygen redefine palaeoatmospheric predictions for the Mesozoic**

C. M. Belcher and J. C. McElwain



- 11:15 Taphonomic controls on trilobite associations in the Silurian reefs of North Greenland**  
Helen Hughes and Alan Thomas
- 11:30 Pioneering Carboniferous ostracods: their first non-marine colonisation**  
Carys E. Bennett\*
- 11:45 Insect traces in Antarctic fossil forests: a comparison with modern forests in Chile**  
Claire M. McDonald\*, Jane E. Francis, Steve G. A. Compton, Alan Haywood,  
Allan C. Ashworth, Luis Felipe Hinojosa and John Smellie
- 12:00 Experimental ichnology – now with crocodiles!**  
Jesper Milàn
- 12:15 Using computer simulation to explain variation in fossil vertebrate tracks**  
Peter L. Falkingham, Phillip L. Manning and Lee Margetts
- 12:30 Lunch**

### ***Biodiversity Change***

- 13:30 A Gondwanan view on the diversity and ecology of Ordovician fish**  
Ivan Sansom, Neil S. Davies, Alex Ritchie, C. Giles Miller, Guillermo Albanesi and  
Robert S. Nicoll
- 13:45 The Ordovician Biodiversification: geologically or biologically triggered?**  
Thomas Servais, David A. T. Harper, Jun Li, Axel Munnecke, Alan W. Owen and  
Peter Sheehan
- 14:00 Recognising the Taghanic Event in the Devonian terrestrial environment and its  
implications for understanding land-sea interactions**  
J. E. A. Marshall, J. F. Brown and T. R. Astin
- 14:15 Growth rates and longevity in ‘Lilliput’ animals in the aftermath of the Late Permian  
extinction event**  
Brett Metcalfe\* and Richard J. Twitchett
- 14:30 Symbiotic bleaching in fossil planktonic foraminifera and extinction in the latest  
middle Eocene**  
Bridget S. Wade, Nadia Al-Sabouni, Chioma Udeze, Richard K. Olsson and  
Christoph Hemleben
- 14:45 Unravelling the history of the Indo–West Pacific marine biodiversity “hotspot”**  
Laura McMonagle\*
- 15:00 Coffee and Posters**

***Evolution and Phylogeny***

- 15:30 Evaluating phylogenetic hypotheses of carroids using stratigraphic congruence indices**  
Imran A. Rahman\*, Mark D. Sutton and Mark A. Bell
- 15:45 Exploration of fossil floras on the volcanic oceanic islands of Macaronesia, as an important part of resolving complex botanical questions and biogeographical patterns**  
Cajsa Lisa Anderson, Alan Channing and Alba B. Zamuner
- 16:00 The deep evolution of Metazoan microRNAs**  
Alysha M. Heimberg, Benjamin M. Wheeler, Erik A. Sperling and Kevin J. Peterson
- 16:15 Hot spring ecosystems through time: Homes for endemics, hot spring specialists or widespread but pre-adapted generalists?**  
A. Channing, A. Zamuner, D. Guido and D. Edwards
- 16:30 Unlocking character preservation before chordate skeletonization: decay of the cephalochordate Branchiostoma**  
Robert S. Sansom, Sarah E. Gabbott and Mark A. Purnell
- 16:45 Dinosaur Origins and radiations: numerical approaches in macroevolution**  
Michael J. Benton
- 17:00 Announcement of prize winners and close of meeting**



# Abstract of Annual Address

**The emergence of tetrapods: how far have we come in the last twenty years and where can we go in the next?**

**Jennifer A. Clack**

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

Twenty years ago, only three genera of Devonian tetrapod were known: one, *Ichthyostega*, was known from extensive specimens though incomplete descriptions but carried the burden of being an icon for early tetrapods; another, *Acanthostega*, was known from two partial skull roofs; the third, *Tulerpeton*, was known from a single partial skeleton and seemed anomalous in several ways. From the ‘fish’ side of the spectrum, a single genus, *Eusthenopteron*, was available as the model from which tetrapods evolved. Many scenarios were postulated to explain the fish–tetrapod or water–land transition, including several ‘hypothetical ancestors’.

Today, the skeletal anatomy of *Acanthostega* is almost completely known; *Ichthyostega* is seen as radically different from its iconic image; and *Tulerpeton* is thought to fit the emerging picture of polydactylous Devonian tetrapods that lived in marginal marine conditions. We have much more detailed knowledge of tetrapodomorph fish with the discovery of *Tiktaalik* and reinterpretations of *Panderichthys*. These have allowed us to construct consensus phylogenies from which we can infer sequences of character acquisition that then lead on to more testable hypotheses of when, where and how come tetrapods evolved. We see that the ‘hypothetical ancestors’ have been proved incorrect in many respects, because they were based on preconceptions about evolutionary drives that are probably invalid.

Ecological information is now coming from many more sites for fossil stem tetrapods and tetrapodomorphs, resulting from the increasing range of taxa now available to represent the transition world wide. Studies of climate change and plant evolution in the Devonian link with morphological changes to the stem group. We are increasingly able to exploit a range of new technologies to explore the fossils in greater and greater detail, allowing histological, microarchitectural, biomechanical and morphometric analyses. Studies of appropriate modern analogues point the way to inferences about how stem tetrapods adapted their physiology and sensory systems that further suggest features of their skeletal anatomy to re-examine. The interface with evolutionary developmental biology has recently been embraced by both sides, with more ‘evolutionarily interesting’ taxa being studied developmentally, with the input from fossils feeding into a more coherent picture. Probably most significant of all, exploration of new geographical areas is uncovering potential sites for collecting more fossils.



# Abstracts of symposium presentations

## Multiple origins of animal skeletons and dynamic adaptive evolution documented by molluscan shell matrix proteins

**Kazuyoshi Endo**

*Doctoral Program in Earth Evolution Science, University of Tsukuba, Japan*

Hard skeletons evolved almost simultaneously in a number of animal lineages *ca* 540 million years ago. Phylogenetic distributions suggest that the hard skeletons evolved not only simultaneously but also independently multiple times. This suggestion underscores the strength of adaptive pressures for skeletal biomineralisation, and is reinforced by sequence comparisons of genes encoding programs for skeletogenesis, including skeletal matrix proteins recently characterized from cnidarians, molluscs, arthropods, echinoderms, and chordates. Even within molluscs, shell matrix proteins such as Nacrein and Dermatopontin evolved more than once independently by gene duplications and subsequent recruitment from carbonic anhydrases and extracellular matrix proteins, respectively. At least for the latter protein, this parallel co-option took place much more recently than the “Cambrian explosion”. Furthermore, highly acidic skeletal proteins evolved rapidly and convergently in molluscs and vertebrates, presumably due to functional constraints and by virtue of their capacity to interact calcium ions. Taken together, the above observations demonstrate that the skeletogenetic machineries controlled by matrix proteins were never built up to perfection at the time of their origins, but have experienced and are still subject to dynamic processes of adaptive evolution.

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## The history of biocalcification in the sea: observations and experiments

**Steven M. Stanley**

*Department of Geology and Geophysics, University of Hawaii, POST Bldg. 701,  
1680 East-West Road, Honolulu, HI 96822*

There have been three Phanerozoic intervals when nonskeletal calcite has formed in shallow seas and two intervals when nonskeletal aragonite has formed, along with high-Mg calcite. For biologically simple organisms, especially ones that have functioned as major reef builders or sediment producers, biocalcification in the ocean has tended to conform to the secular patterns of nonskeletal carbonates. In the modern aragonite sea, for example, the dominant producers of shallow-water carbonate sediment are aragonitic green algae, and the major reef builders are aragonitic corals and coralline algae, which produce high-Mg calcite. In the late Palaeozoic aragonite sea, the dominant reef builders were predominantly aragonitic, whereas in the earlier Palaeozoic calcite sea they were predominantly calcitic. Calcareous sponges may always have produced skeletons with mineralogies favoured by the Mg/Ca ratio of seawater, and cheilostome bryozoans have shifted their mineralogy from predominantly low-Mg calcite to aragonite and/or high-Mg calcite. Laboratory experiments on a wide variety of organisms have illustrated that both the Mg/Ca ratio and the absolute concentration of Ca in seawater influence the rate of growth and mineralogy of skeletolised organisms. Some organisms exert strong control over their skeletal mineralogy; others, to varying degrees, are at the mercy of seawater chemistry.



## Isotope record of Phanerozoic seawater as recorded by fossil shells

**Jan Veizer**

*Ottawa-Carleton Geoscience Center, University of Ottawa, Ottawa, Ontario K1N 6N5, Canada*

The development of a palaeothermometer for ancient oceans has been a prime goal of stable isotope geochemistry since its inception. For the pre-Tertiary times, the earlier limitation of suitable carrier phases for the temperature signal is being slowly overcome by utilising low-Mg calcite shells of oysters, belemnites and particularly brachiopods. The band of baseline data for the Phanerozoic is reasonably well defined and likely represents a primary feature. Oxygen accounts for 60% of all atoms in the calcite (aragonite) lattice and replacement, via dissolution/reprecipitation, by extraneous oxygen would undoubtedly result in disruption of related attributes, such as texture, mineralogy, chemistry and isotopes. Yet the uncontested sulfur, calcium, carbon and strontium Phanerozoic isotope records all emerge from the same collection of shells. A higher order structure of greenhouse and icehouse episodes appears to be superimposed on the general Phanerozoic baseline and Permian data suggest an existence of the latitudinal temperature gradient of about 14°C. Overall, this Phanerozoic pattern shows much better correlation with potential celestial climate drivers than with model concentrations of atmospheric carbon dioxide, with empirical records on shorter time scales providing additional support.

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## Common mechanisms of biomineralization and the implications for the evolution of hard tissues

**Steve Weiner**

*Department of Structural Biology, Weizmann Institute of Science, Rehovot, Israel 76100*

The first demonstration that biological mineralization processes can involve the initial deposition of a disordered phase that then crystallizes into a mature mineral was by Towe and Lowenstam in 1967 for the chiton tooth. In 1997 Beniash *et al.* (1997) showed that echinoderm larvae also form their calcitic spicular skeletons via an amorphous calcium carbonate precursor phase. This strategy for forming mineralized hard tissues has now been identified in many other invertebrate phyla in both larval and adult phases. Most recently, it has also been shown that bone most likely mineralizes via an amorphous calcium phosphate precursor phase (Mahamid *et al.* 2008; Olszta *et al.* 2007).

The mechanisms involved in transforming the precursor phase into a more stable mature phase are not well understood. Specialized proteins, as well as magnesium and possibly phosphate, appear to be involved in both stabilizing the initial phase and somehow subsequently destabilizing it at a later stage. Interestingly, the initial disordered phase already possesses the short range order of the mature phase, namely calcite or aragonite. Detailed mapping of the intermediate phases shows that small packages of mineral about 20 to 40nm in size transform and several intermediates can be identified.

This biological strategy for mineralization offers the advantage of first producing a phase that can be easily shaped, and when it crystallizes, reduces the volume of water that has to be removed from the mineralization site. Clearly the fact that so many different phyla use this unique approach is consistent with a divergent evolutionary scenario, whereby an ancestor of the metazoans evolved the ability to form minerals in this manner.



- BENIASH, E., AIZENBERG, J., ADDADI, L. and WEINER, S., 1997. Amorphous calcium carbonate transforms into calcite during sea-urchin larval spicule growth. *Proceedings of the Royal Society of London Series B*, **264**, 461–465.
- MAHAMID, J., SHARIR, A., ADDADI, L. and WEINER, S., 2008. Amorphous calcium phosphate is a major component of the forming fin bones of zebrafish: indications for an amorphous precursor phase. *Proceedings of the National Academy of Science, U.S.A.* (in press).
- OLSZTA, M. J., CHENG, X., JEE, S. S., KUMAR, R., KIM, Y.-Y., KAUFMAN, M. J., DOUGLAS, E. P. and GOWER, L. B., 2007. Bone structure and formation: a new perspective. *Materials Science and Engineering: R*, **58**, 77–116.
- TOWE, K. M. and LOWENSTAM, H. A., 1967. Ultrastructure and development of iron mineralization in the radular teeth of *Cryptochiton stelleri* (Mollusca). *Journal of Ultrastructure Research*, **17**, 1–13.

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## Trend in limestone formation from the Archaean to the Present

**Peter Westbroek**

*Leiden University*

As rivers steadily carry solubilised calcium (and magnesium) carbonate from the continents into the sea, the ocean water tends to be permanently oversaturated. However, the ocean itself cannot rid itself of this load, because the water contains various inhibitors of carbonate precipitation, including biological slime. This suppression of spontaneous calcification enhances the habitability of the ocean: it prevents sensitive biological surfaces from being covered with harmful crusts of limestone. In actual fact the mineral does form of course, but only inside fluid microcompartments that are secluded from the open seawater. These microcompartments are continuously generated by the calcifying biota. This global regulatory mechanism of carbonate production has not always been around. Archaean and Lower Proterozoic carbonates contain spontaneously precipitated crusts in addition to biogenic limestone. It is likely that in this period the marine biota had to protect itself from overcrusting by the extrusion of slime. I shall argue that two factors were mainly responsible for bringing carbonate production under biological control: improved inhibition of crust formation as well as enhanced efficiency in biological calcification. It should be noted that this trend not only resulted from biological evolution, since it affected all aspects of the carbonate cycle, including the ocean, the atmosphere and the continental surface. This is an example of the ratcheting development of the Earth, for which we have no theory, Darwinian evolution representing only one aspect.



# Abstracts of oral presentations

\* Candidates for the President's Award are marked with an asterisk.

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## Exploration of fossil floras on the volcanic oceanic islands of Macaronesia, as an important part of resolving complex botanical questions and biogeographical patterns

**Cajsa Lisa Anderson**<sup>1</sup>, **Alan Channing**<sup>2</sup> and **Alba B. Zamuner**<sup>3</sup>

<sup>1</sup>*Department of Biodiversity and Conservation, Real Jardín Botánico, Madrid, Spain*

<sup>2</sup>*School of Earth and Ocean Sciences, Cardiff University, UK*

<sup>3</sup>*Departamento de Paleobotánica, Facultad de Ciencias Naturales y Museo, UNLP, 1900 La Plata, Argentina*

The floristic “Rand Flora” pattern – the existence of disjunct distributions across many plant groups between northwest Africa–Macaronesia, Southern Arabia and East–South Africa, is an example of a biogeographical and evolutionary enigma, which we so far have not been able to resolve. Today we finally have the tools (new model-based approaches to biogeographic inference and phylogenetic dating) to start the work of integrating different disciplines to examine the causal factors of such complex botanical patterns. But for this research we desperately need the fossil data.

Fossil floras of the Macaronesian oceanic volcanic islands are so far virtually unexplored, but in 2007 a Miocene–Pliocene fossil flora was found on Gran Canaria. Preliminary work on approximately 20 plant fossil horizons suggests that laurisilva and *Pinus*-dominated ecosystems were established on Gran Canaria between major late Miocene/early Pliocene volcanic events, supporting the concept of these elements of the Islands flora as Miocene relicts. The study furthermore suggests great potential for finding fossil floras associated with other volcanic islands. An exploration of such floras would provide essential data for research on the evolution of island endemic plants and testing of biogeographical hypotheses, and provide age constraints for molecular dating of phylogenies.

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## The Burning Question: New limits for combustion in low oxygen redefine palaeoatmospheric predictions for the Mesozoic

**C. M. Belcher** and **J. C. McElwain**

*School of Biology and Environmental Science, University College Dublin, Belfield, Dublin 4, Ireland*

Numerous studies have sought to test the limits of combustion under varying concentrations of oxygen; however, none have been able to assess these limits within a fully controlled and realistic atmospheric environment. Experimental burns were performed at 20°C at oxygen concentrations ranging from 9% to 21%, and at ambient and high (2000ppm) carbon dioxide, in a new experimental atmospheres and climate facility, equipped with a thermal imaging system and full atmospheric, temperature and humidity control. Our data reveal that the lower oxygen limit for combustion should be increased from 12% to 15%. These results, coupled with a new record of Mesozoic palaeowildfires, are incompatible with the prediction of prolonged intervals of low atmospheric oxygen





levels (10–12%) in the Mesozoic. The palaeowildfire record provides a key means for testing low-oxygen events in the geological record and highlights the need for high-resolution studies of palaeowildfire across major mass-extinction events in order to test current hypotheses that advocate a primary role of short term low-atmospheric-oxygen events in catastrophic faunal diversity loss in the Permian–Triassic and Triassic–Jurassic mass extinction events.

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### Pioneering Carboniferous ostracods: their first non-marine colonisation

**Carys E. Bennett\***

*Department of Geology, University of Leicester, University Road, Leicester, UK.*

The adaption from marine to non-marine aquatic environments is a key step in the evolution of life, paving the way for animals to colonise the land. Ostracods are small aquatic crustaceans, abundant in the fossil record, whose evolution can be traced back to the early Ordovician. However, little is known about their first non-marine colonisation, which occurred during the Mississippian.

The study focuses on an ostracod rich succession from the Mississippian of the Midland Valley of Scotland, which in the Early Carboniferous was a palaeoequatorial restricted marine basin. Deposition took place in a range of environments, from shallow water restricted marine basins to deltaic fluvial channels, lakes and coal swamps. Brackish to freshwater ostracods such as *Carbonita* and *Geisina* occur in non-marine sediments from the Arundian, the oldest recorded occurrence from the Midland Valley of Scotland. Freshwater and brackish conditions are defined by multiple lines of evidence: sediments, ostracods, macrofossils and algal palynomorphs. The isotope results show the importance of a diagenetic study; trends in  $\delta^{18}\text{O}$  previously interpreted as a palaeoenvironmental signal are revealed to be the result of diagenetic cements. Well-preserved calcitic ostracod shells are essential to record the original values of Carboniferous waters.

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### Dinosaur origins and radiations: numerical approaches in macroevolution

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It has sometimes been hard to distinguish macroevolutionary narratives from storytelling, and this has been especially true for dinosaurs and other fossil vertebrates. Cladistics was the first step; appropriate numerical methods now allow palaeontologists to explore aspects of macroevolution in a testable manner. In recent studies, researchers in Bristol have shown that dinosaurs did most of their rapid evolving in the first half of their history, and that they coasted through the Cretaceous Terrestrial Revolution (KTR), the time when angiosperms, herbivorous and social insects, squamates, birds and mammals were evolving fast. Comparison of diversity and disparity can answer questions about radiations and extinctions: dinosaurs, for example, radiated initially in a two-step process, not fully establishing themselves in the Triassic. Sampling is important, especially for studies of terrestrial vertebrates, but analysts must choose appropriate sampling proxies: some proxies are redundant with fossil counts and so prove little. Understanding how palaeontologists name new taxa is a critical aspect of correcting for error, and new studies show that the key to finding *valid* new dinosaurian species is to explore new basins, but that recently-named species of dinosaurs are more likely to remain valid than any similar sample from the past.



## Modes and distribution of exceptional preservation in the Builth Inlier (central Wales): the volcanic connection

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The volcanic–siliciclastic Middle Ordovician sequence of the Builth Inlier includes notable or exceptional preservation at numerous localities from a diverse range of environments. The faunas represented are diverse, but particularly include echinoderm obrution deposits and sponge-dominated communities, with associated taxa such as worms, holothurians, arthropods and hydrozoans. In some cases, unmineralised and labile tissues are preserved, through a range of chemical mechanisms. Many of the deposits are restricted to thin horizons or pockets, with the unusual faunas previously overlooked.

Interpretation of the physical and chemical taphonomy of these biotas leads to a preliminary understanding of their distribution. The most interesting sites are associated either with an interval of constant high sedimentation, or with rapid sediment transport. Pyritization is a factor in almost all occurrences, the iron originating from an andesitic sediment source. In shallow water, exceptional preservation was due to rapid silicification combined with high sediment accumulation rate, related to erosion of a silica-rich volcanic source. The combination of complex topography, unstable slopes and seismic disturbance, high sediment supply and chemical disequilibrium led to the common occurrence of notable to exceptional fossil material. This combination of aspects makes andesitic/rhyolitic volcanic island systems in general likely to yield multiple exceptional biotas.

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## Earliest Cretaceous ‘firestorm amber’ with spiders’ webs, from the ~140 Ma dinosaur trackway beds of Bexhill

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“No organism wholly soft can be preserved” said Darwin in 1859. He was seemingly unaware, though, of the fossil record within the petrified resins of ancient trees – ‘amber’. In recent years, new techniques have allowed the detailed imaging of delicate and seemingly improbable fossil structures, such as spiders’ webs and cell organelles. Most examples of amber with inclusions span only the last ~100Ma, and earlier reports are extremely rare. Pre-Cretaceous reports consist mostly of microscopic amber droplets, yielding only bacterial, protozoan and fungal remains. Inclusions within very ancient amber are here reported for the first time from lowest Cretaceous (~140Ma) alluvial sediments near Bexhill in Sussex. Deposited shortly before the emergence of the earliest flowering plant communities, these ambers coincide with trackways of *Iguanodon*.

Automontage shows vascular tissues, tracheid cells and resin ducts of the parent coniferous trees. The oldest known coiled and paired silk webs occur abundantly. There are also colonies of saprophytic cells. These remains became entombed within resins that seeped through charred bark of coniferous trees subjected to severe fire damage. Such resins may have helped combat damage caused by widespread forest fires, perhaps inflamed by raised levels of atmospheric oxygen in the early Cretaceous.



## New insights into early animal diversity, evolution and ecology from the Lower Cambrian fossil archive of South Australia

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The Lower Cambrian succession in South Australia is replete with some of the best preserved and most diverse fossil assemblages in the world. These rocks represent an ideal archive for investigation of the early development, evolution and diversification of skeletonised metazoan life on Earth. New fossil material derived from a series of 15 stratigraphic sections (supplemented by numerous spot localities) measured through the full range of carbonate dominated facies (shallow platform, bioherms, platform to slope transition, and basin) has greatly increased knowledge about species diversity and ecological constraints of all major bilaterian groups (especially trilobites, bradoriids, brachiopods, molluscs, tommotiids *etc.*) within a much improved biostratigraphic framework.

Importantly, new complete (or partially complete) scleritome material provides vital clues about the zoological affinities and phylogenetic relationships of a wide range of problematic small shelly fossils – groups that have previously frustrated our understanding of early animal evolution. For example, detailed morphological and ultrastructural investigation of tommotiids such as *Micrina*, *Paterimitra*, *Camenella*, *Dailyatia*, *Lapworthella*, and *Eccentrotheca* from South Australia suggest close similarity with stem lophotrochozoans (especially the brachiopod/phoronid clade), but differences in the number and configuration of sclerite morphs for each taxon reflect a wide range of life habits within a paraphyletic Tommotiida.

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## Hot spring ecosystems through time: Homes for endemics, hot spring specialists or widespread but pre-adapted generalists?

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Richly fossiliferous Jurassic hot spring deposits in Patagonia are providing information that allows generalisations to be made about the traits that adapt organisms for life in and around hot springs. These provide a crucial data point between observations of modern thermal ecosystems and the Rhynie Chert. At active hot springs the plants and animals most commonly preserved, and particularly those that are permineralised to the cellular level, are those that live and die in contact with silica supersaturated water of moderate to ambient temperature. These interactions occur frequently in pools on sinter aprons, distal areas of run-off streams, on extensive geothermally influenced wetlands, and where geothermal waters interact with lake/river margin communities. Plants in these settings are commonly flooding-tolerant and capable of withstanding physiological drought brought about by immersion in mineral-rich, brackish water. Plants preserved are representatives of genera with regional, even global distributions, with adaptations to more common



oligohaline–saline habitats, *e.g.* evaporation dominated lakes, or coastal marshes. Similar observations can be made in Patagonia. Hot spring floras are of low diversity, comprising at present only four taxa, commonly growing in monotypic stands. This contrasts starkly with surrounding clastic environments where a broad range of plant groups are present.

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### Spike bivalves: intra-periostracal crystal growth in anomalodesmatans

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The external surfaces of some bivalve shells are studded with small conical spikes, particularly at the posterior end. We investigated the growth and form of these spikes within the anomalodesmatan bivalves where they are common. Electron Back Scattering Diffraction analysis of the spikes of *Lyonsia norwegica* reveal these are prisms of aragonite composed of twinned crystals, with the *c*-axis along the length of the spike. In *Lyonsiella abyssicola* the distal ends may be single crystals. The spikes grow during very early shell growth. Our observations show that they grow initially within the free periostracum prior to the secretion of calcareous shell layers. They are not pre-formed in the mantle as previously suggested. Later they continue growing within the outer shell layer. The surrounding prisms of the shell have identical crystallographic characteristics.

A survey of the occurrence of spikes within the anomalodesmatans reveals that they are present in virtually every family but that their distribution and morphology varies greatly between taxa. Spikes are also present in non-anomalodesmatan heterodonts, for example the gastrochaenid *Spengleria* where the mechanism of secretion appears different. Elsewhere within the palaeoheterodonts, intra-periostracal calcification is known in *Neotrigonia* and indicates that this character may be plesiomorphic for these bivalves.

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### 3-dimensional analysis of dental complexity in high fibre plant feeders

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Bamboos – grasses belonging to the Poaceae – are highly fibrous, with culms containing 50 percent cellulose. This, together with phytoliths, makes bamboo a challenging food. Specialization for bamboo feeding has evolved several times in extant mammals. Primates, bears and muroid rodents all have species that rely predominantly on bamboo. While phylogeny, size and life history are highly divergent among these bamboo specialists, they share some adaptations to bamboo-feeding. One feature is dental morphology, and here we apply a three-dimensional method to assess crown feature complexity, or surface roughness, in bamboo-eating lemurs, pandas and rodents. Our analyses of 3D digital tooth models, generated by surface laser scanning, show that bamboo specialists have highly complex cheek tooth morphology irrespective of taxon-specific morphological details. The high complexity values can be related to the high number of tooth crown features, or ‘tools’, required to process fibrous bamboo. We also assess dental complexity in extinct taxa previously inferred as having high-fibre herbivorous diets, such as rhynchosaurs,



tritylodontids and mammalian groups. Neither bamboo nor other grasses existed coevally with the older, Mesozoic taxa. However, the dentitions of these specimens were sufficiently complex to have processed plant material similarly high in fibre and/or phytolith content to bamboo.

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## Pachythecalids, the rugosan origin of the Scleractinia

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During the last three decades a series of palaeontological and biological results have created a reliable framework allowing a re-examination of the long-standing question of the relationships between the Palaeozoic and modern corals. Newly discovered Triassic families with very unexpected skeletal patterns bring palaeontological support to several investigations based on molecular phylogeny that have repeatedly demonstrated that the classical taxonomy inherited from Vaughan and Wells (1956) was inadequate at the family level. Additionally, knowledge of the fine-scale mode of growth of coral skeletons and progress in understanding the biochemical control during their mineralizing process provide a new set of evidence to discuss the mineralogical change that has occurred during the Permian/Triassic gap. Thus, from both palaeontological and biological viewpoints, the major question in the evolutionary history of corals has to be re-examined, suggesting substantial changes in the concept of Scleractinia itself.

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## A Lower Cambrian radiolarian from Australia with entactinarian affinities: Implications for the emergence of the Rhizaria

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Radiolaria are now considered to represent the most basal branch of the recently established monophyletic protistan group Rhizaria, which also includes the Foraminifera and Cercozoa. The earliest fossil record of polycystine Radiolaria (those secreting siliceous skeletons) is therefore of particular importance for understanding the origin and early body plans of the group, as well as the early evolutionary history of the Rhizarian lineages.

Siliceous spicular microfossils extracted from the lower Cambrian Ajax Limestone of the Mt Scott Range (Australia), previously reported as "clawed spicules" (Bengtson *et al.* 1990: *Mem. Ass. Austral. Pal.* 9), give information about the most primitive Radiolarian body plan. The skeleton architecture of this form is organised in two hemispheres: four slender and distally tapering *apical* rays diverge out of the edges of a median bar (a kind of small 'saddle'), while four other *basal* rays are placed almost perpendicularly in the opposite direction and they display antler-like branching tips. The new form can be assigned to the Radiolarian family Palaeosценидиidae, thus placing firmly the polycystine Radiolaria in the Early Cambrian ecosystems. This finding also suggests that the entactinarian-type Radiolarian skeleton body-plan is the most primitive in the evolutionary history of siliceous biomineralization within Rhizaria.



## Mineralogy of coleoid cephalopod shells: evolution or diagenesis?

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Modern cephalopod shells are aragonite. Fossil shells are either aragonite or calcite. The Chicago PDB marine standard for  $\delta^{13}\text{C}$  is a belemnite, based on the hypothesis that rostra are formed by primary biogenic low-Mg calcite. This hypothesis is so widespread that, when aragonite rostra are found, they are excluded from the Belemnitida and new taxa are created.

Calcite and aragonite rostra are known in fossil Coleoidea. Whereas aragonite and calcite rostra of Aulacocerids and *Belopteryna* were found apart, the coexistence of both minerals in the same rostrum has been reported in true belemnites: *Goniocamax*, *Belemnoteuthis* and *Neohibolites*. Comparisons of the arrangement, structure and composition of cephalopod shells have shown that the coleoid rostrum is the thickening of the outer prismatic layer (Barskov 1973, Dauphin 1983). Moreover, the mineralogy of rostra follows the alternation of calcite and aragonite seas through geological times defined by Sandberg (1983). Thus, microstructural and geochemical analyses favour the hypothesis that belemnite rostra were composed of primary aragonite. If so, most of the phylogenetic and palaeoclimatological conclusions drawn in studies carried out on Belemnites must be reconsidered.

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## Using computer simulation to explain variation in fossil vertebrate tracks

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A vertebrate track may show considerable morphological difference when compared with others, even those formed by the same trackmaker within the same trackway. This variation can be linked to substrate conditions at the time of track formation (and thereafter until burial), limb kinematics, and position within the three-dimensional volume (undertracks). Using computer simulation, in this case the finite element method (FEM), the potential variation in vertebrate tracks can be quantified. Here the FEM is used to quantify variation in morphological features (*e.g.* track length, displacement rim size) over a range of substrate parameters related to moisture content, and depth within the track volume. Simulated tracks show that higher and more extensive displacement rims are good indicators of surface or near-surface tracks. Track length follows the form of a Boussinesq 'pressure bulb', increasing then decreasing in size with increasing depth.

Virtual tracks do not suffer from the ambiguities inherent in defining track outlines of fossil tracks, but the objective measurement of track features is difficult to transfer to real specimens; for example displacement rims may extend beyond observed measurements by >33% as sub-millimetre deformation. This highlights the importance of developing consistent methodologies for measuring tracks, both real and digital.



## Pyritized olenid trilobite faunas of upstate NY: Palaeoecology and taphonomy

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Pyritized olenid trilobites are found at three Upper Ordovician grey-shale localities of the Taconic Foreland Basin: Beecher's Trilobite Bed (BTB) and the newly discovered Gulf Road Site (GR), both in the Frankfort Formation, and the Martin Quarry (MQ) in the Whetstone Gulf Formation. Olenid trilobites have been interpreted as having a symbiotic relationship with sulfur bacteria, allowing them to live in low-oxygen, borderline-sulfidic conditions. Highly reactive iron ( $\text{Fe}_{\text{HR}}$ ), total iron (FeT),  $\delta^{34}\text{S}$ , organic carbon and trace elements were measured to determine if bottom waters were anoxic. Results suggest dysoxia with occasional anoxia. However, the signatures are not simply correlated to palaeoecological data. BTB and GR have a low-diversity and sparse fauna of graptolites, cephalopods, brachiopods, trilobites and rare bivalves. Beds with whole trilobites often have shallow trace fossils at the top. Diversity at MQ is higher, although pyritized trilobites are nevertheless found in otherwise unfossiliferous beds. Pyritization occurred in multiple horizons at all three sites. Beds with pyritized fossils have consistently high ratios of  $\text{Fe}_{\text{HR}}/\text{FeT}$ , high  $\delta^{34}\text{S}$  and low organic carbon. In summary, conditions fluctuated and were occasionally inhospitable requiring at least adaptation to low oxygen and a muddy substrate. Pyritization occurred in distal turbidites with distinctive geochemical signatures.

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## Patterns of shell damage and repair in Recent terebratulide and rhynchonellide brachiopods from Doubtful Sound (New Zealand)

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In order to provide quantitative data concerning patterns of shell breakage and repair in rhynchonelliform brachiopods we studied live and death assemblages from a New Zealand fiord where three species of terebratulide and one rhynchonellide occur in dense mixed beds on the near vertical walls. Few individuals show signs of having been able to repair marginal breaks (<1% for *Calloria inconspicua*, *Liothyrella neozelanica* and *Notosaria nigricans* and c.6% for *Terebratella sanguinea*) but the proportion of individuals showing lethal breakages was high (>55%). Aquarium-based experiments showed that each of the four species was capable of rapid marginal repair when kept isolated in tanks. Damaged individuals maintained in tanks with extra-oral feeding starfish, gastropods or fish from the fiord community rapidly succumbed to these predatory taxa. In marked contrast, no feeding attempts were observed when undamaged brachiopods were offered to these same predators. We discuss the cause of the damage apparent in the death assemblages and implications for understanding patterns of shell damage and repair in other assemblages both living and fossil.



## The function of forks: The asaphid-type hypostome

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The forked morphology of the hypostome of asaphid (Asaphidae) trilobites is enigmatic. Although the trilobite hypostome is analogous to the labrum in other arthropods, the hypostome of *Isotelus* lacks an obvious modern counterpart. The *Isotelus* hypostome has closely-spaced terrace lines on a greatly thickened inner surface of the fork, the scarp of the terrace facing anteroventrally. This is compatible with a grinding function, suggesting possible limb differentiation to complement this structure. The inner face of the fork is also unique in that it has a microstructure perpendicular to the surface of the sclerite. Macro predatory and filter-feeder roles are ruled out, and previous characterizations of the hypostome as knife-like or serrated are rejected. It is concluded that the hypostome of *Isotelus* is unique and lacks modern analogues. The features of the asaphid-type hypostome are compared with those of other trilobites with forked hypostomes and with the labrum of other arthropods. Its function is incompatible with that of other non-asaphid trilobites with forked hypostomes, like the remopleuridid *Hypodicranotus*.

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## The deep evolution of Metazoan microRNAs

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microRNAs are ~22nt non-coding RNA regulatory genes that are key players in cellular differentiation and homeostasis. They might also play important roles in shaping metazoan macroevolution. Previous studies have shown that miRNAs are continuously being added to metazoan genomes through time and are only rarely secondarily lost. However, because these studies were largely based on phylogenetic conservation of miRNAs between model systems, it was unclear if these trends would describe miRNAs in most metazoan phyla. Here, we explore the miRNA repertoires of ten different phyla by combining 454 sequencing of small RNA libraries with genomic searches from taxa whose divergence times are known from either the fossil record and/or a molecular clock. We show that the evolutionary trends elucidated from the model systems are generally true for all miRNA families and metazoan taxa explored: the continuous addition of miRNA families with only rare substitutions to the mature sequence and only rare instances of secondary losses. Finally, we describe a novel miRNA type in demosponges that, although showing a different pre-miRNA structure, shows the same evolutionary dynamics as eumetazoan miRNAs. We propose that miRNAs might be excellent phylogenetic markers, and suggest that the advent of morphological complexity might have its roots in miRNA innovation.





## **An experimental investigation of isotopic changes during early diagenesis: Implications for palaeontological studies**

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The nitrogen and carbon isotopic composition of organic matter has been widely used to trace biogeochemical processes in various environments. We have used these isotopes to investigate processes in the geological past, namely the reconstruction of palaeodiet and palaeoclimate using fossilised bones and scales of fish. To evaluate the information extracted from the fossils accurately, laboratory-based taphonomy experiments were conducted using extant fish to gain a better understanding of how isotopic signatures may vary after death and during early diagenesis. A series of fish were left to decay in controlled conditions over a six month period and the  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  in vertebrae, muscle and scales were measured after ten different time intervals. The effects of temperature, oxygen level and salinity were also explored. Preliminary results suggest that isotopic ratios, particularly of carbon, varied significantly in the bone during the six month time period, indicating that fossil bone may not preserve a reliable record of its chemistry during life. Muscle tissues decayed rapidly and showed significant variation in the isotope values produced. However, fish scales produced consistent data throughout the time intervals examined, and therefore appear to have potential for future isotopic studies of fossil fish.

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## **Taphonomic controls on trilobite associations in the Silurian reefs of North Greenland**

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



## Bivalve sclerochronology and climate change: evidence of global warmth and fluctuating oceanic heat supply from the Pliocene of the southern North Sea Basin

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The Pliocene is the most recent interval during which global mean temperature was significantly higher than at present. The behaviour of the Gulf Stream/North Atlantic Drift (GS/NAD) under these circumstances is a matter of considerable interest. The biota of the Coralline Crag Formation (Suffolk, UK) points to substantially elevated Winter temperatures and hence a vigorous GS/NAD. The oxygen-isotopic composition of *Aequipecten opercularis* and *Arctica islandica* from the Ramsholt Member indicates, however, that Winter temperatures were similar to now in the southern North Sea, and that Summer temperatures were *lower* than at present. This does not appear to be consistent with global warmth, still less with an accompanying strong GS/NAD. Combined isotopic and growth-increment (sclerochronological) evidence suggests, however, that intense thermal stratification occurred during Ramsholt-times such that the isotopic composition of bivalves (benthic) substantially underestimates surface temperature. When the bivalves investigated were alive the annual maximum and range of surface temperature were probably higher than now, a situation accountable to elevated global temperature and a *weaker* GS/NAD. The presence of taxa indicative of warm Winters implies that at other times global warmth was accompanied by substantial GS/NAD heat supply. There may therefore be interesting times ahead for residents of the North Atlantic borderlands...!

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## Using skeletons of extinct and extant bryozoans to test the calcite–aragonite seas hypothesis

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Our goal is to examine secular variations in seawater chemistry (the calcite–aragonite seas hypothesis) using bryozoans. Our first dataset is extracted from the published literature on extinct and extant bryozoan mineralogy. Fossils, although subject to diagenetic bias, indicate that the Phanerozoic pattern of mineralogy in bryozoans does not match the oscillation of calcite and aragonite seas. To avoid bias, we did another analysis predicting secular variation in global sea water chemistry by examining the first appearance datum of extant bryozoan families with different characteristic mineralogies, but this too does not match the pattern of calcite and aragonite seas. The second dataset consists of morphological data from fossils spanning the latest calcite–aragonite sea transition. We used diagenesis-independent degree of skeletonization as a proxy and predicted that calcite taxa would have less robust skeletons in an aragonite sea using low-Mg calcite fossil cheilostomes and cyclostomes from New Zealand. The degree of skeletonization did not significantly decrease from the Calcite II Sea to the Aragonite III Sea. The general secular



trend in bryozoan mineralogy is for increasing variability, not fluctuation along with seawater chemistry. Bryozoans are active mineralizers, and their evolution does not appear to have been driven by seawater chemistry.

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## Taphomorphs and taxonomy of the Ediacara Biota in Avalonia

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One of the most problematic factors in interpreting the Ediacara biota is that of recognising the influence of preservational styles and of post-mortem changes upon the morphology and taxonomy of these organisms. This research explores – by means of field and laboratory studies – the hypothesis that saprophytic degradation of Ediacaran organisms on the palaeo-seafloor can explain the strangely ‘effaced’ appearance of several key Avalonian taxa, such as *Ivesheadia* and *Shepsbedia*. In other words, these important fossils may merely be taphomorphs of other, more widespread taxa. The present authors have observed bedding planes in both the Charnwood and Newfoundland regions of Avalonia that we consider to contain several taphomorphs of a single taxon on the same surface. We consider that these taphomorphs represent a taphonomic spectrum, ranging from finely preserved, non-decayed organisms such as *Fractofusus*, through progressively more decayed stages, to effaced taphomorphs such as *Ivesheadia*. If accepted, then studies of Ediacaran seafloor diversity and biotic density need to consider that preserved Avalonian communities may not represent populations where all observed specimens were alive at the time of burial. This would have concomitant implications for the palaeoecology of the earliest macrobiotic ecosystems.

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## Recognising the Taghanic Event in the Devonian terrestrial environment and its implications for understanding land-sea interactions

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The Taghanic is one of a series of Mid and Late Devonian biotic events of varying severity. Major extinctions in the Taghanic are recognised in the ammonoids, conodonts, trilobites, corals and terrestrial plants. The late Mid Devonian Eday Marl Formation from the Orcadian Basin, Scotland is a terrestrial equivalent of the marine Taghanic Event interval. The Eday Marl from Orkney contains a high-resolution archive of climatic change controlled by the relative strength of the seasonal insolation. This includes several distinct and discrete episodes of basin flooding as demonstrated by the deposition of lacustrine laminites, bedded evaporites, marginal sheet flood sands and marine influenced bioturbated sheet sands. These flooding events are intercalated with intense and sustained episodes of aridity at times of relatively low seasonal insolation and indicating a relatively weak monsoon climate. Analysis of cycles within the Eday Marl demonstrates their climatic origin and suggests that the main event has a duration of some four 405 ky eccentricity cycles. Recognising the Taghanic as a rapid alternation of cool arid and relatively hotter



pluvial events provides a unifying explanation for the associated collapse in the terrestrial vegetation and the parallel faunal changes in the marine realm.

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### Insect traces in Antarctic fossil forests: a comparison with modern forests in Chile

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Insect body fossils from Antarctica are very rare, yet collections of Eocene fossil leaves from Antarctica provide insect trace fossils, indicating that insects were an important component of the unique forests that once grew in south polar regions. These insect traces provide an excellent opportunity to examine the palaeoecology of Antarctica. The fossils studied include Eocene leaves from both Seymour Island and King George Island on the Antarctic Peninsula. A database of all insect traces on the Antarctic fossil leaves was compiled and analysed in terms of the diversity of palaeoherbivory. The fossil leaves are diverse with several different plant families present such as *Nothofagaceae* and *Cunoniaceae*. The range of traces that were found includes leaf mines, leaf galls, general leaf chewing and skeleton feeding, of which both marginal and non-marginal examples were present.

To provide a greater understanding of ancient herbivore intensity and diversity in Antarctica, modern insect traces on *Nothofagus* leaves, and their associated insects, were examined from the temperate forests in Chile, the modern day analogue of the Antarctic forests during the Eocene. Modern traces show a similar diversity of damage types to that seen in the Eocene, but the intensity of damage appears to be greater now.

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### Unravelling the history of the Indo-West Pacific marine biodiversity ‘hotspot’

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Despite the importance of this modern biodiversity ‘hotspot’, the geological origins of the Indo-West Pacific (IWP) marine region remain understudied. It has previously been suggested that the extant biota formed during a diversification event at approximately the Oligocene–Miocene boundary. Studying the coral diversity around this time can test the timing and magnitude of this. The study area is the Gomantong Limestone in Sabah, Borneo. Nannofossil dating shows the area to be mid- to end-Oligocene in age. A collection of zooxanthellate-like coral fossils has been gathered from nine localities, containing over 1,700 specimens and over 70 morphospecies. 61% of the colonies are plate-shaped and 26% are branching. Just 3% are massive, suggesting that the area favoured corals with a high surface area to volume ratio, indicating turbid habitats. This is the most diverse collection of Palaeogene corals from the area and potentially rivals those previously described from the Pleistocene beds of Papua New Guinea (83 species), and from the Lower Pliocene of Java (~70 species). Comparing this fossil fauna to the extant fauna



of the IWP will improve our understanding of the origins of the present-day biodiversity 'hotspot' by complementing studies of the molecular phylogeny of extant taxa.

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### Experimental degradation of vertebrates: taphonomy of keratinous tissues and implications for the fossil record

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To understand better the factors that influence the taphonomy of vertebrates, in particular the fate of keratinous tissues, specimens of zebra finch (*Poephila guttata*) and mouse (*Mus mus musculus* x. *domesticus*) were degraded under controlled conditions for 16 months. Three experiments, each simulating a different environmental setting, were run; keratinolytic bacteria were added to each experimental vessel to stimulate degradation of keratinous tissues. Specimens decay in a consistent pattern within each experimental programme. This pattern, and the rate, of physical degradation is markedly different for birds and mice, and between specimens held in aqueous and in dry conditions; these differences are evident at the macroscopic scale and also in the fidelity of ultrastructural detail revealed by SEM and TEM analyses. Notably, such variation occurs even if the tissues have near-identical compositions (e.g. keratinous). One feature common to all keratinous tissues was the rapid colonisation of their surfaces by rod-shaped keratinolytic bacteria. These bacteria were often organised into patterns that include a strongly developed fabric of closely packed, aligned, bacteria. Similar textures associated with fossil keratinous tissues have been considered to represent fossil bacteria. Our experiments therefore indicate that recent re-interpretations of the latter as fossil melanosomes may not be universally applicable.

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### Growth rates and longevity in 'Lilliput' animals in the aftermath of the Late Permian extinction event

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The Late Permian mass extinction event resulted in an estimated loss of 80–96% of species. Studies show that both the marine and terrestrial ecosystems collapsed simultaneously. In the wake of this crisis, fossils preserved in Lower Triassic strata record a phenomenon referred to as the Lilliput effect, defined as a temporary reduction in size of survival taxa. Previous studies have shown that a short-term reduction in body size in the first two conodont zones of the Triassic affects all marine invertebrate taxa and is followed by a subsequent increase in all groups of organisms. One question is whether the documented size changes are the results of changes in growth rates, or individual longevity, or a combination of both. In this study, dimensions of the bivalves *Claraia*, *Unionites* and *Eumorphotis* and the brachiopod *Lingula* were measured in the field using digital callipers, confirming patterns from previous studies. Laboratory-based growth line studies were conducted on well-preserved specimens in order to determine their rate of growth. Results demonstrate that growth line spacing was similar in the 'Lilliput' animals and their larger-sized conspecifics, suggesting that small size was due to changes in longevity not growth rate; the 'Lilliput' animals died at younger ages.



## Experimental ichnology – now with crocodiles!

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While dinosaur tracks have been the topic of intense research during recent years, tracks and trackways of crocodiles have received less attention, and have on several occasions been misidentified as tracks of pterosaurs or other animals. An ongoing project is set out to document the complete morphological variation in tracks and trackways from extant crocodiles to create an important reference volume for the study of fossil tracks. The project is carried out in cooperation with Crocodile Zoo in Denmark, which houses 21 of the 23 recognized species of extant crocodiles. To obtain the tracks the animals are encouraged to walk through prepared lanes of damp sand. Each trackway is subsequently cast and digitally documented. The preliminary results show significant variation in trackway patterns, placement of feet and hand, and the amount of belly and tail dragmarks preserved in the trackways. Trackways from different ontogenetic stages of the same crocodile species change significantly as the animal grows bigger and tend to drag more of the body.

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## Soft tissue preservation in Late Triassic lacustrine deposits from Solite Quarry, Virginia, USA

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The cuticle of insects and the skin and/or musculature of the tail of the reptile *Tanytrachelos* are preserved as carbonaceous remains in Late Triassic lacustrine deposits in Solite Quarry, Virginia, USA. This mode of preservation is therefore not diagnostic of a particular histology. The external surfaces of both tissues are coated by a structureless thin film of the same authigenic phase, 'biotite'. The 'biotite' pseudomorphs the head and thorax, but not the abdomen, of the insects. In *Tanytrachelos* the 'biotite' occurs on only one side of, and also infills cracks through, the carbonaceous remains; these cracks originated by brittle extensional deformation of the fossilized tissues. The 'biotite' originated during metamorphism, via replacement of a precursor phase. The composition of the latter is unknown; it precipitated during late stage diagenesis or metamorphism. Similar features in non-biom mineralised fossils from the Burgess Shale provide confirmation that some, but not all, of the various aluminosilicate phases originated adjacent, and external, to organically preserved tissues. In these, it is not necessary to invoke the aluminosilicates having replaced the carbonaceous tissues, or infilled voids created by their volatilisation.



## Isotopic analysis of the life history of the enigmatic squid *Spirula spirula*, with implications for studies of fossil cephalopods

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Stable isotopes analyses of *Spirula spirula*, a mesopelagic cephalopod which possesses a coiled internal aragonitic shell, are presented. The data suggest that  $\delta^{18}\text{O}$  is precipitated in equilibrium with the surrounding water. The  $\delta^{18}\text{O}$  trends are interpreted to reveal a life beginning in deep waters characterised by cool temperatures, before rising to warm surface waters to feed during its juvenile stage. Following this brief period in warmer waters the isotopes suggest that the remainder of the organism's life was spent in progressively cooler (deeper) waters. The incorporation of isotopically light metabolic carbon has, however, significantly affected the stable carbon isotope signal recorded in *S. spirula*, effectively obscuring the record of  $\delta^{13}\text{C}$  of seawater dissolved inorganic carbon archived in the shell carbonate. This may relate to the internal position of the shell, whose growing margin is anchored in soft tissue and separated from the ambient seawater within the mantle cavity. Thus,  $\delta^{13}\text{C}$  of extinct cephalopod shells may prove a useful guide to the amount of soft tissue surrounding the growing margin of the shell. Our results have important implications for ancestors of *S. spirula* such as belemnites, in terms of constraining equilibrium precipitation of shell carbonate, required in terms in palaeoenvironmental studies.

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## Doushantuo fossils are not giant bacteria, but bacterial pseudomorphs of animal embryos

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Embryos from the Ediacaran Doushantuo Formation are among the most astonishing examples of exceptional fossilization. However, the mechanism of fossilization is poorly understood, leading directly to debate over the interpretation of the fossils, some authors even questioning their interpretation as embryos. It has been hypothesized that microbial processes are responsible for preservation and mineralization of organic tissues. However, the actions of microbes in preservation of embryos have not been demonstrated experimentally. We show that bacterial biofilms assemble rapidly in marine embryos, forming detailed pseudomorphs of cellular organization and structure. We define three essential steps in embryo preservation: 1) blockage of autolysis by reducing or anaerobic



conditions; 2) rapid formation of microbial biofilms that consume the embryo but form a replica that retains cell organization and morphology; 3) bacterially-catalyzed mineralization. We identified major bacterial taxa in embryo decay biofilms using 16S rDNA sequencing. Decay processes were similar in different taphonomic conditions, but bacterial populations depended on specific conditions. Experimental taphonomy resembles preservation states of fossils. Our data show how fossilization of soft tissues in sediments is mediated by bacterial replacement and mineralization, providing a foundation for experimentally creating biofilms from defined microbial species to model fossilization as a biological process.

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## Evaluating phylogenetic hypotheses of carroids using stratigraphic congruence indices

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The controversial fossil carroids (Deuterostomia) possess a unique anatomy that is difficult to interpret; as a result, there are a number of competing phylogenetic hypotheses for carroid taxa. Stratigraphic congruence indices provide a quantitative means of evaluating alternative cladograms where character coding is contentious; trees that show a statistically significant fit between stratigraphy and phylogeny are better supported by the fossil record. We here test the agreement between stratigraphic and cladistic data for three competing hypotheses for the phylogenetic position of carroids. The results demonstrate that assuming carroids should be interpreted by reference to chordates/hemichordates (rather than echinoderms) leads to a poorer fit with the stratigraphic ordering of fossils. Thus, the disputed calcichordate hypothesis (carroids interpreted as stem- and crown-group chordates and stem-group hemichordates) is much less congruent with stratigraphy than alternative models interpreting carroids as stem- or crown-group echinoderms.

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## A Gondwanan view on the diversity and ecology of Ordovician fish

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Recent years have seen the rapid accumulation of new data which can be used to assess the evolutionary radiation of primitive fish through the Ordovician, although many of these have a Laurentian perspective. The Gondwanan record has been characterised as being dominated by arandaspid and some poorly understood microremains. In order





to address any potential bias, work has been undertaken in the Amadeus Basin (central Australia), the Precordillera and Cordillera Oriental (Argentina and Bolivia), and Oman to collect samples and to assess the palaeoenvironmental settings of each locality. It is evident from these studies that Ordovician fish occupied very similar environmental niches in both Gondwana and Laurentia, and that a degree of ecological segregation had developed between microsquamous lineages and heavily armoured ostracoderms forms within these shallow water palaeoenvironments. The recovery of new taxa, together with revised interpretations of previously described forms, provide the basis for a revised look at the palaeobiogeographical dispersal of early vertebrates, their phylogenetic relationships and palaeoecology.

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### Unlocking character preservation before chordate skeletonization: decay of the cephalochordate *Branchiostoma*

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The crucial stages in the origin and early evolution of chordates and vertebrates pre-date the appearance of a biomineralized skeleton. The poorly understood taphonomy of the soft-bodied fossils from this phase of evolution (e.g. *Pikaia*, *Haikouella*) makes their anatomy ambiguous and their phylogeny contentious. A better understanding of soft-tissue decay can constrain anatomical interpretations and answer the crucial question: does character absence reflect phylogeny or taphonomic loss? In order to resolve the taphonomic sequence of character loss, we experimentally investigated the decay of *Branchiostoma* (a.k.a. Amphioxus, the best extant proxy for the pre-vertebrate chordate condition). Anatomical synapomorphies defining Deuterostoma, Chordata and Cephalochordata are differentially affected by the processes of decay and therefore have different preservation potentials. Correlation between the taxonomic levels at which characters are informative and their relative order of taphonomic loss leads to systematic bias in the identification of putative chordate fossils. Reconsideration of the early fossil record of Chordata in light of this chronic bias highlights difficulties regarding current hypotheses of the affinities of purported stem-chordates and stem-vertebrates.

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### Trilobite eyes and their visual systems

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Because of its minute dimensions the tiny holochroal eye of the juvenile *Ctenopyge ceciliae* Clarkson & Ahlberg, 2003 appears to be far too small to be a truly functional compound eye. The great eye parameter, however, indicates a light gathering, functional system, sufficient enough to work under the bright light conditions beyond the water surface. This suggests that *C. ceciliae* was probably one of the first undoubtedly planktonic trilobites so far known. Some forms of schizochroal eye consist of individual primary calcitic columns, vertically running uninterruptedly throughout the lens. Gaps between them, arising during development, were probably filled with organic material, isolating each column. We have developed the concept that the whole system could have worked as a light guide bundle,



unique in the animal realm. There is another principle in the schizochroal eyes, where the lens is formed by a lens doublet with an aplanatic interface, avoiding spherical aberration and able to focus sharply. Using x-ray tomography we found internal eye-structures, still to be interpreted. The design of this eye is rather similar to that of certain jumping spider eyes, which have an aplanatic lens and an underlying vitreous body; a sharp image is formed onto a retina at the base of the eye.

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## Fossil evidence for the origin of spider spinnerets, and a new arachnid order

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Silk production from opisthosomal glands is a defining characteristic of Araneae. Silk emerges from spigots (modified setae) borne on spinnerets (modified appendages). Spigots from *Attercopus fimbriunguis*, from Middle Devonian (386 Ma) strata of Gilboa, New York were described in 1989 as evidence for the oldest spider and the first use of silk by animals. Slightly younger (374 Ma) material from South Mountain, New York, conspecific with *A. fimbriunguis*, includes spigots and other evidence which elucidate the evolution of early Araneae and the origin of spider silk. No known *Attercopus* spigots, including the original specimen, occur on true spinnerets but are arranged along the edges of plates. Enigmatic flagellar structures originally described as Arachnida *incertae sedis*, are shown to be *Attercopus* anal flagella, as found in *Permarachne*, also originally described as a spider. A new arachnid order, Uraraneida, is erected for a plesion including these two genera based on this combination of characters. Spinnerets originated from biramous appendages of opisthosomal somites 4 and 5; while present in *Limulus*, no other arachnids have opisthosomal appendage homologues on these segments. The spigot arrangement in *Attercopus* shows a primitive state prior to the re-expression of the dormant genetic mechanism which gave rise to spinnerets in later spiders. The inability of Uraraneida to control silk weaving suggests its use as a burrow lining or homing material.

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## The Ordovician Biodiversification: geologically or biologically triggered?

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The Ordovician witnessed the most sustained biodiversification of marine life in Earth history. The International Geoscience Programme project IGCP 410 (1997–2002) focused on this ‘Great Ordovician Biodiversification Event’ and resulted in the publication of diversity curves of all major Ordovician fossil groups. Its successor, IGCP 503 (2004–2008 ‘Ordovician Palaeoclimate and Palaeogeography’), has attempted to find the geological and biological causes for this biodiversification. Increasing sea-levels (with the highest levels of the Phanerozoic during the Ordovician), and warm climates before the end-Ordovician glaciation and its associated extinctions, were long considered to be possible biodiversity



triggers during a period of major continental spreading and dispersal. More recently, the Ordovician climate has been recognized as much more variable than previously thought, and a sustained period of cooling prior to the event has also been postulated. An episode of asteroid impacts in Baltica has been implicated in biodiversification on at least a regional scale, and the effects of major volcanism and orogeny in and around the Iapetus Ocean have also been considered significant. Major evolution of the phytoplankton at the base of the food chain generated a plankton revolution that followed the Late Cambrian and possibly had profound implications for the entire biota.

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## Review of bradoriid and phosphatocopid arthropods from the Early Cambrian of South Australia

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Bradoriids and phosphatocopids are small, bivalved arthropods which were an important component of Cambrian faunal assemblages before disappearing in the early-mid Ordovician. The group had a worldwide distribution and occurs in all of the major Cambrian Lagerstätten, including the Sirius Passet, Chengjiang and Burgess Shale faunas. In Australia, bradoriids and phosphatocopids from the uppermost Lower and Middle Cambrian (Ordian and Templetonian) of Queensland have been well documented, but faunas from Cambrian rocks in other parts of Australia are relatively poorly known. Recent investigations by the authors have revealed well preserved and diverse bradoriid assemblages (including new taxa) in both matrix and acid resistant residues from the Early Cambrian succession of South Australia. The assemblages display similarities to faunas from South China and Antarctica. The biogeographic distribution of the genus *Hipponicharion* is extended to eastern Gondwana. The recognition of distinct bradoriid assemblages associated with the *Abadiella buoi* (Atdabanian), *Pararaia tatei*, *P. bunyeroensis* and *P. janeae* (all Botomian) trilobite biozones indicates great potential for regional, and possibly intercontinental, biostratigraphic correlation. The widespread problematic small shelly fossil *Mongolitubulus* can be definitively referred to the Bradoriida based on the discovery of bradoriid specimens with the spine attached to the central region of the carapace.

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## Determining the microstructure of the lenses in the schizochroal eyes of trilobites.

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High resolution techniques including Electron Backscatter Diffraction (EBSD) have revealed new details of the internal structure of lenses in schizochroal eyes of trilobites, potentially providing a clearer understanding of how this optical system may have functioned. These results show that each lens is not a single crystal as previously reported, but is composed



of an array of micrometre sized sub-crystals. In genera including *Geesops*, *Ananaspis*, *Reedops* and *Boeckops* the sub-crystals vary in their *c* axis orientations along the visual surface, and some specimens also show the same structures along the lens base. Before assessing how these radial arrays of calcite crystals might have functioned, it is essential to ask whether they are primary lens microstructures or diagenetic artefacts. This is addressed using two approaches: (i) the investigation of lens chemistry at micrometre-scales using X-ray microanalysis and cathodoluminescence (CL) spectroscopy, and (ii) the study of petrographic relationships between the radial lens calcite and early diagenetic cements in the enclosing limestone. We hypothesise that if primary, the radial calcite array will be compositionally distinct from other parts of the exoskeleton and that the early diagenetic cements will have adopted the crystallographic orientation of their substrate.

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## Symbiont bleaching in fossil planktonic foraminifera and extinction in the latest middle Eocene

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Planktonic foraminifera underwent a major biotic turnover in the Middle Eocene with extinction of *Morozovelloides* and a significant reduction in the acarininid lineage. Sediments from the western North Atlantic (Ocean Drilling Program Site 1052) were examined at high-resolution (3 kyr) in order to investigate these extinction events. The large acarininids (*Acarinina mcgowrani*) terminate 10 kyr prior to the extinction of *Morozovelloides crassatus*. Preceding the extinction of *M. crassatus* morphometric analysis shows a reduction in test size. We used size restricted carbon isotopes ( $\delta^{13}\text{C}$ ) to track changes in the ontogenetic life strategies and show a long-term (1.5 million year) deterioration of *Morozovelloides* ecology that culminated in their extinction at 38.02 Ma. The decline in ontogenetic  $\delta^{13}\text{C}$  suggests diminished photosymbiotic activity (bleaching) and disruption of foraminiferal ecology. Stable isotope analyses and new Mg/Ca indicate that the extinctions of *M. crassatus* and *A. mcgowrani* occurred during a long-term cooling trend, but the biotic turnover in the muricate group was not related to significant sea surface temperature change. We conclude that the extinction of *Morozovelloides* and their diminutive size in the pre-extinction interval was not associated to temperature decline but directly related to the deterioration of photosymbiotic partnerships with algae.

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## Making ‘census’ of Ediacaran communities in Charnwood Forest

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Ediacaran biotas record a critical interval in life: the transition from predominately mat-based ecosystems to tiered metazoan communities, though there is little consensus regarding the affinities or ecologies of their constituent organisms. The Neoproterozoic strata of Charnwood Forest, near Loughborough (UK), have historically yielded several



cosmopolitan taxa, including the type specimens of the iconic *Charnia* and *Charniodiscus*, but the biota has traditionally been considered low diversity. New, large-scale moulding of multiple bedding-plane surfaces, totalling an area of about 175m<sup>2</sup>, reveals the biota to be of comparable diversity and abundance to those of the classic (palaeogeographically related) sites in Newfoundland. Each bedding-plane preserves a census population of a predominately tethered biota, felled and smothered *in situ* by consecutive low-density turbidites. A number of new taxa are recognised, including notably giant forms. The material provides a significant new window on deepwater Ediacaran biotas which is providing insights into endemism, community structure, ontogeny and taxonomic affinity.

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# Abstracts of poster presentations

\* Candidates for the Council Poster Prize are marked with an asterisk.

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## The effect of volcanic deposits from Montserrat, Lesser Antilles Volcanic Arc, on life on the sea floor

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In December 2008 research cruise JC18 collected marine cores from 35 sites around the volcanic island of Montserrat. Sampling ash-fall and pyroclastic flow deposits, erupted during the most recent collapse of the Soufrière Hills Volcano, this study aimed to assess the impact of volcanic eruptions on life on the sea floor. The devastation, and recolonisation of microfauna, was evaluated from analysis of samples from two of these sites. Within the first core (affected by ash-fall from the 2006 eruption) recolonisation of the sediments is observed to be already occurring. A high number of opportunistic species, typically found in stressful environments, were present, indicating early stages of recolonisation were well under way, less than three years after the volcanic event. However, to the southeast of the island, the second core (affected by flows formed from pyroclastic deposits) showed no signs of recolonisation. Thicker than the ash deposits, these soupy sediments appear unable to support life, and remobilisation of the sediments may cause constant disturbance to the sea floor, preventing recolonisation of the environment. This pilot study has produced a simple model of recolonisation for sediments around Montserrat, and it is this model that will be tested and verified as work continues.

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## Fossil floras on oceanic volcanic islands [part 1]: late Miocene – early Pliocene records of gymnosperms and laurisilva on Gran Canaria

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Fossil plant records from volcanic island archipelagos such as the Canary Islands are rare. This is unfortunate considering their importance in biological studies on biogeography and evolution. On Gran Canaria we have discovered a late Miocene – early Pliocene flora. Approximately 20 plant fossil horizons occur within clastic deposits associated with the end of a *ca.* 4 million year volcanic hiatus. Plants occur as casts of *in situ* tree stumps with associated prostrate logs, or as transported trunks, branches, twigs, leaves, and fruits. Wood fragments include *Tetraclinis* and *Pinus* and angiosperms. The leaf assemblage appears to be dominated by broad-leaved sclerophyllous genera of today's Macaronesian laurisilva. Less common fossils include fruits/capsules [of Lauraceae and eudicots] and monocot stems and leaves. These findings suggest that both laurisilva and *Pinus*-dominated ecosystems were established on Gran Canaria in the late Miocene/early Pliocene, supporting the concept of these elements of the Islands flora as Miocene relicts.



The study suggests great potential for finding fossil floras associated with other volcanic islands. These will provide essential data for research on the evolution of island endemic plants, testing of biogeographical hypotheses, and age constraints for molecular dating of phylogenies, plus climatological and palaeoecological research.

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### Using fossils as historical records of collectors: Charles W. Peach

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Charles W. Peach [1800–1886] retired from the Customs service and moved south from Wick to Edinburgh in 1865. This provided him with new opportunities for fossil collecting and scientific networking. Here he renewed and maintained his interest in natural history and made significant palaeobotanical collections from the Carboniferous of the Midland Valley of Scotland. Many of Peach's fossils have not only the locality detail, but the date, month and year of collection neatly handwritten on attached paper labels; as a result we can follow Peach's collecting activities over a period of 18 years or so. Comments and even illustrative sketches on his labels give us first hand insight into his observations. Novel presentation techniques included the preparation of the palaeobotanical equivalent of herbarium sheets. Peach also ground and prepared his own microscope sections of permineralised plant tissue using whatever materials he had to hand at the time. Study of these collections, now held in National Museums Scotland, reveals a pattern of collecting heavily biased towards those localities readily accessible from the newly expanding railways. These provided Charles Peach with a relatively inexpensive and convenient means of exploring the geology of the neighbourhood of Edinburgh.

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### The evolution of fossil preservation through the Precambrian–Cambrian transition

**Jonathan Antcliffe, Richard Callow and Martin Brasier**

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When did the animals originate? Why do almost the whole range of major animal body plans appear in a geological instant? Or is there a longer fuse to this evolutionary explosion? These are problems that were as significant and puzzling to Darwin as they remain today. To decode these enigmas we must look at the fossil record both before the Cambrian explosion and during these evolutionary events. The worldwide and pervasive preservation of soft-bodied fossils in the Neoproterozoic Era is unique in the history of life. Here the conditions that produced this extraordinary scenario are examined. A unified model is presented that also accounts for the decline of these processes in the Cambrian and later. This model has significant implications for when the animals originated.



## Jugal foramina as phylogenetic information in crocodylian evolution

**Marco Brandalise de Andrade**

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Jugals are particularly important as informative structures in crocodylian evolution. Morphological study of fossil/extant mesoeucrocodylians identified the occurrence and previously unreported diversity of patterns in the distribution of jugal neurovascular foramina. Neurovascular foramina are poorly documented, despite their occurrence in the jugal, premaxilla, maxilla, postorbital, dentary and angular. Jugal foramina are absent in archosauromorphs to basal mesoeucrocodylians, but occur in eusuchians, basal neosuchians and derived notosuchians. Within Eusuchia, small neurovascular foramina (2–5) face ventrolaterally in *Crocodylus* and ventrally in alligatorids, *Osteolaemus*, *Diplocynodon* and *Asiatosuchus*. No foramina were found in *Gavialis gangeticus* and *G. macrorhynchus*, but *Piscogavialis* has two enlarged foramina facing laterally. Basal neosuchians (*Pholidosaurus*, Dyrosauridae indet.) have two ventrally-oriented foramina, supporting phylogenetic proximity with eusuchians. Derived notosuchians (*Mariliaesuchus*, *Sphagesaurus*, *Adamantinasuchus* and *Comabuesuchus*) have a single enlarged and laterally-oriented jugal foramen, which is absent from *Notosuchus* and baurusuchids. Thalattosuchians seem to lack jugal foramina, which could be an atavism, or evidence for a basal position of this clade, within Mesoeucrocodylia. Crocodylians show distinct patterns of jugal neurovascular foramina, consistent with recent phylogenetic proposals. However, jugal foramina are still poorly documented and should be collected for several taxa (e.g. *Allognathosuchus*, *Pristichampsus*, *Bernissartia*, *Isisfordia*, *Sarcosuchus*, *Elosuchus*).

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## Thalattosuchian diversity of Solnhofen and niche partition among Mörsheim crocodylians

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The Solnhofen limestones of the Mörsheim Formation (uppermost Hybonotum zone, early Tithonian) have five species of thalattosuchians, each differing in aspects of feeding mechanics. *Dakosaurus* and *Geosaurus giganteus* were large-bodied (>2.5m) brevirostrine metriorhynchids with laterally compressed non-procumbent serrated teeth. Competition between these top-predators was prevented by differences in the rostrum and dentition (i.e. robust chopping teeth in *Dakosaurus*; blade-like teeth in *G. giganteus*). *Geosaurus suevicus* and *G. gracilis* were small (<2m) longirostrine metriorhynchids with procumbent dentition, piercing uncompressed and non-carinated teeth, indicating a primarily piscivorous diet. The delicate teeth of *G. gracilis* suggest further specialisation towards smaller/softer prey (crustaceans /soft-bodied molluscs). *Geosaurus suevicus* was probably a generalist feeder. *Steneosaurus priscus* combined large size (~4m) with tubular elongated rostrum and uncompressed non-carinated piercing teeth. These indicate a piscivorous diet, but postcranial morphology constrain this teleosaurid to a non-pelagic ambush predatory lifestyle. The extensive body armour of *Steneosaurus* contrasts with the flippers and caudal fin of armour-free metriorhynchids, which were active pelagic hunters. The diverse morphology of teeth, skull, post-cranium and size support the specialisation





towards particular diets among Solnhofen thalattosuchians. Niche partitioning is here hypothesised as the mechanism allowing the co-existence of these crocodylian taxa in the same palaeoenvironment.

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## Two stratophenetic phylogenies of the Cenozoic Planktonic foraminifera

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A stratophenetic phylogeny of the macroperforate Cenozoic planktonic foraminiferal morphospecies has been constructed using available literature. This initial phylogeny has then been transformed into a lineage phylogeny by removing cases of pseudospeciation and pseudoextinction (the appearance and disappearance of morphospecies by phyletic transformation rather than cladogenesis and true extinction). The phylogenies will be used for analyzing the evolutionary pathways and patterns of the planktonic foraminifera over the past 65 million years. They will be used to address key questions about speciation and extinction rates, body size changes, character loss and acquisition, and the adaptive evolution of the group over macroevolutionary timescales. We plan to use the tree to randomly sample the fossil record to select case studies for more detailed analysis (for example, to test Cope's Rule of phyletic size increase).

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## A cluster of *Maccoya* (Echinoidea) from the Carboniferous of County Donegal

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*Maccoya gigas* (M'Coy), the type species of *Maccoya*, is moderately abundant near its type locality in the Lower Viséan Rinn Point Formation, St. John's Point, County Donegal. It has interambulacral zones of four columns, rather than six as previously reported. A bedding surface shows at least 20 compacted but otherwise intact tests of *M. gigas*, in an area of 0.16 m<sup>2</sup>. Four are preserved with the periproct facing upward and the remainder on their sides. One specimen is larger than the others, which are interpreted as not fully grown. Elsewhere in the Rinn Point Formation, disarticulated plates and spines of *Archaeocidaris* sp. occur with *M. gigas*, but they do not occur on this bedding surface. The cluster of tests represents either a living assemblage demonstrating aggregation, or a post mortem accumulation. The upper surfaces of the tests are overlain by shale and in some cases by fenestellid fronds and are preserved intact, indicating that they were covered by sediment soon after death. However, none of the specimens have spines or periproctal plates in place, indicating some post mortem decay before the tests were entombed. The cluster is likely to be a post mortem accumulation resulting from storm current activity.



## Quantitative taxonomic and positional discrimination among hyracoid teeth using 3D Eigensurface analysis

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Tooth morphology and dentitions have contributed much of what we know about both the taxonomic and ecological diversity among Palaeogene hyracoids. The teeth of these once dominant Afro-Arabian herbivorous mammals ranged from bunodont to selenodont and lophoselenodont. Classification of hyracoids often relies solely on the teeth; however the degree of intra-specific variation, as well as issues such as wear, size dimorphism and deciduous dentitions, can be problematic. To help resolve these issues, shape variation across hyracoid teeth has been quantified. Upper molars from several late Eocene and early Oligocene genera from the Fayum Depression, Egypt, were subjected to eigensurface analysis. This method examines variation in surface structure across a sample. Modification to the technique allows points corresponding to the major cusps on each tooth to be constrained in the analysis. This increases the ability of this method to discriminate between groups and, for some taxa, between M1, M2 and M3. The eigensurface ordinations show that tooth shape similarity patterns are broadly consistent with recent phylogenetic hypotheses, and illustrate differences between the dental morphology of the oldest known Fayum genus to that of later Palaeogene hyracoids. These results can also be used to identify isolated molars and specimens of uncertain taxonomy.

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## Reconstructing the locomotor biology of *Acrocanthosaurus atokensis* (Dinosauria: Theropoda)

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I have used laser scanning and computer modelling software to create a 3D musculoskeletal model of *Acrocanthosaurus atokensis* (Dinosauria: Theropoda). The most complete specimen of *Acrocanthosaurus* has been digitized, providing a high resolution skeletal framework around which body cavities and internal organs have been reconstructed, allowing calculation of segment masses, centres of mass and moments of inertia for this animal. A sensitivity analysis has subsequently been carried out, in which the volumes of body segments and respiratory structures were varied in an attempt to constrain the plausible range in mass parameters. Locomotor musculature has been reconstructed on the basis of homologous osteological correlates of muscle-tendon insertions in extant archosaurs. Combining the mass and muscle-tendon reconstructions I have conducted a 3D dynamic simulation of locomotion in *Acrocanthosaurus*. To create stable locomotion, an appropriate muscle activation pattern has been developed by a distributed, parallel Genetic Algorithm (GA) optimization system. The GA system searches for muscle activation patterns that maximize performance according to specific fitness criteria (e.g. maximum running speed), thereby producing explicit quantitative predictions of gait. Sensitivity analysis will be used to quantify the effects of soft tissue and mass inputs on predicted gaits, using the ranges identified in this study.



## Estimating mass properties of dinosaurs using laser imaging and 3D computer modelling

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We used laser scanning and computer modelling to create 3D volumetric models of five specimens of non-avian dinosaur. The laser-scanned skeletal models provide a high resolution framework around which body cavities and internal organs were reconstructed. This allowed calculation of segment masses, centres of mass and moments of inertia for each animal. However, soft tissue reconstructions in extinct taxa inevitably represent best estimate models with an unknown level of accuracy. We have therefore conducted an extensive sensitivity analysis in which the volumes of body segments and respiratory organs were varied in an attempt to constrain the likely maximum plausible range of mass values for each animal. Our results provide wide ranges in actual mass and inertial values, emphasizing the high level of uncertainty in such reconstructions. However, our sensitivity analysis consistently places the centre of mass well below and in front of the hip joint in each animal, regardless of the chosen combination of body and respiratory structure volumes. These results emphasize that biomechanical assessments of extinct taxa should be preceded by a detailed investigation of the plausible range of mass properties, in which sensitivity analyses are used to constrain values to be used as inputs in analytical models.

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## Ferns, fires and disturbed environments: The role of wildfire across the Triassic–Jurassic Boundary in East Greenland

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The Triassic–Jurassic boundary (TJB) is marked by the third greatest ecological catastrophe in the history of life, with the loss of 23% of marine families and 22% of terrestrial families. This mass extinction event coincided with major environmental upheaval, highlighted by a perturbation of the global carbon cycle. Recent studies of the plant macrofossil record in the Jameson Land region of East Greenland have provided evidence of localised ecosystem instability prior to, and following, peak extinction at the TJB, demonstrating that terrestrial vegetation was profoundly disrupted at this time. Fire has played the role of cause, consequence and catalyst to the development of terrestrial life on Earth, yet remains largely unexplored as a potential mechanism of palaeoecological change across the TJB. To investigate these issues, we have undertaken a palynological analysis of the Triassic–Jurassic transition in East Greenland. Our study is based on samples collected from the fluvial–lacustrine Kap Stewart Group at Astartekløft. The fire history of the region, as recorded by fossil charcoal, has been set against the patterns of floral change, to assess the contribution of ancient wildfire to vegetation dynamics at the Triassic–Jurassic transition.

[Note: CMB and LM contributed equally to this work.]



## Macroevolutionary controls over body-size evolution in Palaeozoic Arachnomorpha

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Trilobites, as a highly diverse and long-lived arthropod clade (consisting of ~21,000 species and ~5,000 genera) are an ideal group with which to conduct macroevolutionary studies of size evolution. A database was constructed of dimensions from museum and literature sources. Including more than 12,000 trilobite individuals, this represents the temporal, taxonomic and spatial range of the major trilobite Orders. A history of body size evolution in the Trilobita is presented. A strong relationship with their diversification history is noted; an initial increase during the Early–Middle Cambrian followed by a steady decrease till the Permian punctuated by a rapid increase in the Early Devonian (Emsian). Spearman rank correlations support a highly significant positive correlation between size and diversity at both Class and Order level. The effects of the Ordovician extinction on Laurentian trilobites will be discussed. Finally, a preliminary examination of the Eurypterida suggests a more complex system with the largest pterygotids occurring at times of peak diversity, but with some stylonurids reaching large size during times of lower diversity.

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## Dinosaurs stepping on the conodont animals

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On the roof of a First World War tunnel in the Monte Pasubio (North Eastern Italy), on a supratidal stromatolitic bed of the Dolomia Principale Formation, 11 tracks have been found. Among them occur some clear dinosaurian tridactyl footprints, from small grallatorid-like to medium-large eubrontid, as well as some tetradactyl footprints. This formation contains the principal dinosaur footprints for the Triassic of the Southern Alps. All previous findings were on fallen blocks which, given the poor palaeontological content of the formation, and the lack of a precise stratigraphical position, made their biostratigraphical constraints very difficult to determine. In this case, for the first time, the trampled surface crops out *in situ*, about 500m from the bottom of the formation. Conodont sampling was carried out on the subtidal level just below the trampled surface. Unexpectedly, two conodonts were found: an advanced *Epigondolella praeslovakensis* and a true *Mockina slovakensis*, an association exclusive for the Middle Norian (latest Alauanian). Thus, being so precisely constrained, the ichnoassociation could be used to date the other isolated blocks of the Dolomites. Moreover this co-occurrence of tetrapod footprints and conodonts can be used to confirm the Middle Norian age of the *Eubrontes-Grallator* biochron.



## Planktonic foraminifera ecology and pelagic ecosystem recovery after the K/Pg Boundary Mass Extinction

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The Cretaceous/Paleogene (K/Pg) mass extinction seriously affected the marine ecosystem, with a 90% loss of Cretaceous planktonic foraminifera species. Surface to deep-ocean foraminiferal  $\delta^{13}\text{C}$  gradients and carbonate accumulation records show that this extinction coincided with a crash in organic matter flux to the sea floor and a long (3Myr) delay in recovery. This delay has been attributed to major disruption of the pelagic ecosystem due to extinctions of larger pelagic life that facilitate export of organic matter to the sea floor through faecal material, and the long timescales required for rebuilding complex food webs. This hypothesis, coined the 'living ocean' model, has potential problems. Firstly, benthic foraminifera, which utilise food from surface waters, do not show parallel patterns of extinction. Secondly, the 'final stage' of carbon system recovery coincides with major changes in planktonic foraminifera isotopic signatures as photosymbiotic ecologies diversified in several clades.

Here we present new planktonic foraminifera multispecies carbon and oxygen isotopic data from the lower Paleocene of Walvis Ridge ODP Site 1262, that reveal ecological evolution of the potentially important geochemical proxy species through the critical 'final stage' of carbon system recovery. These time slices provide a picture of depth-controlled thermal stratification of the upper water column compared to conditions at the sea floor, and a relative indication of the depth at which organic recycling was occurring in the water column. This fully astronomically tuned section has huge potential for resolving the detailed timing and palaeoecology of planktonic foraminifera after the K/Pg.

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## An investigation of exceptional, three-dimensional preservation in arthropods from Frome, SW England using synchrotron-based x-ray tomography

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Three-dimensional fossil shrimp, in which parts of the internal anatomy are preserved, often in exquisite detail and life position, have been recovered from Upper Triassic (Rhaetian) strata at Frome, Somerset, England. The host lithologies, thin, un lithified, clay layers, form part of a shallow marine sequence dominated by conglomerates and fine-grained carbonates. Remarkably, the fossils, which do not occur inside concretions, were reworked from another, unknown, possibly evaporitic, setting. Scanning electron microscopy and, in particular, synchrotron radiation x-ray microtomography were used to elucidate the internal structure. Abdominal and cephalothoracic musculature, the hepatopancreas, gonads and, in rare cases, blood vessels are replicated in calcium



phosphate. Nervous tissue and gills are represented by voids inside an extremely fine-grained carbonate infill. The gut and stomach are usually infilled with clay material. All organs are almost always preserved *in situ*; this resulted from the precipitation of carbonate inside the cuticle shortly after death. Notably, this carbonate often enclosed peripheral tissues and organs that decayed subsequently; their former presence is indicated by voids. Carbonate precipitation kept pace with the initial shrinkage of the musculature, then ceased. Subsequent decay of the musculature created voids inside the carbonate infilled partially by the remaining musculature.

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### Towards a solution for Darwin's Dilemma: remarkable preservation in 1 billion year old lake ecosystems in NW Scotland

**Martin Brasier, Leila Battison, Richard Callow and Jonathan Antcliffe**

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In 1859, Charles Darwin was puzzled by a seeming absence of fossils in rocks older than the Cambrian. But he made a prediction: *'The presence of phosphate nodules and bituminous matter in some of the lowest azoic rocks probably indicates the former existence of life at these periods'*. Indeed, in 1899, Archibald Geikie announced the first discovery of genuine microfossils in Precambrian phosphate – within the Torridonian rocks of Scotland. This Mesoproterozoic (~1Ga) phosphate is remarkable for its fidelity of fossil preservation, and also for its non-marine, intermontane lacustrine setting. The microbiology of this lagerstätten is being studied at Oxford, revealing fresh evidence for the earliest known terrestrial ecology. Delicate cellular and subcellular structures are preserved in the phosphate and show evidence for life cycles in cyanobacterial, eukaryotic protist and algal cells.

The ecological structure of these Torridon lake communities is compared with modern, mainly acidophilic lakes. The development of seasonal eutrophication and stagnation in the photic zone of the ancient lakes is expected. Such exceptional preservation in the Proterozoic is part of an emerging picture of better preservation of cells further back in the fossil record, attributed to very early diagenesis in a world before a sediment Mixed Layer.

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### Inside the cupboards of the African fossil mammal collection at the Natural History Museum (London)

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The African fossil mammal collection at the Natural History Museum in London forms an important palaeontological resource. The collection comprises numerous types and figured specimens such as the holotypes of *Megistotherium osteothlastes* (Hyaenodontidae, Creodonta), one of the largest terrestrial carnivorous mammals that ever lived, and the enigmatic *Quarunavus meyeri* (Ptolemaïida, Insectivora?). It is heavily used by researchers and has formed the basis for numerous theses and publications (some of which are pending). The collection is also a valuable historical resource, with a number of significant historical collections being housed here. The aim of the current project is to update the documentation of the African fossil mammal collection, with particular emphasis on improving the quality of the provenance data. It also aims to provide fuller documentation of holotypes in the collection, including producing digital images that can eventually



be uploaded to the web and accessed via a searchable online catalogue. The project is illustrated and discussed with reference to three significant historical collections: the Fayum Collection from Egypt, the Savage Collection from Libya, and the Leakey Collection from Tanzania and Kenya.

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## Modelling cranial sutures in Finite Element Analysis: a validation study using the domestic pig

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The use of Finite Element Analysis (FEA) to investigate feeding mechanics is becoming increasingly common. However, what little work has been done to validate the technique has been conducted almost exclusively on primates. This work represents the first attempt to validate cranial FE models of a non-primate mammal, by comparing specimen-specific models of the domestic pig, *Sus scrofa*, with strain data collected *in vitro*. Cranial sutures have been largely overlooked in FE models, despite evidence suggesting their important structural role as “shock-absorbers”, dissipating dangerously high strains. The pig models were loaded at the tooth row, and potentially functionally important sutures (zygomatic, coronal, maxillary-premaxillary) introduced in one of three ways; fused, open, or assigned elastic properties of collagen within sutures. Results show that sutures notably affect strain patterns throughout the skull, and more attention should be paid to their role in cranial FE modelling.

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## *Hydrobia* as ‘Jonah in the Whale’: Shell repair after passing alive through shelducks

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Vermeij’s use of repaired gastropod shell damage to estimate failed predation stimulated my research. The percentage of shells of the small (~5 mm) and abundant (up to 100,000m<sup>-2</sup>) gastropod *Hydrobia ulvae* in the Wadden Sea showing repair varied between localities from 2.8% to 41.8%. I also studied shell repair in *H. ulvae* after surviving passage through shelduck in the Mok, an embayment of the Wadden Sea on Texel. Shelduck feed by filtering mainly small molluscs from the sediment. *H. ulvae* forms an important food item. Passage of food through a shelduck is rapid. Their droppings collected at low tide consisted of up to 500 mainly crushed *H. ulvae* shells. Part of the shells was still intact even with the animal alive, but their shell had a broken outer lip. In aquaria I observed rapid shell repair, leaving a clearly visible scar on the shell. I conclude that part of the shell repair in *H. ulvae* in the Wadden Sea is related to (failed) shelduck predation. The high (11.2 to 41.8) percentage of repaired *H. ulvae* shells in the Mok as compared to an average of 7.7% at other Wadden Sea locations I relate to the relatively high number of shelduck feeding here.



## The evolution of phosphatic preservation across the Proterozoic–Cambrian transition

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The changing nature of phosphatic preservation of soft tissues between *c.* 1000 Ma to *c.* 450 Ma is outlined using both new and well-known examples. The first significant change is the departure from high-fidelity cellular (and possibly sub-cellular) preservation in the Precambrian, towards low-quality preservation of organic materials in the Phanerozoic. The locus of phosphatization is also observed to change from near-shore settings and close to the sediment–water interface during the Precambrian towards outer shelf environments and at greater depths below the sediment surface in post-Cambrian times. Lastly, we show the change from the phosphatization of photoautotrophic organisms in the Precambrian towards the preservation of faecal matter and processed remains during the Phanerozoic. A model is put forward to link these observations to biological innovations, including the onset of bioturbation and grazing (including zooplankton), and to episodic increases in the degree of mixing and oxygenation of the oceans and sediment.

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## Exceptionally preserved microbes and mats from the late Ediacaran Longmyndian Supergroup, England

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A variety of macroscopic bedding plane markings are common on bedding planes of the late Ediacaran Longmyndian Supergroup. These markings were first described by J.W. Salter in 1856 and were even noted by Darwin in the ‘Origin of Species’. While some of these markings have been interpreted as trace or body fossils, others are now believed to represent the sedimentary expressions of unpreserved microbial mats. Until now, the mat-building microbes themselves have not been widely reported from these sediments. Our study of historic and fresh collections allows us to report the discovery of exceptionally preserved filamentous and sphaeromorph microfossils in the Longmyndian. The microbes are variously preserved as carbonaceous films, by aluminosilicate permineralization and as three-dimensional bedding plane impressions. This preservation has important implications for our understanding of ancient microbial communities and taphonomy during the Ediacaran period. These observations support the long-suspected link between wrinkle markings and microbial mats, and draws attention to the apparent bias towards high-quality soft-tissue preservation in the Ediacaran Period.

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## Late Ordovician (Katian) brachiopods from the Southern Uplands of Scotland: Biogeographic patterns on the edge of Laurentia

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Some 40 brachiopod species are known from the localities of Kilbucho and Wallace’s Cast from the Kirkcolm Formation in the Northern Belt of the Southern Uplands of Scotland.





The fauna is diverse despite the relatively small numbers of brachiopod specimens (*c.* 180) available for study. Much of the fauna was transported downslope and is locally preserved in obrution deposits. It represents a broad census of outer shelf and upper slope palaeocommunities around this part of the Laurentian margin during the early Katian and is dominated by relatively small plectambonitoid brachiopods. A brachiopod-dominated fauna of shallower-water origin (which also includes a polyplacophoran mollusc together with diploporite cystoids) is found mixed with taxa from deeper-water environments. They represent a community that lived above storm-wave base. When compared with other circum-Iapetus assemblages, the brachiopods from the Southern Uplands compare most closely with those from the Bardahessiagh Formation, Pomeroy, Northern Ireland rather than with adjacent, well-known faunas from the Girvan district, SW Scotland. These new data suggest that this part of the Southern Uplands was located in closer proximity to Pomeroy than Girvan, located in deep-water environments similar to those of the upper parts of the Bardahessiagh Formation.

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### Palaeoecology and microfacies analysis of a basal Triassic microbialite from within a Panthalassan seamount setting

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The Griesbachian limestones of the Kamura Formation, southwest Japan, accumulated on a seamount in Panthalassa and preserve a typical low-diversity skeletal assemblage dominated by molluscs, suggestive of the earliest recovery interval after the end-Permian mass extinction. These Griesbachian limestones were also reported to contain unusual microbial ‘bindstone–cementstone’ facies interpreted as ecological ‘disaster forms’ flourishing within the Scythian reef gap. This study combines palaeoecological analysis of fossils in thin section with microfacies analysis of the microbial horizons, in order to: 1) gather palaeoecological index data for comparison with other coeval sections from different settings, and 2) determine the precise ecological controls on the proliferation of the microbial communities to provide a test for the ‘ecological disaster taxa’ model. The results of these two approaches suggest that the Kamura microbialites are a facies-dependent phenomenon existing within a rare depositional environment, with analogous communities in the present day, and therefore do not require special environmental interpretation as ‘disaster taxa’. Furthermore, the unusual carbonate fabrics within the Kamura Formation may provide a unique record of hurricane-strength storms in the Griesbachian of Panthalassa, which have been predicted by theoretical models to have been more frequent, and more violent, than those seen in the present day.

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### Reweaving the tapestry: A species-level supertree of birds

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Supertrees are a useful method of constructing large-scale phylogenies by assembling numerous smaller phylogenies that have some, but not necessarily all, taxa in common. Supertrees have now been produced for a diverse range of taxa including dinosaurs, mammals and crocodiles. Birds are an obvious candidate for supertree construction as they are the most abundant land vertebrate on the planet and no comprehensive phylogeny



of both extinct and extant species currently exists. Here, a species-level supertree has been constructed containing 5,274 taxa from 757 source trees. The tree shows generally-accepted relationships between the main groups, with only a few novel clades, most of which can be explained by a lack of information regarding those taxa. The tree was constructed using a strict protocol, which ensures robust, accurate and efficient data collection and processing. Additionally, it was constructed in a collaborative fashion by placing the source trees and MRP matrix on the World Wide Web for the scientific community to download. No shorter trees were found using this community-based method of tree-building, but it still proved invaluable in identifying taxonomic errors that would otherwise have had a negative impact on the resultant supertree.

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### Muddy Waters to Sandy Shore: numerical analysis of historical data

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Museum collections may be the only source of palaeontological material for localities now unavailable for sampling. The question arises as to whether meaningful palaeoecological signals may be preserved in such historical collections even though they were not sampled for such analysis. The collections of the British Geological Survey reflect the extensive mining, quarrying and sinking of cored boreholes associated with the exploration and exploitation of coal, ironstone and other economic deposits such as limestones in the Carboniferous of the Midland Valley of Scotland from the late 18th to the mid-20th century. Explorative numerical analysis using seriation, cluster analysis and Principal Components Analysis of 116 such samples from 67 localities in the Hurler and Index limestones of Ayrshire yields patterns of taxonomic co-occurrence, trophic structure and links to lithofacies that compare very favourably with the qualitative analyses published by the BGS geologist R. B. Wilson which arose from over forty years of experience on the Carboniferous successions of the Midland Valley. Moreover, draping the geographical distribution of the clusters of taxa for each limestone over a 3D computer model of the subsurface illustrates the influence of penecontemporaneous fault movement over the palaeoenvironments.

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### Palaeoecology of the *Chaetetes*-Band: a numerical approach

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The *Chaetetes*-Band, a highly fossiliferous sponge biostrome commonly occurring near the base of the upper Mississippian (Serpukhovian) Great Limestone of northern England, comprises a range of fossiliferous limestone facies. Explorative numerical techniques applied to samples from seven localities on the Alston Block reveal contrasting links to lithofacies in the benthic and conodont faunas and enable species and genus-level associations, trophic structures and palaeogeographical distributions amongst the benthos to be determined. The biohermal 'Coral-band' facies characteristically includes species of the corals *Diphyphyllum*, *Lonsdaleia*, *Actinocyathus* and *Dibunophyllum*, with some species of *Diphyphyllum* restricted to the facies, and pelagic conodonts including species of *Kladognathus*, *Gnathodus* and *Vogelgnathus*. The biohermal '*Chaetetes*-band' facies characteristically includes



benthic *Chaetetes*, with the coral *Syringopora*, the brachiopod *Schizophoria* sp. and bivalve *Dunbarella radiatus* restricted to the facies, and pelagic and nekto-benthic conodonts including species of *Gnathodus*, *Kladognathus* and *Cavusgnathus*. Encrusting *Chaetetes* is absent from both the 'Coral-band and Bioclastic' and 'Bioclastic' limestone facies, which may have been deposited in higher energy environments. Cluster analysis of the numbers of benthic genera in higher taxa provides six clusters. Dominant throughout are epifaunal suspension feeders, though four clusters apparently include an increased proportion of detritivores, and two of them also show an increased proportion of predators.

## How good is preservation of biodiversity in dead shell assemblages of bivalves? The case study of Touho Lagoon (Northeast of New Caledonia)

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Reliability of fossil assemblages for diversity estimates and palaeoenvironmental reconstructions depends on how well the original properties of local biodiversity are sampled. Preservation quality should vary according to environmental and sedimentary parameters. We test this assumption in the Touho area that offers a high diversity of molluscs and a wide range of ecosystems from mangrove to reef flat, beach, pass, estuary, mudflat, etc. The dataset combines information from more than 83,000 bivalve shells collected from 37 stations. Each shell is identified at the species level and counted as dead or alive. Each station is described by complementary measures of living biodiversity and of its preservation in the dead assemblages: species richness, standardized diversity, rarefaction curve, PIE index of evenness, and the fidelity indices of Kidwell & Bosence (1991). As expected, the preservation of biodiversity is highly variable. For example, the percentage of living species found dead at the same station fluctuates from 18% to 100%. On average, preservation is higher in fine sands, and decreases conversely to grain size. Communities typical of mangrove are poorly preserved *in situ* due to dissolution and transport. All metrics of biodiversity are significantly altered in dead assemblages, evenness being the most conservative.

## Stars of the Caribbean Miocene: Grand Bay Formation, Carriacou, The Grenadines

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Hitherto, the fossil record of asteroids (starfishes) and ophiuroids (brittlestars and basketstars) in the Antilles consisted solely of disarticulated plates (ossicles). Asteroid and ophiuroid ossicles are widely distributed in the Upper Cretaceous and Cenozoic of



the Antilles, but have received little attention and remain essentially unknown in the fossil record here. The first 'starfish bed' to be recognized, in the Cenozoic of Carriacou, is therefore significant. The Middle Miocene Grand Bay Formation comprises beige to light brown, fine- to coarse-grained volcanoclastic sandstones with intercalated horizontally and finely laminated to massive silty and sandy mudstones and calcareous mudstones, associated with sporadically developed volcanogenic pebbly sandstones and conglomerates. It is abundantly fossiliferous. Previous fieldwork on Carriacou led to a better understanding of the sedimentological and tectonic evolution of the Grand Bay Formation (Donovan *et al.* 2003, *Lethaia*, **36**, 255–272), deposited at 150+ m depth in a turbidite basin with siliciclastics derived from a single volcanic source (Jackson *et al.* 2008, *Caribbean Journal of Science*, **44**, 116–124). This combination of turbidite basin deposition in a region of active volcanism led to the formation of a rare deposit, a starfish bed. A goniasterid asteroid and an ophiothrid(?) ophiuroid are currently being described.

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### Responses to differences in habitat: Ecophenotypic variations of *Encrinurus liliiformis* (Echinodermata: Crinoidea) from the middle Triassic of the Central European Basin

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*Encrinurus liliiformis*, a well known crinoid from the middle Triassic Muschelkalk of the Central European Basin, shows a great variation in crown morphology. In order to quantify these differences in crown shape, a statistical analysis of distinct populations from two localities in Southwest Germany was conducted. The population from Crailsheim reflects a shallow water habitat on a carbonate ramp, whereas the Neckarwestheim population shows a deeper basinal environment. The comparison led to a distinction of two ecophenotypes adapted to the varying habitats: 1) an ecophenotype originating in shallow water showing shorter brachia with less ornamented surfaces of brachials, and 2) an ecophenotype originating in a deeper water environment showing longer brachia and a higher degree of ornamentation on brachial surfaces. Possible interpretations of these differences refer to a reaction to predatory pressure and water flow energy, which is important for food resources of the filter feeding animals. Additional *Encrinurus* crowns from a third population (Mistlau) reflecting a deeper water environment were included in the study because of their high degree of ornamentation on the brachials. The analyses of this population show an intermediate position concerning morphology with strong ornamentation patterns but arm ratios similar to those of shallow water specimens.

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### A Faith and Fossil Network: Proposal for public engagement of Palaeobiology

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We approach the Darwin celebrations in 2009 with the scientific basis for evolution strengthened from all branches of scientific endeavour, not least palaeontology. Ironically, anti-evolutionary notions appear to be more prevalent now than ever. In particular, the fossil record has been misrepresented perhaps more than most fields. To engage more



fully with public understanding of evolution, palaeontology and science we propose to establish a network to provide: 1) corrections to arguments pertaining to the fossil record used to deny evolution; 2) the gold standard for fossil evidence of evolution to those who are sceptical or confused in a manner that is non-threatening to a religious worldview; 3) a project to demonstrate in 'real time' a new fossil discovery being understood and how this reinforces, fits or revises current understanding; 4) an accurate and scholarly background on some of the historical and philosophical aspects that is likely to be outside the training of most palaeontologists. The overall aim is to provide excellent science education in a forum that is credible to scientists and religious people. Such a programme would be a fitting tribute to Darwin who painstakingly developed the case for evolution while displaying a degree of sensitivity to the religious perspectives of his day.

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### The early Ordovician diversification and dispersion of the Orthoceratoidea (Cephalopoda)

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The cephalopod assemblages of the Early Ordovician of England & Wales and the Durness Limestone of Northwest Scotland (early Floian) contain what are currently believed to be the oldest known members of the cephalopod Class Orthoceratoidea. Despite separation by an ocean, many of the taxa present in each area are similar and coeval. No definite members of the Orthoceratoidea are known from coeval or older strata elsewhere. This suggests that the origination, diversification and dispersal of the Orthoceratoidea was (in terms of geological time) extremely rapid.

The Orthoceratoidea are clearly distinct from the Nautiloidea, as indicated by a variety of characters. A number of characters blur this distinction and have led to the proposal of alternative phylogenetic models for the early Orthoceratoidea that suggest that they are either paraphyletic or monophyletic. This is further complicated by the proposal of a Palaeocephalopoda and Necephalopoda, the division between which lies within the Orthoceratoidea. A review of these models in the light of the recent discoveries (above) suggests that the group is monophyletic. Eustatic sea-level rise is considered to have had a role in their diversification and dispersal.

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### Bringing the Thylacocephala out of their shell: Enigmatic arthropods and tomographic reconstruction

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The Thylacocephala are an enigmatic arthropod class with a combination of primitive and derived features. There is limited knowledge of the group's anatomy and origins, largely because an all-encompassing carapace hinders the recovery of key pieces of morphological data, such as the attachment position of appendages. The result has been three decades of debate over thylacocephalan affinities and palaeobiology. Tomographic reconstruction allows anatomy hidden within the carapace to be studied. Computer models of a three-dimensionally preserved Middle Jurassic thylacocephalan (*Dollocaris ingens*, from the La Voulte-sur-Rhône Lagerstätte, France) are presented. These were built from physical-



optical tomography (serial grinding) and X-ray microtomography, and document – for the first time – the internal anatomy of the Thylacocephala. This includes structures associated with derived crustaceans such as pleurobranch gills, hypertrophied eyes and a complex digestive system, but also seemingly primitive ones such as an undifferentiated trunk. The findings add significant information to the body of knowledge surrounding the Thylacocephala, but data do not yet allow an authoritative inference of their phylogenetic position. This study also demonstrates the power of ‘virtual palaeontology’ to resolve problematic anatomy, especially where three-dimensional exceptionally-preserved fossils are available.

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### Computer reconstruction of Carboniferous trigonotarbids

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Many Carboniferous Konservat-Lagerstätten host three-dimensionally preserved fossils within siderite (FeCO<sub>3</sub>) concretions. To work with this material, palaeontologists have traditionally relied upon physically splitting the nodules and optically studying the sections through the fossil thus exposed; anatomy not revealed by the split remains hidden. In this project high-resolution X-ray computed tomography was used to reconstruct three-dimensional computer models of fossils preserved in this manner in the Coseley Lagerstätte, West Midlands, UK (Upper Carboniferous). Material studied comprised several species of the extinct arachnid order Trigonotarbida, an important group in Coal Measures ecosystems. New details on the anatomy of *Anthracomartus bindi* were documented, and strong similarities to *Cleptomartus plautus* were apparent. Species of the genera *Eophbrynus* and *Anthracosiro* were also reconstructed, providing new anatomical data. The models provided valuable new information on the interrelationships between trigonotarbid genera. This study represents the first ‘virtual palaeontology’ work undertaken on the Trigonotarbida, and has demonstrated that previous problems reported with X-ray microtomography of siderite concretions can be overcome with modern, high-resolution equipment; it is now possible to successfully extract fine three-dimensional anatomy from even decimetre-scale siderite concretions.

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### Biomarkers in coprolites – a new approach to determining the diet, digestive processes and gut microbiota of extinct animals

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Biomarkers are molecules that can be attributed to a biological source on the basis of their chemical structure. Biomarker analysis can extend the utility of coprolites as repositories of palaeobiological information by identifying dietary components, specific digestive processes and gut microbes, with reference to modern analogues.



A suite of modern faecal samples from herbivorous mammals was analysed and a clear difference in biomarker content between foregut-fermenting animals and hindgut fermenters was found, namely the presence of the archaeal biomarker 'archaeol' in the former group only, attributed to digestive tract methanogens. Thus, the occurrence of archaeol in a coprolite may be evidence that the producer was a foregut fermenter. We also found a consistent relationship in hindgut fermenters' faeces between mean ingesta retention time and the ratio of  $5\beta$ -epistigmastanol/ $5\beta$ -stigmastanol, which may allow the mean ingesta retention time of extinct animals to be determined. Analysis of a coprolite of the ground sloth *Nothrotherium shastaensis* found the biomarker profile dominated by epismilagenin, a product of structural modification in the gut of smilagenin, a secondary metabolite found in some plant taxa including the genus *Yucca*. The biomarker evidence therefore supports previous interpretations of a yucca-rich diet for *Nothrotherium shastaensis* based on genetic and other evidence.

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### Inside and out: the lower jaws of two basal mammals

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Two of the first mammals, *Morganucodon* and *Kuehneotherium*, are found in Early Jurassic fissure deposits from South Wales and, although the bones are fragmented, the abundance of material offers a unique opportunity to study individuals at varying stages of their growth and tooth replacement. We use high-resolution CT images and 3-D reconstructions to provide new insights into the jaw and dentition of these mammals.

Complete lower jaws of *Morganucodon* and *Kuehneotherium* are digitally reconstructed in 3-D to illustrate differences in both external morphology and internal structure. Synchrotron-radiation X-ray tomographic microscopy (SRXTM) provides a powerful non-destructive tool to reconstruct histological details such as Lines of Arrested Growth (LAGs) and these are mapped on the reconstruction to reveal the remodelling of the dentary during life. A notable feature of the *Kuehneotherium* reconstruction is the enlarged mandibular canal, which carries the mandibular artery and trigeminal nerve, suggesting increased support for sensory receptors. The pattern of tooth replacement is of interest in such basal mammals, where diphyodonty is just being established. High-resolution scans of different growth stages illustrate the development of replacing teeth and the shedding and resorption of the anterior premolars.

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### Organic-walled microfossils from the Forteau Formation: Fleshing out an Early Cambrian shelly biota

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Shales of the Forteau Formation (western Newfoundland, Canada) preserve a decidedly unremarkable roster of Early Cambrian macrofossils: trilobites, hyoliths, inarticulate brachiopods, and the agglutinating problematicum *Salterella*. However, hydrofluoric acid maceration yields a suite of diverse and well-preserved organic-walled microfossils. Alongside more conventional palynomorphs such as acritarchs and



cyanobacterial filaments, the acid preparations contain organic components derived from the biomineralized portions of trilobites, hyoliths, brachiopods, palaeoscolecid and hexactinellids, as well as teeth, spines and sclerites of various non-mineralizing taxa – notably scalidophoran worms, non-trilobite arthropods, and the lophotrochozoan *Wiwaxia*. Further new additions to Forteau diversity include probable organic-walled variants of ‘small shelly’ fossils, including siphonochitid sclerites and a variety of ornamented cones; the affinities of other forms remain entirely obscure. The extent to which the small-scale organic fossils share a taphonomic pathway with more fully expressed (*i.e.* macroscopic) Burgess Shale-type preservation is uncertain, although their presence in the Forteau Formation clearly indicates a less restricted distribution. Indeed, as a potentially widespread phenomenon in the marine fossil record of the Proterozoic and early Palaeozoic, fine-scale organic preservation promises to be a rich source of insight into large-scale palaeobiological patterns across this key transition in Earth history.

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### Preservation of biomarkers in Green River fossil fish and sediments

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Nitrogen and carbon isotopic ratios have been used to investigate the community structure and palaeoenvironmental changes within the Green River Formation, Wyoming, USA. Given that nitrogen and organic carbon are present in Green River fossils, one of the fundamental questions posed by this research concerns the nature of the organic matter in which they are preserved, and whether these bulk isotope signals are from original fish organic matter. Organic biogeochemical analyses were carried out in order to assess the composition and preservation of the organic matter from which the N and C<sub>org</sub> isotopes were derived. Total organic carbon content was high in both fossil fish and the surrounding sediment, but nitrogen was found only in the fish samples. Lipids were successfully extracted from the fish and the fatty acid methyl ester profiles were quantitatively and qualitatively different to those from the surrounding sediment, confirming the presence of organic carbon in the 50 million year old fossil fish. Dinosterane was found in all samples and is the diagnostic biomarker for dinoflagellates, indicating an abundance of dinoflagellates at time of deposition. This suggests harmful algal blooms could be a possible causal mechanism for the fish mass mortality events in Eocene Fossil Lake.

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### The Early Cambrian tommotiid *Micrina*, a sessile bivalved stem group brachiopod

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The tannuolinid *Micrina* belongs to the tommotiids – a common and widely-distributed, but poorly understood group of Early Cambrian fossil metazoans with external





organophosphatic sclerites. Findings of sessile articulated tommotiid scleritomes indicate that previous reconstructions of tommotiids as slug-like bilaterians with a dorsal cover of sclerites require detailed re-evaluation. Ultrastructural work has already indicated that the tommotiids might be a sister group to the Brachiopoda, with *Micrina* representing the most derived and brachiopod-like bimembrate tommotiid. Here we further develop and strengthen this controversial phylogenetic model with a new reconstruction of *Micrina*, where the two types of sclerites – mitral and sellate – belong to a near bilaterally symmetrical bivalved sessile organism. This new scleritome configuration was tested by recreating an articulated bivalved *Micrina* from isolated mitral and sellate sclerites; both sclerites have muscles that would have enabled movement of the sclerites. The mitral and sellate sclerites of *Micrina* are considered to be homologous with the ventral and dorsal valves, respectively, of organophosphatic linguliform brachiopods, indicating that simple filter-feeding within an enclosed bivalved shell had started to evolve in derived tannuolinids. The new reconstruction indicates that the phylogenetic range of ‘bivalved’, sessile lophophorates is larger than previously suspected.

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### Subcellular structures in Ediacaran fossil cleavage embryos

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The Ediacaran Doushantuo phosphoritic deposits in southern China hold exquisitely-preserved microfossils, and a large number of papers on this biota have been published. The controversial cleavage embryos, preserved as diagenetically phosphatized replacements and encrustations, have been proposed to belong to animals, but no co-occurring adult forms have yet been identified. Recent studies, in which fossil embryos were analysed with synchrotron-radiation X-ray tomographic microscopy (srXTM), have shown that with this technique it is possible not only to distinguish between taphonomic and diagenetic features, but also to depict cellular and subcellular details of the internal structures. In this study, we describe some of the diversity of internal morphological features found in early-stage cleavage embryos by use of srXTM. A few exceptionally-preserved four-cell stage specimens exhibit subcellular structures indicative of eukaryotic affinity, such as complex nucleus-like structures, which are centrally located in each cell. One of these displays a spiral structure on the surface of each blastomere, suggesting affinity with *Spirallicellula* Xue *et al.* 1995. Other specimens display spheroidal and ovoidal structures interpreted as lipid vesicles or yolk granules. In 2007, Bailey *et al.* (*Nature* 445) published an alternative interpretation, in which they propose that the alleged cleavage fossils represent giant sulphur-oxidizing bacteria. However, recent decay studies of modern animal embryos in combination with the likely eukaryotic subcellular features described here support the interpretation that these Ediacaran fossils from the Doushantuo Formation are in fact of embryonic nature.



## What makes a species a species? Testing the validity of morphological characters in fossil and recent isocrinid crinoids

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The fossil record of post-Palaeozoic crinoids tends to be fragmentary, so studies on fossil crinoids have conventionally used these elements for systematic purposes. Many taxonomic studies have employed the number of internodals (IN) along the stem as an important diagnostic character. However, recent research on two modern taxa (*Neocrinus* and *Endoxocrinus*) from the Bahamas revealing large morphological variation in IN, has cast doubt on this idea. This study investigates the validity of the hypothesis that IN is a key character in modern crinoid taxonomy, using the PAST statistical software to produce a multiple component plot of modern crinoids collected off Japan and Australia. This survey uses five different species belonging to two distinct genera (*Metacrinus* and *Saracrinus*), inhabiting seven communities at varying depths. Results suggest that, despite apparent variability within each individual segment, values of IN are statistically strongly correlated within species and are thus consistent. The results also indicate that individuals with greater IN present a broader range of variability within species. In terms of distinguishing species however, separating values from parts of the crinoid which have lower IN appears problematic. Significantly, this study suggests great difficulty in identifying fossil forms from fragmentary material within the Mesozoic.

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## Palaeoecological change through the Permian–Triassic Mass Extinction Event: Comparison of methods

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Different authors use different methods to assess Permian–Triassic palaeoecological changes, yet no comparative study of different methodologies has been published. We compared two methods of assessing palaeoecological parameters such as diversity, richness and skeletal abundance from limestone thin sections: point counting and an equal-area approach. Results demonstrated that there are significant differences between methodologies. Point counting is relatively ‘quick and dirty’. It is somewhat biased with respect to organism size, by overemphasizing larger taxa/bioclasts, and underemphasizing smaller taxa/bioclasts. Some point counting ‘palaeoecological’ data are not considered useful for measuring biotic recovery, as previously suggested by some authors, because they are affected by taphonomic processes. The presence of diagenetic veins may reduce apparent abundance; winnowing may increase it. Trends in abundance between locations and regions through time, however, tend broadly to agree between methods, although we recorded Early Triassic samples with much higher skeletal abundances (up to 75%) than in previous published studies. Data from locations in Italy, Oman and USA were compared. The most diverse samples are Griesbachian in age from Oman, whilst the Dienerian–Smithian samples from western USA are less diverse. These data agree with previously published inferences of varying recovery rates based on analysis of tiering and trace fossils.



## The stratigraphic and palaeogeographic occurrence of the Mid-Permian pollen grain ?*Florinites balmei*

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Palynological assemblages from the thin dark shale-sandstone interbeds of the Sardhai Formation, lying between the Amb Formation limestones and red-beds of the Warcha Formation in the Salt and Khisor ranges of Pakistan, contain abundant bisaccate pollen grains and few spores. In particular, well-preserved specimens of ?*Florinites balmei*, a bilaterally symmetrical monosaccate pollen, are common. This pollen was first described by Stephenson and Filatoff in 2000 from the basal Khuff clastics of Saudi Arabia, and since that time it has also been described from Oman. As yet unpublished data show that ?*F. balmei* occurs in the Kas Formation of southeastern Turkey, the Nesen Formation of Iran and the basal Khuff clastics of the United Arab Emirates. Specimens very similar to ?*F. balmei* but described as *F. millotti* also occur in the Chia Zairi Formation in northern Iraq. Apart from palynological similarity, Permian lithologies are also similar between Arabia (Saudi Arabia and Oman) and Pakistan: both have successions of glacial diamictites at the base, continuing with red beds, followed by distinctive dark shale-sandstone interbeds and concluding with thick limestones. The presence of ?*F. balmei* suggests that the Sardhai Formation can be assigned to the Arabian OSPZ6 biozone, indicating a probable Wordian or Capitanian age.

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

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

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## Asynchronous response of Caribbean and Southeast Asian coral reef ecosystems to Cenozoic global change

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Analysis of specimen-based compilations of reef-coral species occurrences indicates widely differing Late Oligocene to Recent trajectories for coral reef ecosystems in Southeast



Asia and the Caribbean. Caribbean reef ecosystems were altered by regional extinction during the Oligocene/Miocene and the Pliocene/Pleistocene. The Oligocene/Miocene extinction was associated with the collapse of reef building in the region, but contrary to expectations, the Pliocene/Pleistocene extinction is associated with regional reef recovery. The depauperate extant Caribbean biota includes survivors of this extinction, and very few new species have appeared since. In Southeast Asia, there was an expansion in reef carbonate development during the Oligocene/Miocene that coincides with diversification of reef biota. No intervals of accelerated extinction have been discovered in the Southeast Asian Neogene, suggesting that the high diversity of the regional reef biota is a function of continuous diversification, and that reefs in the region were not substantially affected by Neogene climate change. These results suggest that the regional response of coral reef ecosystems to global environmental change is strongly modulated by regional historical factors. Attempts to understand long-term global patterns of diversity and ecosystem distributions are enhanced by analysis of variation at non-global scales.

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### Testing hypotheses of conodont ecology using tooth microwear analysis

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Tooth microwear and surface damage analysis is becoming an increasingly important tool in unravelling the trophic ecology of vertebrates. The fossil record of conodont teeth is the best of any vertebrate group, yet no systematic analysis of wear and surface damage on their skeletal elements has hitherto been conducted. We have undertaken the first quantitative analysis of the frequency of occurrence and degree of damage and wear in conodont elements. The work was based on large numbers of very well-preserved  $P_1$  elements from a variety of late Palaeozoic taxa hypothesised to occupy different environments. Elements were imaged using high-resolution focus-variation optical microscopy, a faster and cheaper alternative to SEM photomicrography. Our results indicate that microwear varies between taxa, and that this reflects differences in their niches. The success of this technique has wide-ranging implications for unlocking the fossil record of conodonts, providing palaeoecological information that can be used to constrain oxygen isotope palaeo-thermometry derived from conodont element apatite, offering a means of validating functional hypotheses and furnishing direct information on diet-mediated processes driving observed patterns of evolutionary change.

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### Stepwise changes in the diet of the plant eating mammal *Plagiolophus minor* across the Eocene–Oligocene transition

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Changes in the diet of *Plagiolophus minor* (Mammalia: Perissodactyla) occurred in two major steps across the Eocene–Oligocene transition of Europe. The first significant change in dental mesowear and microwear occurred in the Late Eocene when cusp roundness, pit number and mean pit size increased, and occlusal relief decreased. These all indicate a browsing diet and suggest a major increase in the consumption of abrasive material. The second step occurred across the mammalian faunal turnover, the Grande Coupure, during the earliest Oligocene. There was a continuation of the trend in increased abrasiveness



shown by the decrease in occlusal relief and increase in pit number. However cusp roundness, scratch number and the size of pits did not change. Immediately after the Grande Coupure, there was no significant change in any of the dental wear variables. The timing of the dietary changes corresponds to stepwise changes in ice volume and global temperature, including the Oi-1 glaciation, which was coincident with the Grande Coupure. The lack of dietary change immediately after the Grande Coupure occurs at a time when there were no major steps in ice volume and temperature. The increase in abrasiveness reflects the general cooling trend across the Eocene–Oligocene transition.

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### The first micro-tomographical studies of a eurypterid

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An unusually well-preserved sea scorpion (Chelicerata: Eurypterida) from the Hunterian Museum, Glasgow was restudied using micro computed-tomography ( $\mu$ CT). Provisionally labelled as *Rhenopterus* sp., this Early Carboniferous specimen from Montagne Noire, France is probably an *Adelophthalmus*. Such three-dimensional fossils of eurypterids are extremely rare and this is the first time that one has been reconstructed using this methodology. New insights into internal morphology were gained. The prosoma is dominated by leg coxae with internal apophyses. Lamellate structures were observed in the mesosomal region which resemble the primary respiratory organs of Recent chelicerates (xiphosuran book gills or arachnid book lungs). Similarities between these lamellate organs in shape and location in fossil and Recent taxa suggest that book gills evolved within the chelicerate stem-lineage.

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### Moscovian macrofloras from South Wales, UK

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



## Significance of non-trilobite arthropods from the Devonian Hunsrück slate of Germany

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The Lower Devonian Hunsrück Slate is one of the most important Lagerstätten for exceptionally-preserved marine fossil arthropods of late Palaeozoic age. Although commercial exploitation has ceased, new material remains to be described from the quarries at Bundenbach. These fossils preserve details that are important for determining the phylogenetic position of known Hunsrück Slate arthropods and also include new taxa. Twenty specimens of *Vachonisia rogeri*, for example, are now available compared to the five previously known. A new investigation reveals ontogenetic stages, clarifies the morphology and arrangement of the appendages, and throws new light on the affinities of this remarkable arthropod, including its phylogenetic position relative to the Marrellomorpha. *Devonohexapodus bocksbergensis* Haas *et al.*, 2003 was interpreted as a marine stem lineage representative of the Hexapoda, indicating that terrestrialisation took place twice in Ateloceratan evolution. Reinvestigation of the specimen, however, together with those of *Wingertshellicus backesi* Briggs & Bartels, 2001, also from the Hunsrück Slate, prompts a re-evaluation of *Devonohexapodus* and its significance.

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## The Portishead eurypterid *Drepanopterus abonensis*: implications for stylonurid phylogeny

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*Drepanopterus abonensis*, a stylonurid eurypterid (Arthropoda; Chelicerata) from the Late Devonian Old Red Sandstone (Famennian) of Portishead, UK, is redescribed. New material reveals *D. abonensis* to be a primitive sweep-feeder, a precursor to the large, bizarre sweep-feeding hibbertopterids that ranged from the Carboniferous to the end-Permian. The new reconstruction differs drastically from the previous one; *D. abonensis* was a deep-bodied creature with a length of *c.*40 cm, shorter than previously considered. Inclusion within a phylogenetic framework resolves *D. abonensis* at the base of the hibbertopterids, sharing the synapomorphies of a cleft metastoma and blades (blunt modified spines) on the anterior prosomal appendages. A well-resolved stylonurid phylogeny also enables macroevolutionary implications to be addressed. A trend towards sweep-feeding is observed throughout stylonurid evolution, with lauriepterids, hardieopterids and hibbertopterids each independently adopting this feeding mode. This particular ecological niche could explain why the Stylonurina persisted through the Carboniferous whereas the Eurypterina went into decline during the Devonian; unable to compete for prey with their more manoeuvrable nektonic eurypterine brethren, stylonurids adapted to occupy a distinct sweep-feeding habit and so were unaffected by the competition from jawed vertebrate and other invertebrate predators that contributed to the decline of the Eurypterina.



## Ordovician brachiopod faunal provinces and palaeogeography

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Cluster, Principal Coordinates Analyses (PCO) together with Seriation were performed by PAST on global distribution data for Ordovician brachiopod genera for three time slices: the Dapingian–Darriwilian, the Sandbian–early Katian, and Hirnantian. For the first time, localities are defined by precise geographical coordinates, giving a more accurate and more highly resolved overview of the brachiopod provinces than previously. Localities together with faunal provinces indicated by the multivariate analyses were plotted on new global reconstructions provided by Trond Torsvik. The following provinces were interpreted from the analyses: Dapingian–Darriwilian (four provinces): the Celtic, the Toquima–Table Head, the Baltoscandian provinces, and the Laurentian platform province. Sandbian–early Katian (four provinces and one deep-water faunal belt): the marginal Gondwanan, tropical province, the Baltoscandian/Avalonian province, the Scoto–Appalachian province, the marginal Gondwanan, polar province, and a deep-water belt containing the *Foliomena* fauna. Hirnantian (two major and one minor plus a deep-water belt): the major provinces are the Midcontinent and the Kosov provinces wherein the *Hirnantia* fauna was globally distributed. The Kosov province is associated with one minor province and one deep-water belt: a marginal Gondwanan, polar zone, the Bani province, with a very low-diverse, cold-water *Hirnantia* fauna, and a deep-water belt dominated by a relatively low-diverse, deep-water *Hirnantia* fauna.

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## Stable isotope evidence for an amphibious phase in early proboscidean evolution

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Evidence from geological, embryological, molecular and palaeontological studies has suggested that the Order Proboscidea, consisting of modern elephants and their extinct relatives, may have an aquatic ancestry. We present isotopic evidence obtained from the tooth enamel of the late Eocene proboscideans *Moeritherium* and *Barytherium* which supports this hypothesis. Analysis of stable carbon isotope ratios within the enamel suggests that these herbivores were consuming a diet of freshwater plants and/or C<sub>3</sub> vegetation. The variation exhibited by oxygen isotope ratios within the sampled populations is intermediate between the values seen in modern fully aquatic and fully terrestrial mammals. When compared with the results from contemporary Eocene terrestrial taxa (hyracoids and anthracotheres), the values indicate a more aquatic mode of life for the proboscideans. When taken together with dental, sedimentological and morphological evidence, we suggest that the early proboscidean *Moeritherium* led a semi-aquatic lifestyle in fluvial or lacustrine/swamp environments.



## Dinosaurs and the Cretaceous Terrestrial Revolution

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The observed diversity of dinosaurs reached its highest peak during the mid- and Late Cretaceous, the 50Myr that preceded their extinction, and yet this explosion of dinosaur diversity may be explained largely by sampling bias. It has long been debated whether dinosaurs were part of the Cretaceous Terrestrial Revolution (KTR), from 125–80Myr ago, when flowering plants, herbivorous and social insects, squamates, birds and mammals all underwent a rapid expansion. Although an apparent explosion of dinosaur diversity occurred in the mid-Cretaceous, coinciding with the emergence of new groups (*e.g.* neoceratopsians, ankylosaurid ankylosaurs, hadrosaurids and pachycephalosaurs), results from the first quantitative study of diversification applied to a new supertree of dinosaurs show that this apparent burst in dinosaurian diversity in the last 18 Myr of the Cretaceous is a sampling artefact. Indeed, major diversification shifts occurred largely in the first one-third of the group's history. Despite the appearance of new clades of medium to large herbivores and carnivores later in dinosaur history, these new originations do not correspond to significant diversification shifts. Instead, the overall geometry of the Cretaceous part of the dinosaur tree does not depart from the null hypothesis of an equal rates model of lineage branching. Furthermore, we conclude that dinosaurs did not experience a progressive decline at the end of the Cretaceous, nor was their evolution driven directly by the KTR.





## Land plant spore biochemistry detects long-term changes in UV-B radiation

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The stratospheric ozone layer shields the Earth's biota from the harmful effects of UV radiation. The thickness of this layer and thus the flux of UV-B radiation reaching the Earth's surface are governed by a variety of natural processes including solar cycles, volcanic aerosols and anthropogenic ozone-depleting substances. However, diagnosing the role of these processes prior to instrumental records requires the development of well-constrained proxies. Plants, as sessile organisms that are dependent on sunlight, face a trade-off between maximising photosynthetic carbon gain whilst at the same time protecting themselves from the deleterious effects of UV-B radiation. One method of protection that has been widely adopted by a variety of plant groups is the use of UV-B absorbing compounds. Therefore the quantification of the UACs within plant tissue offers the potential to develop a proxy to track changes in UV-B radiation.

Here we show that the UV-B absorbing compounds (*p*-coumaric and ferulic acid) of the spores of *Lycopodium* (Lycophyta) from the high-latitudes of the northern and southern hemispheres are strongly regulated by historical variations in UV-B fluxes. As proof of concept, we present a spore-based multi-decadal historical ozone and UV-B reconstruction for Greenland (1907–1993) validated against Dobson spectrophotometer measurements from Norway and surface UV-B estimates from Sweden. Our results indicate that Earth's UV-B history is retained in herbaria records and opens the possibility of using the fossil and sub-fossil record of plant spores to track changes in UV-B radiation.

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## Palaeosaurus Eight Years On

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It is now almost eight years since the launch of the BGS "Palaeosaurus" initiative (<[www.bgs.ac.uk/palaeosaurus/home.cfm](http://www.bgs.ac.uk/palaeosaurus/home.cfm)>) to database details of the British Geological Survey palaeontological collections. With an estimated three million specimens these represent the most comprehensive biostratigraphical collection relating to Great Britain and its continental shelf, and comprise the second largest fossil collection in the UK. Already containing data describing more than 125,000 specimens from the BGS Museum collection, ranging in age from Neoproterozoic to Quaternary, *Palaeosaurus* offers a formidable



curatorial and research resource. Nevertheless, the time is now right to take stock of this highly successful enterprise and consider its future development.

Cutting-edge methodologies offer the promise of powerful new ways to access, combine and analyse palaeontological data from multiple, distributed databases. Currently maturing web service technology will be considered, alongside newly developed standard data interchange formats, such as those for systematic data (for example, biodiversity information standards at <[www.tdwg.org](http://www.tdwg.org)>) and geoscientific data (as characterised by the OneGeology initiative, <[www.onegeology.org](http://www.onegeology.org)>). Alongside such technical innovations, lateral approaches to dataset enhancement will be introduced, adding value to *Palaeosaurus* by allowing web database visitors to annotate existing records with their own additional information.

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### Accidental agglomerations or regional radiations? Combining phylogenies and palaeobiogeography to evaluate competing models of rapid Early Triassic ammonoid recovery

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Early Triassic ammonoids recovered rapidly from the End-Permian mass extinction. A basin-level study of Early Triassic ammonoid diversity found a strong Olenekian diversity gradient, linked to SST variations. New genus-level phylogenies were combined with palaeobiogeographical analyses to discriminate between two evolutionary modes potentially responsible for this pattern: 1) Regional diversity ‘hotspots’ result from many unrelated genera migrating into a basin; 2) ‘Hotspots’ result from major endemic radiations. Cluster analyses and PAE supported previous reports of unstructured Induan palaeobiogeographical units, with the more structured palaeobiogeographical units emerging during the Olenekian. PAE trees all had C.I.s > 0.5, indicating a strong phylogeographical signal. However some clusters are not explicable by larger-scale palaeobiogeographical patterns, e.g. Arctic provincialism or simple palaeogeographical proximity. Relationships among Olenekian basins are more predictable and stable. Both PAE and cluster analyses indicate that Olenekian diversification in western Tethyan basins is a real phenomenon. New phylogenies allow testing of the two competing hypotheses of regional diversification. Regional ‘hotspots’ are generally driven by immigration of multiple ammonoid lineages into regions, rather than by rapid radiation of individual lineages within isolated areas. Combining palaeobiogeographical and phylogenetic data has demonstrable potential for advancing process-based understanding of diversification events in the fossil record.

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### The Late Triassic Crisis and the Lazarus Effect: Evidence from the Bivalve Fossil Record of Northwest Europe

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The quality of the Triassic–Jurassic bivalve fossil record in Northwest Europe has been measured using the Simple Completeness Metric (SCM). The SCM has been applied



to the fossil record of total bivalve richness and to the records of different ecological guilds. Palaeoecological analyses of the Late Triassic crisis in SW UK have demonstrated that a significant bio-event took place during the latest Rhaetian. SCM data from the present study indicate that this event is unlikely to be an artefact of reduced fossil record completeness. The 'Pre-Planorbis Beds' of the lower Lias Group, however, witness a precipitous decline in the completeness of most bivalve guilds, and emigration of taxa due to localized marine anoxia is a likely cause. Neither variation in lithofacies, shell mineralogy, sedimentary rock outcrop area, nor sequence architecture can convincingly explain the observed patterns of completeness. Our SCM data reveal that the Early Jurassic fossil record of infaunal suspension-feeding bivalves is significantly poorer than that of epifaunal bivalves. Any differences in the apparent Rhaetian extinction rates between these two guilds should therefore be viewed with caution. Analyses of selectivity during the Late Triassic mass extinction based on global databases appear robust in light of our SCM data.

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## Aspidin – The Earliest Vertebrate Skeletal Tissue is Acellular Bone

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Aspidin, the hard tissue comprising the integument of the earliest skeletonising vertebrates, has been the subject of vigorous debate over its biology and homology for the last 60 years, having been identified as a form of dentine, cementum and cellular or acellular bone. Previous workers failed to reach consensus on the nature of structures present in the tissue or resolve aspidin's homologies, in part hindered by the limited technology of the day. We have revisited this debate and used new techniques to elucidate the true function of these structures, and use this to draw further conclusions about the placement of aspidin in the development of skeletonisation in the vertebrates. Etched histological specimens were investigated using SEM to examine and characterise aspidin in the main groups of heterostracans, with SRXTM imaging used to create a 3D model revealing the architecture of the heterostracan dermoskeleton. This has allowed us to conclude that the structures that typify aspidin include: a linked osteonal network, individual or woven bundles of unmineralised intrinsic fibres, and extrinsic fibres of attachment. This is consistent with aspidin being a form of acellular bone.

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## Sauropod forelimb flexibility deduced from deep manus tracks

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Sauropods are often considered to have very limited mobility and reduced limb flexibility, mainly due to their giant size and consequent weight. In the Upper Jurassic Lourinhã Formation, central-west Portugal, deep vertical natural casts of sauropod manus tracks are often preserved as the infills of the original tracks. These manus tracks are vertical-walled, with marks of the striations of the skin scales, showing that the movement of the sauropod



manus impacting and exiting the mud was totally vertical with no horizontal component of the stride. Some tracks are up to 66 cm deep, which is equivalent to the height of whole sauropod manus. This means that sauropods could lift their anterior feet in a complete vertical manner. Such movement is only possible if there is mobility at elbow and shoulder articulations in a higher degree than previously thought for sauropods. Our vision of sauropod limbs as inflexible columns has to be updated to a more dynamic model for limbs and body.

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### First record of the stegosaurian ichnogenus *Deltapodus* from the Upper Jurassic Morrison Formation, Utah, USA

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We describe the first American stegosaur track of the ichnogenus *Deltapodus brodricki* Whyte and Romano, collected in the Upper Jurassic Morrison Formation of San Juan County, southeastern Utah, USA. The track is preserved as a natural cast on the underside of a slab of fluvial sandstone, and consists of a well-preserved pes track and the eroded remains of a manus. The pes track is tridactyl, sub-triangular in outline, 31 cm long and 22 cm wide, mesaxonic and widest across the digits, which are short and blunt. *Deltapodus brodricki* was originally described from the Middle Jurassic floodplain deposits of the Yorkshire coast of England and later found in similar Upper Jurassic deposits of Portugal and Spain. Previous reports of stegosaur tracks from the Morrison Formation all differ significantly from the morphology of *Deltapodus*. The new discovery thus substantially extends the geographic record of this ichnogenus, and highlights the similarities between the Late Jurassic dinosaur faunas of North America and western Europe.

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### Silurian (late Sheinwoodian and Homerian) palaeocope ostracods from Arctic Canada

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A new silicified ostracod assemblage from Silurian (Wenlock) limestones and calcareous shales of the Cape Phillips Formation, Arctic Canada spans the interval of the late Sheinwoodian and Homerian, including the globally recognized Homerian regression. The ostracods, collected from Baillie Hamilton Island and on the Abbott River, Cornwallis Island, can be linked with previously described graptolite, trilobite and micro-vertebrate biozonal schemes. Some seventeen species are present, including the new taxa *Beyrichia marssae*, *Gabrielsella copelandi* and *Platybolbina adraini* which are indicative of the perneri-opimus to ludensis graptolite biozones. The ostracods, though largely endemic to the Cape Phillips Formation, include two taxa common to the Wenlock of the Avalanche Lake area, North West Territories, Canada, while some suggest correlation with other Silurian successions in Northern Canada and the Baltic. Sparse ostracod faunas characterise the level of a marked positive carbon isotope excursion recognized in this



succession at the level of the early *ludensis* graptolite biozone. However, there is a mixed response in palaeocope diversity in the succeeding interval, with some taxa continuing to be present and others becoming extinct. This contrasts with the sudden occurrence of a new pervasive Homerian ostracod fauna in other sections in Northern Canada.

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### Palaeoenvironments and biota of the Jurassic Dos Manantiales hot spring complex, Deseado Massif, Argentine Patagonia

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The Deseado Massif of southern Argentine Patagonia is characterized by long-lasting, Middle to Late Jurassic bimodal volcanism that created numerous and widespread Au-Ag epithermal deposits. Some of these have extensive and well preserved surficial deposits including silica (sinter) and carbonate (travertine) mounds and aprons and distally thermally influenced wetlands/lakes. At Dos Manantiales, sinter outcrop facies mapping and initial microscopic investigation reveal several, often intercalated, fossiliferous hot spring sub-environments. These include proximal (mid-temperature) to distal (lower temperature) sinter aprons, supra-apron pools, geothermal wetlands and silicified clastic sediments. The hot spring biota includes mat-forming bacteria, aquatic macro-algae, higher plants, plus aquatic arthropods and their coprolites. Higher plants, dominantly sphenophytes and gymnosperms, occur almost exclusively at the margins of the sinter apron complex in geothermal wetlands or in cooler supra-apron pools where aquatic macro-algae form dense carpets. Poorly preserved microbial mat fabrics dominate on the sinter apron. Many of the sedimentological and biological features associated with the sinter deposit have characteristics favourably comparable with more extensively studied Palaeozoic hot spring deposits, *e.g.* the Rhynie Chert, Scotland (Devonian) or Drummond Basin, Queensland, Australia (Dev/Carb) and more recent deposits of New Zealand (Neogene) and active hot spring areas such as Yellowstone, USA.

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### Geomorphic morphometrics: Defining early land plant species using principal component analysis

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Palaeontological taxonomists rely on morphological characteristics to distinguish between groups of organisms. Unfortunately, early land plants have few diagnostic characters, traditionally defined by terminal sporangia morphology and size. This is particularly the case when studying coalified compressions, as often the only part remaining are thin films of coal with little information regarding original anatomy or *in situ* spores. In previous investigations, sporangia morphology has been determined by observational and traditional univariate analysis (*e.g.* width:height ratio) and personal interpretation of shape definition. Morphometric analysis has now advanced, with the capacity to make multivariate datasets based on shape geometry much more visual. Using Principal Component Analysis, each shape can be represented as a point in multidimensional space, with groups of points



forming ‘point clouds’. An attempt to quantify the variance in sporangia from a collection of early land plants is made. Using Principal Component Analysis, sporangia shape and size changes resulting from varying degrees and combinations of Principal Components are visualised. Both inter-species and intra-species models have been generated. The model has the capacity to classify new specimens according to their Principal Components.

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### New data on the Early Ordovician pelagic faunas of Sarydzhas, eastern Kyrgyzstan

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The Ordovician Oldzhobai Formation comprises basin plane and outer-fan fringe siliciclastic lithofacies deposited on the margin of the Karatau–Naryn micro-continent facing the major oceanic basin. It also includes thin layers of radiolarian cherts containing low diversity conodont and radiolarian faunas. Conodonts represent two succeeding associations. The lower one is almost monospecific, comprising abundant *Paracordylodus gracilis* and a few *Drepanodus* cf. *arcuatus*. In the radiolarian cherts of Kazakhstan, associations dominated by *Paracordylodus gracilis* are characteristic of the upper *Paroistodus proteus* Biozone (uppermost Tremadocian to lower Floian). Succeeding conodont fauna contains *Prioniodus*, *Periodon*, *Oelandodus*, *Protoprioniodus* and *Paroistodus*, suggesting the early Floian age. Moderately well-preserved radiolarians were recovered from two horizons in the middle and upper part of the Oldzhobai Formation. The lowermost radiolarian fauna occurs together with the conodonts *Drepanodus arcuatus*, *Paracordylodus gracilis* and *Prioniodus* cf. *oepiki*, suggesting the lower Floian. The radiolarian assemblage from the uppermost Oldzhobai Formation is probably of upper Floian to Dapingian in age. The radiolarian fauna is in general dominated by members of the family Inaniguttidae which could possibly be assigned to *Inanigutta*, *Inanibigutta* and *Oriundogutta*. Interestingly, it also appears to contain a number of new, previously unknown, morphotypes.

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### Lower Cambrian bio- and chronostratigraphy in Scandinavia

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A detailed sequence stratigraphical framework comprising sixteen third order transgressive–regressive sequences forming three supersequences has been developed for the Lower



Cambrian of Scandinavia. The sequence stratigraphical correlation is crudely constrained by acritarch and trilobite biozones. Revision of the existing trilobite zonation is proposed by merging the *Holmia kjerulfi* and the lower part of the 'Ornamentaspis' *linnarssoni* zone into one informal zone, for the time being referred to as the *H. kjerulfi*-*O.* *linnarssoni* zone. The upper part of the traditional 'O.' *linnarssoni* Zone is separated as a new informal *Comluella?*-*Ellipsocephalus lunatus* zone. The *Holmia inusitata* Zone is abandoned as it overlaps with the upper part of the *H. kjerulfi*-*O.* *linnarssoni* zone. The stages defined for the Lower Cambrian of Eastern Europe are adopted also for Scandinavia, viz. the Rovnian, Lontovan, Dominopolian, Ljubomlian, Vergalian, Rausvian and Kibartian stages. The latter contains *Volborthella* and rare olenellid trilobites, and is considered of Early Cambrian age. The Scandinavian Lower/Middle Cambrian boundary corresponds to the Kibartai/Deimena transition in the East Baltic area.

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### A case of heterochrony in Lower Palaeozoic echinoderms: the solute *Dendrocystites* (Blastozoa) from the Upper Ordovician of Bohemia

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Solutes are a class of asymmetrical Palaeozoic echinoderms (Middle Cambrian – Early Devonian). Their anatomy consists of three regions: 1) a single feeding appendage (brachiole); 2) a flattened body (theca); 3) a locomotory stem-like appendage (stele). The genus *Dendrocystites* comprises the two species *D. sedgwicki* Barrande and *D. barrandei* Bather, both from the Upper Ordovician of Bohemia. *Dendrocystites barrandei* (Letná Formation, late Sandbian) was originally described for small to medium-sized solutes, with unornamented thecal plates, and a proximal stele made of well-organised imbricated rings. *Dendrocystites sedgwicki* (Zahořany Formation, early Katian) corresponds to large solutes, with strongly ornamented thecal plates, and a polyplated, unorganised proximal stele. Re-examination of more than 250 specimens of Late Ordovician Bohemian solutes shows that: 1) all specimens from the Letná Formation follow the description of *D. barrandei*; 2) three distinct morphotypes are present in the younger Zahořany Formation, with the co-occurrence of *D. barrandei*-like solutes (small specimens), *D. sedgwicki*-like solutes (largest individuals), and finally, solutes intermediate in morphology between *D. barrandei* and *D. sedgwicki* (medium-sized specimens). Consequently, all Bohemian solutes are here interpreted as belonging to a single species (*D. sedgwicki*), and the largest, strongly ornamented individuals as hyperadult forms (hypermorphosis).



## New crocodyloid eggs and eggshells from the Upper Cretaceous of Brazil (Bauru Group)

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The record of fossil crocodyloid eggs is scarcely documented and poorly understood, not matching the wide diversity of crocodylomorph taxa known, a problem partially attributed to the proportionally thin eggshell of extant crocodilians. A new Upper Cretaceous (Adamantina Formation, Bauru Group) outcrop yields a remarkable association of crocodyloid eggshells, eggs and egg clutches. Several associations of eggs are distributed in a relatively small area and at different horizons. At least two egg clutches were associated with articulated remains of *Baurusuchus pachecoi*. The new eggs show a particularly thin eggshell (0.15–0.25 mm), elliptical or teardrop-shaped pore openings (30–80 µm in length) and a tightly packed arrangement of the basic units. These features contrast with other known types of fossil crocodyloid eggshells (e.g. *Krokolithus wilsoni*, *K. helleri*), which always possess well-developed interstices and usually subcircular pore openings. The Bauru Group is the only geological unit to show two distinctive types of crocodyloid eggs, as well as dinosaurian eggs. The occurrence of two types of crocodyloid eggs in the Bauru Group is expected because it includes no fewer than seven different genera of fossil crocodylians. These eggs provide valuable information on the palaeobiology of the Bauru Group crocodylian fauna.

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## Ecospace utilisation in the Mesozoic: changes in the modes of life of marine organisms

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Ecospace can be represented as a combination of the three axes of tiering, motility and feeding, each divided into six subcategories. From the Cambrian to Recent, ecospace utilisation has tripled, however the trend through the Phanerozoic remains unclear. We analysed stage-by-stage occupation of ecospace for the marine fauna from the Late Permian to Early Jurassic. 3,181 genera were recorded from Sepkoski's compendium, and each one classified according to the autecological information derived from the Paleobiology DataBase and published references. Finally, average relative abundance for each





subcategory was calculated and we evaluated the trends in tiering, predation and motility. 31 modes of life were recorded. Ecospace utilisation increases from the Guadalupian to Sinemurian. In the three main categories of tiering, motility and feeding, the most common subcategories (>15% of taxa) are, respectively: 'shallow infaunal', 'fast mobile' and 'predation'. Ecospace utilisation decreased 35% and 16% at the end of Permian and Triassic respectively. There was a significant, positive correlation between abundance of predators and both infaunalisation and prey motility. The appearance of marine reptiles and adaptations in the ichthyofauna to new trophic niches, like durophagy, presumably increased predation pressure and drove the increase in benthic infaunalisation.

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## Evidence for diverse life modes of Mesoproterozoic acritarchs

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The Lakhanda Formation and the overlaying Ui Group (Uchur–Maya Region, East Siberia, Russia) constitute a Mesoproterozoic Lagerstätte. The recovered microfossils make up three distinct biotas differentiated by their lithological context. Forms common to all three assemblages are leiosphaerid acritarchs (ranging in size from 15.2µm to 827.5µm) and putative cyanobacterial sheaths. All the Leiosphaerids seem to exhibit a mode of size increase which would be compatible with growth during ontogeny. Possession of this trait would oppose their most common interpretation as phytoplankton cysts, although it does not rule out a planktonic life mode. The exceptional preservation of the Lakhanda Formation and the Ui Group also enabled recovering probable benthic mat communities with *in situ* acritarchs. Applying appropriate statistical analysis of the distributional patterns can permit distinguishing random fallout from the water column from deterministic growth of organisms on the sea floor. Such a study combined with a taxonomical analysis can offer the first qualitative and quantitative evidence for benthic life modes in the Mesoproterozoic.

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## Stratigraphy and taphonomy of Miocene fossil mammal assemblages from Damiao, Inner Mongolia, China

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This study introduces preliminary results from a field investigation of a fossil-bearing sedimentary sequence, exposed at the Damiao area of Inner Mongolia, China. The fluvio-lacustrine strata, ranging from the Early to the Late Miocene, record a change in the depositional regime, and consequently, taphonomic modes. Systematic excavations at the Early Miocene locality DM-16 revealed a rich collection of micromammals and a minor proportion of large mammals set in siltstone-dominated slightly calcareous matrix. The highly fragmentary nature of the bones, coupled with the simultaneous absence of surface degradation, suggests trampling. The presence of associated bone parts in small mammals



translates into rapid burial and *in situ* preservation of predator accumulations. Collectively, deposition took place in an ephemeral lake within the distal part of a floodplain. Thus, the DM-16 fossil site represents a low energy setting with waning stream power. In contrast, the Middle and Late Miocene fossil localities DM-01 and DM-02 show a transition toward higher energy conditions. The large mammal assemblages are probably allochthonous. The bones are derived from a black, nodule-rich, fluvial conglomerate, and display a high degree of fragmentation, weathering, and abrasion. The small mammal teeth could have a scatological origin with subsequent fluvial transport.

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## A revision of the chimaeroid fishes (Chimaeroidei) from the Stonesfield Slate (Middle Jurassic, Bathonian) of Oxfordshire, England

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Prior to revision, the chimaeroid fishes from the Middle Bathonian (*Procerites progracilis* zone) Stonesfield Slate (Sharp Hill Formation) of Oxfordshire consisted of ten nominal tooth-based and two fin spine-based species, all of which were described in the mid 19th Century (Agassiz, 1843; Egerton, 1843, 1847). During the revision, all available specimens at the NHM, London [all types]; Sedgwick Museum, Cambridge; Oxford University Museum; and BGS, Keyworth; were examined; a total of 100+ specimens. As a result, the Stonesfield Slate chimaeroid assemblage has been rationalized to just three species, all of the family “Edaphodontidae”. These are *Ischyodus tessonii* Buckland *in* Agassiz, 1843, *Elasmodectes falcatus* (Egerton, 1843) and ‘*Ischyodus*’ *curvidens* Egerton, 1843 (gen. nov.). All other nominal species names are junior synonyms and *nomena dubia* (*Ischyodus bucklandi* and *I. emarginatus*). Junior synonyms for *Ischyodus tessonii* are *Ganodus oweni*, (?) *Ischyodus colei* and (?) *Leptacanthus serratus* [fin spine]; for *Elasmodectes falcatus* are *Ganodus psittacinus* and *Leptacanthus semistriatus* [fin spine]; for ‘*Ischyodus curvidens*’ are *Ganodus dentatus*, *G. neglectus* and *G. rugulosus*. This chimaeroid assemblage, dominated by young individuals of *Ischyodus* and small specialized ‘edaphodontids’ with cutting dentitions, reflects a near-shore environment and a habitat and reproductive strategy similar to that of the Recent rabbitfish *Callorhynchus*.

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## Deciphering floral diversity and palaeoclimate signals from the mid Palaeocene floras of the Isle of Skye, Scotland

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Fossil floras are preserved within Tertiary volcanic deposits of the Isle of Skye, Scotland. The fossils represent vegetation that grew in a volcanic landscape during quiescent intervals between eruptive episodes. Lava sequences containing the floras have been dated as 60–58Ma, mid Palaeocene. The fossil plant assemblages on Skye are preserved in small outcrops of finely laminated sandstones and siltstones that may represent rivers and ponds on the volcanic surface. New collections of fossil plants have been assembled from Allt Mor, Allt Geodah a Ghamhna and Glen Osdale, Skye. The leaves are being described in



order to determine the overall composition and diversity of the vegetation. Angiosperm leaves are the most abundant and diverse components of the floral assemblages and show similarities to members of the Corylaceae, Fagaceae, Tiliaceae, Ulmaceae, Cornaceae, Cercidiphyllaceae, Juglandaceae and Platanaceae. Conifers are also present and represent forms similar to the Cupressaceae (syn. Taxodiaceae). The angiosperm leaves will provide palaeoclimate information using CLAMP, LMA and other techniques.

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## Isolated archosaur teeth from the Lower Jurassic of South Wales

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Lower Jurassic fissure fills from South Wales have yielded three distinct microvertebrate faunas. A depauperate fauna contains three tetrapods: the pleurodont lepidosaur *Gephyrosaurus* and two mammals, *Morganucodon* and *Kuehneotherium*. A wider fauna is dominated by the sphenodont *Clevosaurus* and in addition to the taxa of the depauperate fauna it also contains the tritylodont *Oligokyphus* and the haramiyid *Thomasia*. Recently a third intermediate fauna has been described, containing the same faunal elements as the wider fauna but with faunal proportions more similar to the depauperate. The differences between the three faunas have been suggested to be temporal and show a reduction in biodiversity or a taphonomic bias such as predator selection. Isolated archosaur teeth were also found in all three faunas and reported to be from a theropod dinosaur, sphenosuchid crocodylomorph and a pterosaur. Recent qualitative and quantitative work on the teeth has revealed a more diverse archosaur fauna than previously thought. Nine morphotypes have been described, relating to a minimum of four taxa, including previously un-described herbivorous teeth. The archosaur morphotypes are also more diverse in the wider fauna fissures, suggesting the change in the three faunas is temporal and reflects a drop in biodiversity.

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## Middle Ordovician conodont biofacies and palaeoenvironments across Baltica

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An evaluation of the palaeoenvironmental distribution of conodont biofacies during the Dapingian and early Darriwilian across the Baltoscandian platform has involved twelve sections from Estonia in the East to South-central Norway in the West. The database consists of more than 90,000 specimens representing 11 selected genera from 348 samples. Detrended Correspondence Analysis (DCA) and Unweighted Pair Group Average cluster analysis using Spearman's rank order coefficient show significant differences in the composition of conodont communities across the platform. During the Dapingian, a relatively shallow-water conodont community characterised by *Scalpellodus*, *Baltoniodus*, *Protopanderodus*, *Microzarkodina* and *Drepanoistodus* dominated localities from the Oslo Region through central Sweden to Öland and Estonia. Intervals with more oceanic conditions demonstrate a more complex pattern. The genera *Periodon* and *Costiconus* characterised the platform margin areas of the Caledonides, whereas *Paroistodus* dominated the more oceanic intervals on the proximal part of the platform. Three distinct conodont assemblages occurred in the Darriwilian. The *Gothodus*–*Nordiora* community



characterised the most distal (coolest) platform margin settings of the Caledonides together with Scania; the *Periodon–Protopanderodus* community was common in the distal parts of the platform, whereas the *Baltoniodus–Drepanoistodus–Scalpellodus* community dominated the more proximal parts of the platform.

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## Geochemistry of the Herefordshire (Silurian) Lagerstätte host deposit and its implications for a taphonomic model

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The Herefordshire Lagerstätte has revealed an array of exceptionally three-dimensionally preserved fossils of a range of invertebrate groups. The style of preservation is unique: calcite casting 3D anatomy of hard and soft parts in exquisite detail in host nodules set within a volcanoclastic deposit. Geochemical analysis of the host volcanoclastic unit is vital in order fully to understand the taphonomy of this Lagerstätte.

XRF analysis indicates that an andesitic volcano(es) produced the host ash. Double normalised data of major elements from the deposit provide an insight into the taphonomic pathways involved in preservation. A significant deficiency in sodium suggests that this was one of the key factors responsible for driving up the pH, which is one of the conditions required for calcite precipitation. A deficiency in calcium further supports the notion that the calcium for the calcite was sourced from weathering minerals within the volcanoclastic sediment. XRD analysis of the whole rock and clay fraction denotes that the host unit lacks the geochemical characteristics of other bentonite deposits of similar age.

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## The phylogeny of delthyridoid spiriferids (Brachiopoda, Devonian) – a new interpretation

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Evolutionary studies of a group of multiplicated delthyridoid spiriferids have resulted in the identification of a group with a plicated sulcus and fold as well as bifurcating and/or trifurcating plications on the flanks. Although the scarcity of material complicates the interpretation of this group and the poor knowledge of some genera precludes a fundamental cladistic analysis, certain evolutionary trends are recognizable regarding the pattern of the micro-ornamentation and the development of costae. Two main evolutionary branches are the Fimbrispiriferidae, with a fimbriate micro-ornamentation, and the Costispiriferidae, Elymospiriferidae and a new family with capillate micro-ornamentation. At present the following new taxa are recognized: two new genera in the Fimbrispiriferidae with three new species, one new subfamily in the Costispiriferidae with one new species, one new subfamily in the Elymospiriferidae with one new genus, and one new family based on the genus *Multispirifer*. Biogeographically, the faunal relationships suggest pathways between Nova Scotia and Turkey, eastern North America and North Africa, and Turkey and North Africa. At the beginning of the Late Emsian an eastward migration of taxa from North Africa to South China is proposed.



## The origin of *Cyrtospirifer* (Brachiopoda) from the Middle Devonian of the Western Sahara (Northwest Africa)

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A brachiopod faunule from Givetian-age carbonate and clastic rocks on the southeast flank of the Tindouf Syncline in the Western Sahara (Northwestern Africa) has yielded the oldest species of *Cyrtospirifer*. It is proposed that the origin of cyrtospiriferid brachiopods lay in North Africa instead of western Europe as hitherto assumed. The new species of *Cyrtospirifer* differs in its smaller number and coarser medial and flank plications and equibiconvex shell profile from the other Givetian species of *Cyrtospirifer* that all occur in Europe and to which the new species has given rise. The new implications of the proposed phylogeny of the earliest cyrtospiriferids and their origin in the Western Sahara are discussed. The palaeogeographical distribution of the cyrtospiriferids during the Givetian and Frasnian is shown, as well as its migration routes in relation to global transgression and regression cycles, first from North Africa to Europe and later to North America and Asia.

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## A new species of *Quiringites* (Brachiopoda) from the Middle Devonian of Morocco

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A new species of *Quiringites* from the Middle Devonian (Eifelian) of the Maïder and the Dra Valley (southern Morocco) is similar to the slightly older type species *Quiringites elegans* to which it is externally very similar. The new species is compared to specimens of *Q. elegans* from the Eifel Region (Germany), the Ardennes (Belgium), the Montaña Cantábrica (Spain), and the Gory Swietokrzyskie (Holy Cross Mountains, Poland). Studies of the internal morphology on internal moulds and on serial sections show that the new species differs from *Q. elegans* in that it shows a stronger development of secondary shell material in the apical region, imbedded crural and dental plates, and two spirals more on each spirallium. The internal morphological differences are demonstrated by computer-supported 3D reconstructions of the two taxa studied. A howellellid origin of *Quiringites* is proposed, however the phylogenetic lineage of this genus remains unknown.

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## A new technique for revealing the internal anatomy of articulated brachiopods

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Knowledge of the internal anatomy of brachiopods is of critical importance for accurate taxonomic identification. Until now steinkerns and latex casts as well as two-dimensional



acetate peels of serial sections have been used to determine the internal characters. The anatomy has been illustrated via drawings made from peels using a microscope-mounted camera lucida or as photographs of polished sections of the actual specimens. A new method for generating detailed three-dimensional reconstructions of the internal skeletal features of brachiopods using the custom SPIERS software is presented. The software can be adapted for registration, virtual preparation, and interactive visualization after digitization of acetate peels using a digital camera. This software system generates detailed 3-D images of internal structures such as dental plates, cardinalia, and brachidia. Pairs of images generated by the SPIERS software can also be used to illustrate three-dimensional aspects of internal skeletal structures using split-screen or anaglyph stereo images. Palaeozoic brachiopods from Lower Devonian strata in Germany, Morocco and South China, and Mesozoic taxa recently discovered in Jurassic strata from Jordan, have been successfully sectioned using this new method.

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### Playground of morphological variation: *Valvata* sp. from the Plio-Pleistocene Koobi Fora Formation of the Turkana Basin, N-Kenya

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Species of *Valvata* are known to be highly variable in shell morphology. Even open-coiled morphotypes and species are known today. *Valvata* sp., however, is the first fossil member of that genus exhibiting open coiling. Other morphotypes within the species include trochospiral and planispiral shells. Within individual populations of that species, all transitions from trochospiral to planispiral and open-coiled morphotypes are evident. As the transitions are gradual, it is therefore not possible to separate several species. Among 117 studied specimens from our own collections, about 20% of the shells show various degrees of open coiling. Two hypotheses are suggested to explain the morphologic pattern of *Valvata* sp.. First, the uncoiling of *Valvata* sp. in the Turkana Basin may be a simple ecophenotypic response to high environmental stress. Second, the uncoiling may be an adaptation to an endobenthic life style. As *Valvata* sp. invaded the Turkana Basin about 1.9 Ma ago, the morphological changes may be the reaction to the new environmental conditions. Obviously, the species failed to survive for a long time as its first and last occurrence are only a few metres apart in the sedimentary succession.

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### Diversity and disparity in ancient lakes: The molluscs of the Koobi Fora Formation of the Turkana Basin, N-Kenya

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The Plio-Pleistocene Koobi Fora Formation of the Turkana Basin yields numerous shellbeds with high abundance of well-preserved freshwater molluscs. The study of their diversity and disparity in concert with sedimentological and taphonomical data based on own fieldwork eventually results in the reconstruction of the hydrology and palaeoenvironmental evolution of the Turkana Basin. First evaluation of the stratigraphical distribution of mollusc taxa between about 2.0 and 1.6 Ma shows faunal changes through time. The lower and upper part of the succession is dominated by *Melanooides tuberculata*, *Pseudobovaria* sp. and *Coelatura bakeri*. In between, *Bellamyia unicolor* and *Cleopatra* sp. are dominant. The first faunal transition is associated with new taxa not present before



in the Turkana Basin, like *Valvata* sp. or *Coelatura monceti*. At the same time, changes in shell morphology and disparity of certain taxa are evident. At the moment, *M. tuberculata* and *Pseudobovaria* sp. are studied extensively using a geometric morphometric approach. Both taxa exhibit significant morphological changes associated with a significant increase in morphological disparity. Further studies are still in progress. According to our working hypothesis, immigration and extinction of species and related ecological processes are responsible for the changes in faunal composition and shell morphology.

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## Geometric morphometrics and the growth of temnospondyl skulls

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Temnospondyls are the most species-rich and morphologically diverse group of early tetrapods, with a long evolutionary history ranging from the Lower Carboniferous to the Lower Cretaceous. Uniquely among most Palaeozoic and Mesozoic early tetrapods, numerous temnospondyls are known from well-documented growth stages. Growth series of twelve taxa are studied herein using a geometric morphometric approach. Their distribution in morphospace and their ontogenetic trajectories reflect the phylogenetic relationships of the Stereospondylomorpha, Euskelia, and Dissorophoidea. All Stereospondylomorpha show a significant increase of the length of the preorbital region of the skull. Eryopidae and Zatracheidae show very short trajectories and are separated in morphospace from the Stereospondylomorpha and Dissorophoidea. Outgroup comparison indicates that a long trajectory is the plesiomorphic condition of temnospondyls. The short trajectories of the Dissorophoidea, for example, reflect a derived condition. They occupy the morphospace of larval stereospondylomorphs. In addition, a larval and postlarval development can be distinguished in representatives of the Amphibamidae and Branchiosauridae, suggesting that these forms evolved a kind of 'abrupt' metamorphosis. These results support the hypothesis based on morphological data that branchiosaurids and amphibamids are closely related to some or all groups of modern amphibians.

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## Charred Veg in Pothole Surprise

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Our knowledge of ancient vegetation comes from plants living in lowland basin sites. Our understanding of extra-basinal vegetation, and upland vegetation in particular, is limited. At the end of the Mississippian, Lower Palaeozoic limestones surrounding the Illinois Basin were karstified during a sea-level low and a wet climatic phase. Subsequently, caves and fissures in these limestones were filled with clastic sediment eroding from extra-basinal areas. Extensive caves with cave-fill deposits have been discovered north of the Illinois Basin within Ordovician limestones. Based on litho- and biostratigraphy, the fill is assigned to the middle part of the Tradewater Formation and dated as Atokan (late Bashkirian



– early Moscovian). The sediments comprise coaly-sediments at the base, sandstones, siltstones and fine clays at the top of the cave-fill sequences, and contain abundant plants and arthropods. These are uncompressed and have undergone minimal thermal alteration. Charcoal occurs throughout the sedimentary sequences but becomes increasingly abundant near the top of the cave fills. The charcoaled plant assemblages in the upper part are dominated by cordaites and conifers. The conifers are the oldest known from North America. This floral assemblage is the remains of an extra-basinal, possibly upland vegetation, which was frequently ravaged by wildfire.

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### The usage of foraminifer species presence–absence data in Late Quaternary palaeoenvironmental reconstructions

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In Late Quaternary palaeoenvironmental reconstructions using foraminifera as proxies, the relative abundances of species are used to indicate various palaeo-zones down-core. The basic data gathering techniques involve counting of 250 to 300 specimens per sample and calculation of relative abundances of the identified species. These data are then used for palaeoenvironmental interpretation. In such analyses, there is often a bias towards using the species that exhibit high to medium relative abundances for delineating palaeo-zones. The species with low abundances are prone to exclusion from the analysis, perhaps under the assumption that their contribution is of little value. In order to evaluate the significance of the whole dataset, foraminiferal counts from sediment-cores collected from the Sunda Shelf, South China Sea, were analysed using relative abundance as well as presence–absence of species. There was an overall agreement between the two analyses. However, the presence–absence data determined species associations more consistently, which had implications for the palaeoenvironmental reconstruction.

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### The control of sedimentary facies in preservation and distribution of ichnofossil assemblages in Parahio Formation, Zaskar Basin, Northwest Himalaya: Integrated approach from sedimentology and ichnology

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The siliciclastic–carbonate successions of the Parahio Formation in southeastern Zaskar represent episodically deposited, storm-influenced, shoaling cycles ranging from offshore marine to shore-face to fluvial environments. Integrated sedimentological and ichnological studies on a measured part of the Parahio Formation along the Purni–Phuktal section (Southeastern Zaskar) show that alternating energy conditions due to recurring storm events superimposed on fair-weather sediments were among the key controlling factors for trace fossil distribution and preservation. Environmental conditions in the offshore transition and the upper offshore are more uneven and reflect the alternation of high-energy storm events (deposition of sandstone and shale intercalation) and low-energy fair-weather (deposition of shale & grey-green silt streaked shale) sediments. The storm-related *Skolithos* ichnofacies is preserved with the overlying fair-weather assemblage of





*Cruziana* ichnofacies that reaches a diversity maximum in the upper offshore deposit. The intercalation of grey-green silt-streaked shale in the upper part of the section (deposited closer to the fair-weather wave base) contains the most diverse and varied behavioural strategies of the *Cruziana* ichnofacies, such as locomotion (*Diplichnites*, *Monomorphichnus*), pascichnia (*Dimorphichnus*) and burrows (*Bifungites*). The interbedded shale and sandstone (thin to medium) characterized by the presence of wave ripples and hummocky cross-stratification was deposited under high energy, storm dominated shelf conditions (between FWWB and SWB) and contains a monospecific ichnofossil assemblage of the *Skolithos* ichnofacies (vertical dwelling traces). The high-energy conditions prevailed in lower and middle shore-face environments and bioturbation is restricted to only vertical burrows (*Skolithos*).

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### A placozoan affinity for *Dickinsonia* and the evolution of Late Precambrian metazoan feeding modes

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The Ediacaran taxon *Dickinsonia* has endured a controversial taxonomic history. From the trace and body fossil record, it is clear that: 1) it had two axes of symmetry; 2) it had the ability to move; and 3) it digested the ubiquitous Ediacaran microbial mats with its entire lower surface and thus fed extracellularly (*i.e.*, saprobically). These three characteristics preclude an affinity within crown-group Eumetazoa or within any living sponge lineage, but *Dickinsonia* could lie between “Porifera” and Eumetazoa on the animal tree. We believe it can be most readily interpreted as having affinities with the Placozoa, a small phylum whose modern representatives feed saprobically on biofilms. Our hypothesis predicts then that placozoans are the sister group of the eumetazoans. We performed a phylogenetic analysis using seven nuclear housekeeping genes and find Placozoa to be above a paraphyletic “Porifera” as the sister taxa to Eumetazoa, consistent with the hypothesis that *Dickinsonia* is allied with the Placozoa, either as a stem-group member or as an extinct lineage lying one node higher or lower on the metazoan tree. Our data suggest that all three modes of metazoan feeding, microphagy (sponges), saprobic (placozoan) and macrophagy (eumetazoan), were in place by the end of the Ediacaran.



## A deep water trilobite fauna from the Coldwell Formation (late Wenlock/early Ludlow), of the Lake District Basin

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In the Howgill Fells of Cumbria, North-west England, the 10 m thick Coldwell Formation comprises a graptolitic mudstone separating two calcareous members, each containing a rich shelly fauna including disarticulated trilobites and brachiopods. Trilobites are dominant, with *Decoroproetus scrobiculatus* Owens, *Delops nobilis marri* Rickards, and *Struveria howgillensis* Rickards being the most abundant. *Miraspis*, *Scotoharpes* and *Sphaerocoryphe* are represented by only one specimen each. There are also specimens of *Decoroproetus* distinguished from *D. scrobiculatus* by glabellar and pygidial axis morphology. These may represent one or more additional species. Additionally several specimens of *Delops* resemble *Delops nobilis nobilis* Thomas from shales of Wenlock age near Bülth. The Swedish Colonus shale bears taxa that also occur in the Coldwell Formation. The fragmentary nature of the assemblage along with the disparity between the number of *Decoroproetus* cephalata and pygidia suggests sorting. Transport, however, was probably local, as none of the taxa described are known from platform or shelf environments. The fauna of the Coldwell Formation appears to have inhabited deeper-water settings, below storm wave-base. The lower member formed during a time of eustatic lowstand, but the upper member represents a local shallowing event reflecting the foreland basin setting of the Lake District Basin.

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## Evidence of trophic collapse as a forcing factor in the Late Devonian mass extinction

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Acritarch species richness yields a first order metric of marine primary productivity of large phytoplankton in the Palaeozoic oceans. Acritarchs decline smoothly over a period of 100 Myr (ca. 425Ma to 325 Ma), from a Silurian high of 27 genera/Myr to 1 genus/Myr. The robustness of this data set yields a unique opportunity to look at the Devonian mass extinction as caused by partial trophic collapse in marine ecosystems, based on a cascading effect of declining large phytoplankton. The loss of phytoplankton as a food resource should have had a more direct effect on those organisms living entirely in the water column than those in benthic communities. This allows for a simple predictive model which has two components: 1) the cause of extinctions would have been entirely gradual, representing a long-term forcing gradient, and 2) the zooplankton and nekton, as members of the neritic and pelagic marine realm, should have suffered greater levels of extinction than benthic marine organisms. While it is difficult to find a simple metric to document this latter prediction, three groups of neritic/pelagic organisms – graptolites, chitinozoans and fishes – do exhibit major changes in their evolutionary history at the end of the Devonian.



## Dinosaur tracks and possible lungfish aestivation burrows in a shallow coastal lake; lowermost Cretaceous, Bornholm, Denmark

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The Mesozoic succession of the island of Bornholm in the Baltic Sea has hitherto yielded scarce remains of terrestrial vertebrates. We describe a new find of a well-exposed vertebrate trample ground and large, densely spaced, vertical to inclined burrows from shallow lake deposits belonging to the Berriasian Skyttegård Member of the Rabekke Formation. The trampling ground is exposed in a vertical section at the boundary between light grey, fluvial sand and dark-brown, organic-rich lacustrine mud. The tracks are bowl-shaped, have an irregular flat or slightly conical base, are on average 22 cm deep and 43 cm wide at the tracking surface, but some reach widths up to about 1 m. The morphology of the tracks suggests that they were made by dinosaurs, most likely sauropods.

The lacustrine mud contains numerous curved, J-shaped or spiraling, unbranched, cylindrical burrows, on average 4.4 cm wide and 45 cm deep. The burrows have a passive infill of dark mud and irregularly alternating laminae of white sand and terminates in a rounded, concave-up, commonly slightly enlarged chamber. The burrows are similar to burrows referred to lungfish or crayfish, and they are with hesitation interpreted as representing lungfish aestivation burrows based on the morphological characteristics.

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## The Lagerstätte of algal flora from the Silurian of Estonia

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The Palaeozoic fossil record of macroscopic algae contains mostly taxa with calcified thalli; knowledge of non-calcareous algae is poor. A diverse flora of non-calcareous thallophytic algae was recovered in the Kalana Quarry, central Estonia. The fossils occur in a shallowing upward sequence of shelf carbonates of the early Aeronian, in interbeds of brown organic-rich, microlaminated limestones alternating with micritic limestones. Algae are preserved as brown kerogenous and black-coloured carbonized compressions, being represented by compacted 'stems' and sporangia, but occasionally also by laterals or entire thalli. Over ten morphological groups (species) can tentatively be assigned to the Rhodophyta and Chlorophyta, representing several previously known and new genera.

Only 14 species of noncalcified thallophytic algae have previously been reported from the entire Silurian System, and Kalana is far the richest Silurian Lagerstätte of thallophytes. Most abundant is *Leveilleites* (?) *hartnageli* (Rhodophyta, corallinaceans?). A species with leaflike/phylloid thallus, 2–5 mm wide, shows occasionally groups of ovoid structures (about 50x100 µm) interpreted as reproductive structures. In our interpretation there are male plants bearing spermatangia formed on spermatangial mother cells and female plants (carposporophytes) bearing carposporangia. Some taxa are assigned to formerly reported genera of Chlorophyte order Dasycladales (*Inopinatella* sp., *Chaetocladus* sp., *Medusaegraptus* sp.).



## Comparison of morphometric techniques for shapes with few homologous landmarks and their effect on the morphological complexity bias

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Biometric analyses are essential for the study of organisms, their phylogenetic affiliation and the pattern and rate of their evolution. However, a pervasive bias due to differences in morphological complexity among taxa exists, especially in palaeontology. Although geometric quantifications seem to allow the characterisation of certain taxa as biological species in the fossil record, more featureless taxa, even under optimal circumstances both in terms of abundance and preservation, are difficult to characterise with homologous landmarks. We address biometric quantification of taxa with few unambiguously identifiable landmarks (<15) utilising ornamented and unornamented gastropod shells. Quantitative comparison of landmark analysis (LMA) with its potentially strongest competitor, elliptic Fourier analysis (EFA), utilising learning algorithms indicates that EFA yields significantly better results. This suggests that it is the better alternative in cases of scarcity of unambiguously identifiable homologous landmarks. Although both LMA and EFA document general shell shape similarly, both techniques failed to reproduce the biometric signal of ornamentation as obtained with detailed traditional morphometrics.

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## Chitinozoans and the age of the Soom Shale, an Ordovician black shale Lagerstätte, South Africa

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Isolated chitinozoans from the Soom Shale Member of the Cedarberg Formation, SW South Africa, are described and provide a date of the latest Hirnantian – earliest Rhuddanian. The recovered chitinozoans are typical of the *Spinachitina oulebsiri* Biozone and represent only a very short time span (less than 1My) across the Ordovician–Silurian boundary. This is currently the highest biostratigraphic resolution attainable for the Soom Shale Lagerstätte. Correlation of the Soom Shale chitinozoans with identical assemblages in postglacial, transgressive deposits of Northern Africa is possible; both faunas occur in shales that overlie glacial diamictites of the Hirnantian glaciation.



## Taphonomy of starfish ossicles: bitten, crushed, rotten, squatted, but still something to tell

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Starfish skeletons are generally disaggregated rapidly after death and every individual ossicle can experience numerous outrages before being occasionally preserved as grain in the sediment. Isolated ossicles are common and easily sorted from unconsolidated sediments. SEM observation of their surface allows recognition of traces distinctive of taphonomic processes such as bite marks of predators and scavengers, post-mortem settlement of encrusting and boring organisms, mechanical abrasion, and early diagenesis. Quantitative assessment of the taphonomic features provides insightful information about palaeoecology as well as sedimentary processes. Two examples taken from the Jurassic clay deposits of Poland and a third from the Cretaceous chalk of France demonstrate the potential outcomes of the method. At Częstochowa, aggregations of fossils show taphonomic signature of predator regurgitates; a behaviour otherwise difficult to demonstrate in the fossil. At Lukow, the ossicles record distinct taphonomic histories, so that the high local diversity derives from mixing of material from shallow to offshore settings. At Meschers, the mean quality of ossicle preservation varies along a sedimentary sequence, which suggests that the time of residence on sediment surface has changed with decreasing and increasing sedimentary rate.

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## Fossil feathers and their colour

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Feathers are characteristic appendages of birds and theropod dinosaurs and have been found as carbonized imprints in a number of fossil localities. Studies have demonstrated that these organic imprints consist of micron-sized oblate structures, which were interpreted previously as fossil feather-degrading bacteria. Our new investigation shows that these structures are the melanin-containing melanosomes that imparted colour to feathers.

The discovery of preserved melanosomes opens up the possibility of reconstructing the original plumage patterns of extinct birds and dinosaurs, with obvious implications for understanding their ecology and behaviour. Such reconstructions would not rely solely on a comparison with modern counterparts. There are two distinct melanins: eumelanin, which gives rise to black colour, and pheomelanin which makes reddish colours. Eumelanosomes are oblate whereas pheomelanosomes are spherical. Thus recognizing their morphology under the SEM would provide an indication of colour. Different concentrations and combinations of these melanosomes give plumage patterns ranging from buff yellow to grey and to rusty red and pitch black. Distinct alignment of eumelanosomes gives rise to iridescent colours, which might also be recognizable in fossils. Pheomelanosomes have not been recognized in any fossils at this stage and no studies have been made to quantify the amount of melanosomes to the generated colour. Therefore, further studies on fossil feathers and the melanin content in modern birds are necessary in order to be able to make any reliable predictions of plumage colours of feathered dinosaurs in the future.



## The fossil record of the bivalve *Limopsis* (Arcoidea: Limopsidae) in the Antarctic

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*Limopsis* (Arcoidea: Limopsidae) is an abundant and relatively diverse genus of Recent Antarctic bivalve, with nine known species and a further three known from the adjacent Magellan region. However, only three fossil species have been described from the Antarctic, and a few fossil fragments have been assigned to an extant species. These *Limopsis* fossils are not abundant; approximately twenty-five specimens have been identified, and many of them are incomplete. To this scant record, nine new specimens of *Limopsis* have been added, discovered by the British Antarctic Survey from the Cape Melville Formation of King George Island, South Shetland Islands. From this material a new species has been identified, adding to the sparse fossil record of this genus.

The distribution pattern of *Limopsis* in the Southern region has changed markedly from the Tertiary to the present, probably due to climatic and tectonic changes such as the opening of the Drake Passage, the establishment of the polar front, and fluctuations in temperature. Some of the most dramatic of these changes occurred at the time of deposition of the Cape Melville Formation, a scarce early Miocene unit in Antarctica, which is now known to preserve limopsid and other rare fossils.

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## Inferring Mesozoic conifer diversity from analysis of cuticle under Scanning Electron Microscopy and determining the family affinity of form genera

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The taxonomy of Mesozoic conifers has been hindered by the grouping of fossil species into 'form' genera, where the specimens are placed into genera according to leaf shape as opposed to a natural classification. This, combined with the fact that much of the taxonomy of plants is linked to the presence of sexual organs, has mired the study of Mesozoic conifers. Two of these form genera are *Brachyphyllum* and *Pagiophyllum*. The study aimed to analyse specimens of *Brachyphyllum*, *Pagiophyllum* and *Lindleycladus* from Bristol City Museum and Art Galleries under the Scanning Electron Microscope (SEM) in an effort to determine family affinity. The analysis of the specimens showed *Pagiophyllum*, *Brachyphyllum* and *Lindleycladus* to be part of the families Araucaria, Cheirolepidiaceae and Podocarpaceae respectively. In addition to identifying the family affinity, *Brachyphyllum* was identified as *Brachyphyllum desnoyersii*, which was shown to have a new diagnostic character made up of multiple rings of subsidiary cells around the stomatal aperture. A phylogenetic analysis supported this conclusion with the fossil taxa grouping near their extant relatives. Despite the success of the study, the cuticle is too variable to be a definite character used alone in phylogenetic study, as it only suggests the relative family affinity.



## Taphonomic analysis of Ediacaran acritarchs and its importance for taxonomy, biostratigraphy and global correlation

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In this study we analysed the taphonomic degradation history of a diverse assemblage of Ediacaran (late Neoproterozoic) acritarchs from the Centralian Superbasin and Adelaide Rift Complex in Australia. Taphonomic features observed include compression features, folding and tearing of vesicle walls, pitting, perforation, abrasion, exfoliation, shrinking, twisting, splitting, curling, shredding, pyritization, particle entrapment, and thermal maturation effects. The physical and chemical structure of the vesicle wall determines the degree of taphonomic damage. Consistent associations allowed identification of degradation series which incorporate previously described individual species and provide a framework for taxonomic revision. Recognition of taphonomic variants is an important first step in systematic studies, and tracking degradational pathways for particular species resulted in more precise taxonomic identification. Other biostratigraphically useful fossils are uncommon in the Neoproterozoic which means that considerable reliance will be placed on acritarch biostratigraphy for future global correlations. It is vital, therefore, that the significance of taphonomic degradation, for both taxonomy and palaeoenvironmental analysis, is given adequate recognition. Identification of taphonomic variants is critical for taxonomic studies and must be considered before making biostratigraphic subdivision of the Ediacaran System.

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## Evolutionary reduction of the first thoracic limb in butterflies

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One of the factors contributing to the evolutionary success of the arthropods is their segmented body plan. Most segments bear a pair of appendages, and anterioposterior differentiation of appendages in arthropods (tagmosis) is a feature of their evolution. Adult insects have three pairs of legs, one on each thoracic segment. The first thoracic (T1) limb of butterflies in the family Nymphalidae is reduced so much that it cannot be used for walking; it gives the family the common name “brush-footed butterflies”. SEM of the T1 leg in the nymphalid butterfly *Bicyclus anynana* shows the absence of all five tarsal limb segments, and the two claws at the distal terminus. Proportionally, there is a significant reduction in the length of the distal segments of T1 compared with T2 and T3. In contrast, in the pierid butterfly *Pieris rapae* (an outgroup of Nymphalidae) all tarsal segments are present. In Libytheinae (the most basal subfamily of Nymphalidae), only males have reduction of T1 limbs. Fossil Nymphalidae that preserve the “brush-foot” morphology, especially Libytheinae, provide geological dates for the appearance of this character in the Oligocene. This may elucidate the process by which anterior specialization of limbs (e.g. crustacean maxillipeds, branchiopod first antennae) occurs.

