The Palaeontological Association

50th Annual Meeting 18th–21st December 2006

University of Sheffield

**ABSTRACTS** 



## The Palaeontological Association

# 50th Annual Meeting 18th–21st December 2006

# Department of Animal & Plant Sciences, University of Sheffield

The programme and abstracts for the 50th Annual Meeting of the Palaeontological Association are outlined after the following summary of the meeting.

### Confirmation of registration

Confirmation of registration bookings will be sent out by early November. The deadline for registration and booking accommodation is **Friday 24th November**.

#### Venue

The meeting will take place in the University of Sheffield Union of Students that is located on the main University campus. Information on the University of Sheffield can be obtained from <http://www.sheffield.ac.uk/>.

### Accommodation

All delegates — except those making their own arrangements — will stay in Tapton Hall of Residence. Further details on Tapton Hall of Residence are available at <a href="http://www.sheffield.ac.uk/housing/">http://www.sheffield.ac.uk/housing/</a>>.

### Travel

Travel details and maps for the University of Sheffield are available at the following website: <http://www.sheffield.ac.uk/travel/>. These include details of how to get to the main University campus (where the conference will take place) and Tapton Hall of Residence (where delegates will be accommodated). Details of how to get to the reception (Sheffield Botanical Gardens) and annual dinner (the Cutlers' Hall) will be provided at the meeting.

### Registration

Registration will commence on the afternoon of Sunday 17th at Tapton Hall of Residence. On Monday morning it will move to the meeting venue for the Special Symposium where it will be available from 08.00.



### Seminar

A special seminar on 'Macroevolution' will take place in the Auditorium in the University of Sheffield Union of Students on the main campus, beginning at 11.20 on Monday 18th. This will be followed by a reception in the Pavilions of Sheffield Botanical Gardens.

### Oral and poster contributions

All oral contributions will take place in the Auditorium in the University of Sheffield Union of Students on the main campus, beginning at 08.45 on Tuesday 19th, and continuing on Wednesday 20th. Posters will be exhibited in the Foundry in the University of Sheffield Union of Students (where tea/coffee breaks will take place). Details regarding the presentation of talks and posters will be sent to all contributors.

### Annual address

The annual address will be given at 17.15 on Tuesday 19th by Art Boucot on "What can be included in taxonomic descriptions?".

### Annual dinner

The annual dinner will take place in the Cutlers' Hall from 19.00 on Tuesday 19th.

### Field excursion

There will be a field excursion collecting Coal Measures plant fossils and visiting the National Coal Mining Museum on Thursday 21st (approximately 08.00 to 17.00).

#### **Charles Wellman**

# Schedule of events and timetable for presentations

### **Sunday 17th December**

Room registration will be available from 14.00 at Tapton Hall of Residence.

Meeting registration will take place between 14.00 and 21.00 at Tapton Hall of Residence.

Evening meal will be available at Tapton Hall of Residence, for those who have booked, between 18.00 and 19.00.

Bar will be open from 19.00.

### **Monday 18th December**

Room registration will be available from 08.00 at Tapton Hall of Residence.

Meeting registration will take place between 10.00 and 18.00 at the University main campus (where the meeting will take place) and between 18.30 and 21.00 at Tapton Hall of Residence.

#### 11.20-17.30 Seminar: Macroevolution

Oral presentations in the Auditorium in the University of Sheffield Union of Students.

11.20–11.30 Introductory remarks.

Philip Donoghue

Macroevolutionary perspective

11.30–12.00 Do emergent properties block attempts to reduce macroevolution?

Todd Grantham

**Species and Species Interactions** 

- 12.00–12.30 The macroevolutionary consequences of ecological differences among species.

  Mark McPeek
- 12.30–13.00 Autecology, radiations and the filling of ecospace and change: critical intervals

13.00-14.00 Lunch

Tempo and Mode

14.00-14.30 Macroevolution through deep time.

Nicholas Butterfield

**Diversity** 

14.30–15.00 How did life get to be so diverse? the fossil evidence.

Mike Benton

15.00-15.30 Molecular phylogenetics and the dynamics of diversification.

**Brent Emerson** 



### MONDAY 18th December, continued

15.30-16.00 Tea

Disparity

16.00-16.30 Why so many gaps? Morphologic disparity in the fossil record

Douglas Erwin

16.30-17.00 microRNAs and metazoan evolution

Kevin Peterson

**Macroevolutionary Synthesis** 

17.00-17.30 Scale and hierarchy in macroevolution

David Jablonski

### 19.30-21.30 Reception at the Pavilions of Sheffield Botanical Gardens

Evening meal will be available at Tapton Hall of Residence for those who have booked from 18.00 to 19.00.

Bar will be open in Tapton Hall of residence from 21.00.

### **Tuesday 19th December**

Room registration will be available from 08.00 at Tapton Hall of Residence.

Meeting registration will be available from 08.00-18.00 at the University main campus (where the meeting will take place).

Oral and poster presentations in the Auditorium in the University of Sheffield Union of Students.

- 08.45 Welcome
- 09.00 The role of parasites in macroevolution.

Adolf Seilacher, Wolf-Ernst Reif and Peter Wenk

09.15 Pyritization of soft-tissues: an alternative model.

Philip R. Wilby, Alex Page and David A. Riley

09.30 Birds across the Cretaceous-Paleogene boundary.

Gareth Dyke

09.45 Reef-coral diversity is inversely related to coral-reef building in the Caribbean Cenozoic.

Kenneth G. Johnson

- 10.00 Seed plant phylogeny: the root of the problem, or the problem of the root? Jason Hilton and Richard M. Bateman
- 10.15 How can we make evolutionary sense of the Ediacara biota? The puzzle of Dickinsonia.

Jonathan Antcliffe and Martin Brasier

#### 10.30 Coffee and posters

#### 11.00 Crystallographic conservatism in Ordovician Craniid brachiopods.

Jennifer England, Maggie Cusack and Alberto Pérez-Huerto

### 11.15 Community evolution of micromammals from Langebaanweg and other west coast fossil sites (Mio-pliocene to the Holocene) Cape Province, South Africa.

Thalassa Matthews

#### 11.30 Life history evolution of tropical American Cupuladriid bryozoans.

Aaron O'Dea and Jeremy B. C. Jackson

### 11.45 Critically evaluating position of ovule attachment in basal seed plants.

Leyla J. Seyfullah

#### 12.00 A new look at the 'basal' molluscs.

Mark Sutton and Julia Sigwart

### 12.15 Organic-sheathed hexactinellid sponge spicules from the Early Cambrian Forteau Formation of Newfoundland.

Thomas H. P. Harvey

#### 12.30 Palaeozoic phytoplankton diversity patterns.

Gary L. Mullins, Richard, J. Aldridge, Ken J. Dorning, Alain Le Hérisse, Malgorzata Moczydlowska-Vidal, Stewart G. Molyneux, Thomas Servais and Reed Wicander

#### 12.45 Lunch

### 14.00 Food, Feeding and tooth microwear in ornithopod dinosaurs.

Vincent Williams and Mark A. Purnell

### 14.15 X-ray microtomographic studies of exceptionally preserved three-dimensional Triassic Shrimp.

Aoife K. Braiden, Patrick J. Orr, Paul Tafforeau and Stuart L. Kearns

#### 14.30 Fossil bryophytes record ancient carbon dioxide levels.

Benjamin J. Fletcher, Clive W. Anderson and David J. Beerling

### 14.45 Eiffelia and the early evolution of sponges.

Stefan Bengtson and Jakob Vinther

#### 15.00 Spiral-shaped graphoglyptids from an Early Permian tidal flat.

Nicholas J. Minter, Luis A. Buatois, Spencer G. Lucas, Simon J. Braddy and Joshua A. Smith

### 15.15 Character acquisition through geological time.

Graeme T. Lloyd

#### 15.30 Tea and posters



### TUESDAY 19th December, continued

16.00 The importance of being pedunculate: First record of a linguloid with pedicle from the Middle Cambrian Burgess Shale.

Lars Erik Holmer and Jean-Bernard Caron

16.15 Macroecological responses of terrestrial vegetation to environmental change across the Triassic-Jurassic mass extinction boundary in East Greenland.

Jennifer McElwain and Peter Wagner

- 16.30 New data on Early Devonian mites (Acari) from the Rhynie chert, Aberdeenshire. Jason A. Dunlop, Hans Kerp and Hagen Hass.
- 16.45 Annual General Meeting
- 15.15 Annual Address: What can be included in taxonomic descriptions?

  Art Boucot
- 19.00-24.00 Annual Dinner at the Cutlers' Hall (where a late bar will be available).

### **Wednesday 20th December**

Room registration will be available from 08.00 at Tapton Hall of Residence.

Meeting registration will be available from 08.00-18.00 at the University main campus (where the meeting will take place).

Oral and poster presentations in the Auditorium in the University of Sheffield Union of Students.

09.00 Patterns of origination and extinction in the Solent Group Cerithioidea (Caenogastropoda) reflect wider patterns of molluscan origination and extinction in the Late Eocene to Early Oligocene.

**Martin Munt** 

09.15 The formation of lava trees.

Andrew C. Scott, Don Swanson and Allan MacIntyre

09.30 Brood care in a Silurian ostracod.

David J. Siveter, Derek J. Siveter, Mark D. Sutton and Derek E. G. Briggs

09.45 Taphonomy of exceptionally preserved tadpoles from the Miocene Libros fauna, Spain: ontogeny, ecology and mass mortality.

Maria E. McNamara, Patrick J. Orr, Stuart L. Kearns, Luis Alcalá, Pere Anadón and Enrique Peñalver-Mollá

10.00 Habitat tracking during climate change: evidence from cryptic species in planktic foraminifers.

Daniela N. Schmidt and Sabrina Renaud

- 10.15 The rise and demise of microbialites in the Cambro-Ordovician of Laurentia.

  \*Robert Raine\*
- 10.30 Coffee and posters
- 11.00 Testing hypotheses of functional morphology: a dental microwear investigation into feeding ecology in a fossil fish community.

David C. Baines and Mark A. Purnell

11.15 Just eye-catching: Monocular crustacean from the Upper Cambrian 'Orsten' of Sweden.

Joachim T. Haug, Dieter Waloszek and Andeas Maas

11.30 The graptolite synrhabdosome: evidence of cooperation between automobile colonies.

Alex Page, Rachel Backus, Barrie Rickards and Jan Zalasiewicz

- 11.45 Chitinozoan biozonation and facies analysis of the Llanvirn to Llandovery of the Condroz Inlier (Belgium): implications for Condroz-Brabant basin evolution.

  Jan Vanmeirhaeghe
- **12.00** Extraordinary high innovation rate in late Early Devonian cephalopod evolution. *Björn Kröger*
- **12.15** Parallel three-dimensional finite element analysis of dinosaur track formation. *Phil Manning, L. Margetts, J. M. Leng and I. M. Smith*
- 12.30 New Zealand subantarctic phytoliths and their potential for past vegetation reconstruction.

Vanessa Thorn

- 12.45 Lunch
- 14.00 Trouble in t'Toarcian of Tibet.

  Paul Wignall, Tony Hallam, Rob Newton and Sha Jingeng
- 14.15 Osteostracan evolution through space and time: a phylogenetic approach.

  Robert S. Sansom
- 14.30 Evolution of the shell in aculiferan molluscs (Polyplacophora + Aplacophora).

  Jakob Vinther
- 14.45 A new U/Pb date for the basal Meishucun section and implications for the timing of the Cambrian explosion.

Bjorn-Gustaf J. Brooks, James L. Crowley, Samual A. Bowring, Cinzia Cervato and Yugan Jin

15.00 Life on land during the Cambrian Period.

Paul K. Strother



### WEDNESDAY 20th December, continued

- 15.15 Deep sea bonanzas (sunken wood and whales): munchies for molluscs.

  Steffen Kiel and James L. Goedert
- 15.30 Tea and posters
- **16.00 Poriferan paraphyly and its implications for Precambrian palaeobiology.** *Erik A. Sperling and Kevin J. Peterson*
- 16.15 Fire regimes and palaeoenvironments across the Paleocene/Eocene thermal maximum, S. England.

Margaret E. Collinson, David C. Steart, Luke Handley, Richard D. Pancost, Andrew C. Scott, Ian J. Glasspool, Jerry J. Hooker and Andy Stott

16.30 Cellular and subcellular structure of Neoproterozoic animal embryos.

Neil J. Gostling, James W. Hagadorn, Shuhai Xiao, Philip C. J. Donoghue, Stefan Bengtson, Maria Pawlowska, Elizabeth C. Raff, Rudolf A. Raff, F. Rudolf Turner, Yin Chongyu, Chuanming Zhou, Xunlai Yuan, Matthew B. McFeely, Marco Stampanoni and Kenneth H. Nealson

16.45 Phenotypic variation (macro- vs. micro-environmental sources) in a modern bryzoan: implications for fossil species concepts.

Steven J. Hageman and Christopher D. Todd

- 17.00 Bugs and the barrel: palaeontological data in the hydrocarbon industry.

  Craig Harvey
- 17.15 Cranial mechanics of Dicynodontia using finite element analysis and quantitative histology.

  Sandra Jasinoski, Emily Rayfield and Anusuya Chinsamy
- 17.30 Palaeontological significance of material properties of brachiopod shells.

  Albert Pérez-Huerta, Maggie Cusack and Wezhong Zhu
- 17.45 Announcement of prize winners and close of indoor sessions

Evening meal will be available at Tapton Hall of Residence for those who have booked, from 18.00 to 19.00.

### **Thursday 21st December**

Field excursion – Yorkshire Coal Measures fossils and a trip to the National Mining Museum.

08.30 Depart. Return at approximately 17.00.

Leader: Ken Dorning.

# **Abstracts of seminar presentations**

Autecology, radiations and the filling of ecospace: critical intervals

### Richard K. Bambach<sup>1</sup>, Andrew M. Bush<sup>2</sup>, Douglas H. Erwin<sup>3</sup>

- <sup>1</sup> Botanical Museum, Harvard University, USA
- <sup>2</sup> Department of Ecology and Evolutionary Biology and Center for Integrative Geosciences, University of Connecticut, USA
- <sup>3</sup> Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, USA

All possible combinations of six tiering positions in relation to the substratum/water interface, six motility levels, and six feeding strategies define a complete theoretical ecospace of 216 potential modes of life for marine animals. The number of modes of life actually utilized specifies realized ecospace. Due to constraints of effectiveness and efficiency the modern marine fauna utilizes only about half the potential number of modes of life, two thirds of which (62 of 92) are utilized by animals with readily preserved, mineralized hard parts. Realized ecospace has increased markedly since the early evolution of animal ecosystems. The Ediacaran fauna utilized at most 12 modes of life; with just two practised by skeletal organisms. A total of 30 modes of life are recorded in the Early and Middle Cambrian, 19 of which were utilized by skeletal organisms. The other 11 are documented from soft-bodied animals preserved in the Chengjiang and Burgess Shale Konservat-Lagerstätten. The number of modes of life utilized by skeletal organisms increased by more than 50 per cent during the Ordovician radiation to a Late Ordovician total of 30. Between the Late Ordovician and the Recent the number of utilized modes of life has doubled again.

### How did life get to be so diverse? - the fossil evidence

#### Mike Benton

Department of Earth Sciences, University of Bristol, UK

The long-term diversification of life probably cannot be modelled as a simple equilibrial process: the time scales are too long, the potential for exploring new ecospace is too large, and it is unlikely that ecological controls can act at global scales. The sum of many clade expansions and reductions, each of which happens according to its own dynamic, probably approximates more a damped exponential curve when translated into a global-scale species diversification curve. Unfortunately, it is not possible to plot such a meaningful global-scale species diversification curve through time, but curves at higher taxonomic levels have been produced. These curves are subject to the vagaries of the fossil record, but it is unlikely that the sources of error entirely overwhelm the biological signal. A phylogenetic approach to the study of modern organisms, and an appreciation of longer time scales, allows palaeontologists and biologists to explore together why some clades are highly speciose and others are not.



### Macroevolution through deep time

#### Nicholas J. Butterfield

Department of Earth Sciences, University of Cambridge, UK

The fossil record documents two mutually exclusive macroevolutionary modes separated by the transitional Ediacaran Period. Despite the early appearance of crown eukaryotes and an oxygenated atmosphere, the pre-Ediacaran biosphere was populated almost exclusively by microscopic organisms exhibiting low diversity, no biogeographic partitioning, and profound morphological/evolutionary stasis. By contrast, the post-Ediacaran biosphere is characterized by large, diverse organisms, bioprovinciality and conspicuously dynamic evolution. The difference can be understood in terms of the unique escalatory co-evolution accompanying the early Ediacaran introduction of eumetazoans, and their early Cambrian (Tommotian) radiation into the pelagic realm. Eumetazoans revolutionized macroecology through their construction of multi-trophic food webs, which in turn gave rise to large body size, life history trade-offs, ecological succession, biogeography, fundamental increases in standing biomass, the invention of eukaryote-dominated phytoplankton, and the potential for mass extinction, all of which would have fed back on contemporaneous biogeochemistry, organismal ecology and macroevolution. Both the pre-Ediacaran and post-Ediacaran biospheres were inherently stable, but the former derived from the simplicity of superabundant microbes exposed to essentially static, physical environments, whereas the latter is based on eumetazoan-induced diversity and dynamic, biological environments. The c. 100 million year Ediacaran transition (extending to the base of the Tommotian) can be defined on evolutionary criteria, and might usefully be incorporated into the Phanerozoic.

### Molecular phylogenetics and the dynamics of diversification

#### Brent C. Emerson

Centre for Ecology, Evolution and Conservation, School of Biological Sciences, University of East Anglia, UK

Molecular phylogenetics is increasingly being applied to questions of diversification, from below the species level, above the species level, and even at community levels. Why lineages radiate is a fundamental question at the heart of understanding the dynamics of diversification. Does lineage diversification only occur when the external and internal conditions are right: a new territory or ecospace becomes available, and the lineage has acquired a number of characters that open up a new diet or mode of life? Modern high levels of diversity in certain speciose clades may depend on such an ancient opportunity taken. Dramatic climatic changes through the Quaternary must have driven extinctions and originations, but many species responded simply by moving to more favourable locations. What are the consequences of this for diversification? At one extreme ecological communities may be no more than merely chance associations of species, but there may be real interactions among species. Ironically, high species diversity may lead to more speciation, not, as had been assumed, less: more species may create more opportunities for other species, rather than capping diversity at a fixed equilibrium level. This talk will look across these different scales of analysis (below the species through to communities) concentrating on some of the broader implications of these studies for a general understanding of the process of diversification and the factors that are believed to promote it.



### Why so many gaps? Morphologic disparity in the fossil record.

### Douglas H. Erwin

Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, USA

The distribution of organic forms is clumpy at any scale from populations to the highest taxonomic categories, and whether considered within clades or within ecosystems. The fossil record provides little support for expectations that the morphologic gaps between species or groups of species has increased through time as it might if the gaps were created by extinction within a more homogeneous distribution of morphologies. As the quantitative assessments of morphology have replaced counts of higher taxa as a metric of morphologic disparity, numerous studies have demonstrated the rapid construction of morphospace early in evolutionary radiations, and have emphasized the difference between taxonomic measures of morphologic diversity and quantitative assessments of disparity. Other studies have evaluated changing patterns of disparity across mass extinctions, ecomorphological patterns and the patterns of convergence within ecological communities, while the development of theoretical morphology has greatly aided efforts to understand why some forms do not occur. A parallel, and until recently, largely separate research effort in evolutionary developmental biology has established that the developmental toolkit underlying the remarkable breadth of metazoan form is largely identical among bilateria, and many components are shared among all metazoa. Underlying this concern with disparity is a question about temporal variation in the production of morphological innovations, a debate over the relative significance of the generation of new morphologies versus differential probabilities of their successful introduction, and the relative importance of constraint, convergence and contingency in the evolution of form.

### Do emergent properties block attempts to reduce macroevolution?

#### **Todd Grantham**

Department of Philosophy, College of Charleston, USA

Whether macrovolution is reducible to microevolution is one of the persistent debates in evolutionary biology. Although understanding emergence is important to answering this question, the concept has not been extensively discussed within palaeobiology. To clarify the ways in which emergence relates to this debate, a range of different conceptions of emergence are discussed and a general taxonomy of emergence concepts is presented. Weak emergence is a particularly helpful way to understand the hierarchical nature of biology: it captures the ways in which higher-level traits depend on lower-level processes, while recognizing that emergent traits can nonetheless provide the basis for autonomous higher-level theories. A brief review of the biological literature suggests that geographic range size is weakly emergent. While some concepts of emergence do not block the attempt to reduce macroevolution, weak emergence does. Thus, if geographic range is emergent in this sense, it provides a basis for arguing that macroevolutionary phenomena cannot be fully explained by microevolutionary processes.



### Scale and hierarchy in macroevolution

### David Jablonski

Department of Geophysics, University of Chicago, USA

The incorporation of processes that operate across hierarchical levels and a range of temporal and spatial scales has expanded and enriched our understanding of evolution. Expansion of temporal and spatial scales reveals evolutionary patterns and processes that are virtually inaccessible to, and unpredictable from, short-term, localized observations. These larger-scale phenomena range from evolutionary stasis at the species level and the mosaic assembly of complex morphologies in ancestral forms to the nonrandom distribution in time and space of the origin of major evolutionary novelties, as exemplified by the Cambrian explosion and post-extinction recoveries of metazoans, and the preferential origin of major marine groups in onshore environments and tropical waters. Virtually all of these phenomena probably involve both ecological and developmental factors, but the integration of these components with macroevolutionary theory has only begun. Evolution by natural selection can occur at any level where there is heritable variation that affects birth and death of units by virtue of interaction with the environment. Operationally, emergent species-level properties such as geographic range can be recognized by testing whether their macroevolutionary effects are similar regardless of the different lower-level factors that produce them; geographic range can also be shown to be heritable at the species level. The potential for organismic traits to hitch-hike on other factors that promote speciation or damp extinction is high. Temporal and spatial patterns in the origin of major novelties and higher taxa are significantly discordant from those at the species and genus levels, suggesting complex hierarchical effects that remain poorly understood. Not only are many of the features promoting survivorship during background times ineffective during mass extinctions, they are replaced in at least some cases by higher-level, irreducible attributes such as clade-level geographic range.

### The macroevolutionary consequences of ecological differences among species.

#### Mark McPeek

Department of Biological Sciences, Dartmouth College, New Hampshire, USA

Explaining patterns of species richness and diversity is the ultimate goal of scientists working in a number of disciplines. In particular, community ecologists, palaeontologists, and molecular systematists are all trying in one way or another to understand the processes by which species are made, interact with one another and eventually are lost from the Earth's biota. In this presentation, I will explore whether various types of community organization leave characteristic signatures in data that can be obtained from fossils or molecular phylogenies. Specifically, different shapes in the distributions of species longevities in the fossil record and distributions of external branch lengths from molecular phylogenies result from different mechanisms structuring biological communities. In particular, macroevolutionary processes that define the ecological similarity of new species shape these distributions and the resulting mechanisms that define community structure. These results argue for greater integration and exchange of data and ideas between these three fields.



### microRNAs and metazoan evolution

#### **Kevin Peterson**

Department of Biological Sciences, Dartmouth College, New Hampshire, USA

How complex body plans evolved in animals such as fruitflies and vertebrates, as compared to the relatively simply jellyfish and sponges, is not known given the similarity of developmental genetic repertoires shared by all these taxa. Here, we show that a core set of 18 microRNAs (miRNAs), non-coding RNA molecules that negatively regulate the expression of protein-coding genes, are found only in protostomes and deuterostomes and not in sponges or cnidarians. Because many of these miRNAs are expressed in specific tissues and/or organs, miRNA-mediated regulation could have played a fundamental evolutionary role in the origins of organs such as brain and heart – structures not found in cnidarians or sponges – and thus contributed greatly to the evolution of complex body plans. Furthermore, the continuous acquisition and fixation of miRNAs in various animal groups strongly correlates both with the hierarchy of metazoan relationships and with the non-random origination of metazoan morphological innovations through geologic time.



### **Abstracts of oral presentations**

How can we make evolutionary sense of the Ediacara biota? The puzzle of *Dickinsonia*.

#### **Ionathan Antcliffe\* and Martin Brasier**

Department of Earth Sciences, University of Oxford, UK.

The interpretation of the Ediacara biota is critical to our understanding of the dramatic events at the base of the Cambrian. We here investigate *Dickinsonia*, of the Ediacara biota, in terms of its history of study, growth and development. We present the first detailed description of the Oxford *Dickinsonia* material, and its associated wrinkle structures, from the type Ediacara locality, and discuss its relevance to the wider problems facing Ediacaran taxonomy. The specimens are examined using the new techniques of laser scanning, serial Automontage and serial photography allowing the complex morphology to be exhumed. Morphospace analysis of *Dickinsonia* indicates that various interesting palaeobiological conflicts have arisen from the limits of preservation within sandstones of the Rawnsley Quartzite. We also examine extant annelid material for comparative purposes. From this analysis, we find that *Dickinsonia* was not an annelid worm, as has for long been believed by many workers.

Testing hypotheses of functional morphology: A dental microwear investigation into feeding ecology in a fossil fish community.

#### David C. Baines\* and Mark A. Purnell

Department of Geology, University of Leicester, UK

Aspects of the ecology of extinct species are often inferred from an analysis of functional morphology, but this type of analysis can provide us with only indirect evidence of what an animal was actually doing while alive. Tooth microwear, however, provides direct evidence, and recent work on extant fishes has shown that it varies according to how and where individuals fed (Purnell *et al.* 2006; Journal of Animal Ecology). This breakthrough now allows us to rigorously investigate trophic resource use in fossil fish communities by application of quantitative dental microwear techniques. We present an investigation of tooth microwear in the fossil fish community of the Jurassic Solnhofen Limestone, Germany. Previously these fishes have been assigned to feeding guilds based on their functional morphology and limited evidence of stomach contents (Joomun 2003; MSc Dissertation, Bristol). Because of the exceptional quality of preservation and large numbers of specimens, the Solnhofen fishes offer a unique opportunity for us to apply our methods and provide us with an opportunity to test hypotheses of ecological interrelationships derived by more conventional means.



### Eiffelia and the early evolution of sponges

### Stefan Bengtson<sup>1\*</sup> and Jakob Vinther<sup>2</sup>

- <sup>1</sup> Department of Palaeozoology, Swedish Museum of Natural History, Stockholm, Sweden
- <sup>2</sup> Department of Geology and Geophysics, Yale University, New Haven, USA

The Cambrian sponge Eiffelia, first described by Walcott from the Burgess Shale, has generally been regarded as a heteractinid because of its calcareous hexaradiate spicules. Recently, (2005; PNAS 102:5, 1554-1559) it was discovered that in addition to the hexaradiates, the spicular skeleton of Eiffelia also contains hexactinellid-type tetracts. They also pointed out resemblances in the skeletal structure, with spicules forming a single layer of a globose body, Eiffelia strongly resembles the coeval hexactinellid Protospongia. Botting and Butterfield further noted evidence of a bilayered structure of the hexaradiate spicules, hypothesizing this to reflect a dual mineralogical composition: a core of magnesium calcite being overlaid by an opaline siliceous envelope. In their view, siliceous sponges (hexactinellids and demosponges) were likely derived from early calcareous sponges by silicification of the skeleton. We have investigated the mineralogical structure in Eiffelia spicules from the Lower Cambrian carbonate sequences of South Australia. Like various calcareous skeletons in these deposits, the spicules are preserved in calcium phosphate. In addition, however, spicules preserve a siliceous core, which is strictly localized to the centre and does not appear to be of diagenetic origin. Botting and Butterfield's proposal of a dual mineralogy of Eiffelia spicules appears correct, but the Australian material suggests that the mineral phases were inversed from what they assumed. We investigate the implications of spicule homology between calcareous and siliceous sponges involving a transition from siliceous to calcareous mineralogies.

# X-ray microtomographic studies of exceptionally preserved three-dimensional Triassic shrimp

### Aoife Braiden<sup>1\*</sup>, Patrick J Orr<sup>1</sup>, Paul Tafforeau<sup>2,3</sup> and Stuart L. Kearns<sup>4</sup>

- <sup>1</sup> Palaeobiology Research Group, School of Geological Sciences, University College Dublin, Ireland
- <sup>2</sup>Laboratoire de Géobiologie, Biochronologie et Paléontologie Humaine, Université de Poitiers, France
- <sup>3</sup> European Synchrotron Radiation Facility, Grenoble Cedex, France
- <sup>4</sup> Department of Earth Sciences, University of Bristol, UK

Three-dimensionally preserved arthropods were collected from Triassic shoreface clays near Frome, Somerset, England. Initial SEM analyses of a fractured cross-sectional abdominal surface of one specimen revealed detailed preservation of muscle fibres (replicated in calcium phosphate), and the gut (thought to be infilled by ingested clay). Specimens were then imaged using high-resolution x-ray microtomography (at 0.7µm and 1.4µm per voxel) at the European Synchrotron Radiation Facility, Grenoble, France. Studies of the entire fossil (approximately 20mm long) confirmed that not only is muscle replicated throughout the specimen, but that individual muscle blocks, and on a micron-scale their fibres, can be identified. Similarly, the wall of the gut continues in three-dimensions and is replicated in detail (rather than being simply an infill of the original structure). X-ray microtomographic studies also revealed similar high fidelity preservation of extremely labile tissues such as digestive organs and nervous tissue *in situ*, within the body cavity. Using these datasets, detailed three-dimensional computer reconstructions were produced, thus allowing virtual

dissection and examination. X-ray microtomographic studies of such rare, small, fossils, (particularly when used in conjunction with histological sections and decay experiments of comparable modern fauna), are invaluable in understanding the relative timing and taphonomic processes involved in such exceptional preservation.

A new U/Pb date for the basal Meishucun section and implications for the timing of the Cambrian explosion

Bjorn-Gustaf J. Brooks<sup>1\*</sup>, James L. Crowley<sup>2</sup>, Samuel A. Bowring<sup>2</sup>, Cinzia Cervato<sup>1</sup>, Yugan Jin<sup>3</sup>

- <sup>1</sup> Department of Geological and Atmospheric Sciences, Iowa State University, USA
- <sup>2</sup> Department of Earth, Atmospheric and Planetary Sciences, Massachusetts Institute of Technology, USA
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The Early Cambrian of southern China has long been recognized to record the spectacular transition from microscopic small shelly fossils to a fauna characterized by large, diverse higher bilaterians during part of the Early Cambrian evolutionary explosion. Understanding the timing and rate of this evolutionary transition has been aided through the integration of U/Pb geochronology into Cambrian fossil biozones establishing strong tie-points between platforms. The Meishucun section (Yunnan, China) is one of the units that best preserves what could be considered the prelude to the Cambrian explosion. Several attempts at dating volcanic horizons within this section have resulted in U/Pb zircon dates that range from 538 to 525 Ma, making correlation of Meishucun to sections further afield problematic. This new high-precision U/Pb date of 533 Ma for Meishucun's Bed 5 is in broad agreement but considerably more precise than previous U/Pb ages. It indicates that the low diversity fauna of the Anabarites trisulcatus-Protohertzina anabarica zone persisted for no less than the first 9 m.y. of the Cambrian in China. The Anabarites fauna in combination with this new date may serve as a useful lower bracket for the emergence of higher bilaterians (e.g. trilobites, soft-bodied fauna) traceable throughout Yunnan. Furthermore, a date of 533 Ma indicates that considerable time passed within the first Meishucunian fossil assemblage zone, which has important implications for the overall duration of the Meishucunian stage and its calibration to Siberian stages such as the Nemakit-Dalydnian and Tommotian.

Fire regimes and palaeoenvironments across the Paleocene/Eocene thermal maximum, S. England

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We report qualitative and quantitative coal petrological analyses and compound-specific carbon-isotope analyses from the Cobham Lignite Bed (Cobham, Kent, England). Carbon isotope analyses of  $C_{29}$  and  $C_{27}$  n-alkanes exhibit a negative shift in  $^{13}$ C of c. 3%, confirming the presence and stratigraphic location of the onset of the Paleocene–Eocene thermal maximum (PETM) near the top of the laminated lignite. The laminated lignite



has inertinite-rich and poor layers, indicative of episodic fires and post-fire erosion. The inertinite clasts are predominantly charred herbaceous fern leaf stalks and angiosperm wood from living or recently senesced plants. This assemblage indicates a low-diversity source vegetation, possibly adapted to fire disturbance and seasonal surface wildfires. In contrast, the overlying blocky lignite is derived from decomposed plant material and lacks charcoal; changes most likely to result from increased rainfall. The absence of charred peat raises doubts over burning of Paleocene peats as a contributing factor to the negative carbon-isotope excursion. Carbon-isotopic analyses of bacterially-derived hopanes reveal a major shift in microbial metabolism from heterotrophy to methanotrophy. This is consistent with methane release being a key factor in inducing rapid global warming at the PETM onset and suggests that the terrestrial biosphere could have played an important role.

### New data on the Early Devonian mites (Acari) from the Rhynie chert, Aberdeenshire

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Mites (Arachnida: Acari) can be broadly divided into two major lineages; with debate about whether together they form a natural (i.e. monophyletic) group. Anactinotrichids include opilioacariforms, predatory gamasid mites and ticks. They have a rather short and sparse fossil record, only extending back to the Cretaceous. Actinotrichids encompass all remaining mites and are better represented as fossils with a putative Ordovician example and numerous records, mostly from Tertiary ambers. Until recently, the oldest recorded mites were those from the Early Devonian Rhynie cherts of Aberdeenshire, Scotland. Restudy of the original types together with new material has enabled us to confirm some earlier suggestions about their affinities and the presence of the pachygnathoid group Nanorchestidae (readily identifiable by their unique setae) is a particularly remarkable occurrence. The Rhynie mites are found largely within the sporangia of Horneophyton or Aglaophyton plants which implies that they were strongly associated with, if not feeding directly on, their spores. Further support for an intimate ecological association comes from the presence of multiple instars – an immobile prelarva and a larva, both with only six legs - within sporangia; suggesting that much of the life cycle may have taken place within its confines.



# Birds across the Cretaceous-Paleogene boundary Gareth Dyke

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The pattern of the modern avian radiation across the Cretaceous-Paleogene (K-P) boundary has been hugely debated - molecular estimates for the temporal extent of modern avian lineages differ wildly from fossil ages. The most complete yet assembled compendium of temporal, phylogenetic and geological data, sampling across avian history, illustrates that the bulk of sediments yielding fossil birds from the earliest Paleogene (65–49 MYA) are aquatic: marginal marine or lacustrine. This does not reflect avian preservation potential; older birds from the Mesozoic (146–65 MYA), where there are lower volumes of aquatic rocks, are known across all sedimentological environments. Because global sea level is known to have fallen from the Cretaceous into the Paleogene, leading to an increase in terrestrial rock volume with respect to marine, the presence of more birds in aquatic environments is interpreted to be independent of preservation potential. This suggests that either taphonomic effects bias our interpretation of avian evolution across the K-P boundary or that more 'waterbirds' were actually present in the early Paleogene. Existing geological and palaeontological data actually does support a 'shorebird' or 'waterbird' transition in the aftermath of the K-P extinction, albeit in the absence of clear phylogenetic control.

### Crystallographic Conservatism in Ordovician Craniid Brachiopods

### Jennifer England, Maggie Cusack\* and Alberto Pérez-Huerta

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The relatively sudden emergence of organisms with complex mineralised skeletons in the Early Cambrian (~550 Ma) marks one of the major events in the evolution of life and provides some of the most challenging questions for researchers in the study of biominerals: Why and how did this onset occur? To understand how early biominerals formed, we require detailed knowledge of their composition and ultrastructure as well as evidence of how these early structures relate to modern biominerals. Such direct knowledge is difficult to obtain and is therefore often limited. Since the knowledge of how mineral-producing organisms exert precise control on their crystallographic orientation is one of the most fundamental issues in biomineralisation, this study applies electron backscatter diffraction (EBSD) to compare the crystallography of the Late Ordovician Craniid brachiopod *Petrocrania scabiosa* with that of the modern species *Novocrania huttoni*. EBSD analyses of *P. scabiosa* shell indicate that the calcite *c*-axis is parallel to the outer surface of the shell as in calcite semi-nacre of modern Craniids. This suggests that in the case of Craniid brachiopods the biomineralisation mechanisms involved in shell formation have not altered since the Ordovician.

### Fossil bryophytes record ancient carbon dioxide levels

### Benjamin J. Fletcher<sup>1\*</sup> Clive W. Anderson<sup>2</sup> and David J. Beerling<sup>1</sup>

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Resolving the causes of climate change in the geologic past requires knowledge of Earth's ancient atmospheric carbon dioxide ( $\rm CO_2$ ) content. We used the stable carbon isotope fractionation ( $\rm \Delta^{13}C$ ) of fossil liverworts to reconstruct atmospheric CO<sub>2</sub> concentrations from the Mesozoic (200 million years ago, Ma) to the early Cenozoic (50 Ma). Variations in liverwort physiology and environment were accounted for with a model of plant physiology, evaluated against measurements of liverwort photosynthesis and  $\rm \Delta^{13}C$  under a range of atmospheric CO<sub>2</sub>, O<sub>2</sub>, temperature and irradiance. Our results demonstrate that the CO<sub>2</sub> concentration rose from 500 parts per million (ppm) in the Triassic to a peak value of 1300 ppm in the mid-Cretaceous (~100 Ma) before declining back to 750 ppm in the early Paleogene (~60 Ma). The record supports an enhanced long-term sink for CO<sub>2</sub> through heightened weathering driven by the abundance of fast-weathering volcanic rocks over this interval. Radiative forcing by our Mesozoic atmospheric CO<sub>2</sub> record explains a large proportion of the variance in pH-corrected marine oxygen isotope temperatures, indicating CO<sub>2</sub> was a primary control on the evolution of global climate in the Mesozoic.

### Cellular and Subcellular Structure of Neoproterozoic Animal Embryos

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Stereoblastic embryos from the Doushantuo Formation of China exhibit occasional asynchronous cell division with diminishing blastomere volume as cleavage proceeds. Asynchronous cell division is common in modern embryos, implying that sophisticated mechanisms for differential cell division timing and embryonic cell lineage differentiation evolved before 551 Ma. Subcellular structures akin to organelles, coated yolk granules, or lipid vesicles occur in these embryos. Paired reniform structures within embryo cells may represent fossil evidence of cells about to undergo division. Embryos exhibit no evidence of epithelial organization, even in embryos composed of ~1000 cells. Many of these features are compatible with metazoans, but absence of epithelialization is only consistent with a stem-metazoan affinity for Doushantuo embryos.



# Phenotypic variation (macro- vs. micro-environmental sources) in a modern bryozoan: implications for fossil species concepts

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The degree to which variation among environments can affect the phenotypes of a population is critical for an understanding of palaeontological species concepts (skeletal phenotype). This study evaluates the hierarchical influence of large and small scale environmental variation on skeletal morphology of the modern bryozoan Electra pilosa L. Completely random nested analysis of variance was used to partition a hierarchy of environmental variation. Results suggest that most systematic variation among zooecia occurs within colonies at single localities (ultra-microenvironmental variation and packing). More variation occurs among colonies over small spatial scales (50 cm) than at mid-scale (10 m to 1 km) or large scale (20 to 300 km). It is likely that this small scale variation reflects genotypic differences among colonies, but could reflect microenvironmental differences. No systematic variation was observed among colonies at the 10 m to 1 km scale, but significant differences were recognized among specimens at the extremes of 20 to 300 km scale and are attributed to macroenvironmental differences. Systematic differences were not observed in redeployment of colonies to a common garden. Variation among five other Electra species shows that all observed variation within E. pilosa remains orders of magnitude less than the variation among related species.

# Bugs and the Barrel: palaeontological data in the hydrocarbon industry Craig Harvey

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The positive economic impact of applied palaeontology and biostratigraphy during hydrocarbon exploration and production will be highlighted. Palaeontology lays the foundation for much of geoscience and a commonly posed question in the subsurface environment is "what age is this sequence and what were the depositional environments?" Disciplines such as palynology, micropalaeontology and nannopalaeontology can help answer such questions in a hydrocarbon habitat context. Explorationists often refer to taxa from these disciplines as 'bugs'. These 'bugs' are, of course, what palaeontologists would call 'fossils' and just as seismic tools measure acoustic properties of strata, fossils reveal a biologic signal than can be integrated into geological models. Utilizing palaeontological data can provide solid well ties and when integrated with sedimentology, sequence/ seismic stratigraphy and reservoir modelling scenarios, its value in subsurface evaluation and drilling operations is clear. In addition to optimizing palaeotological data, clear communication of results to non-palaeontologists is just as critical. The importance of 'keeping it simple' cannot be overstated; ironically this means the fewer the fossil names the better. But what is the true value of all this? Case studies will be presented from North Sea regional exploration to the production of deepwater Norwegian gas.



# Organic-sheathed hexactinellid sponge spicules from the Early Cambrian Forteau Formation of Newfoundland

### Thomas H. P. Harvey

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New palynomorphs recovered from shales of the Early Cambrian Forteau Formation, western Newfoundland, represent external organic sheaths of sponge spicules. Spicule morphologies include hexactines and pinular pentactines which are restricted to and characteristic of hexactinellid sponges, but spicules of crown-group hexactinellids do not possess sheaths: this new taxon exhibits an extinct character combination. The sheaths must originally have been constructed from a decay-resistant biomacromolecule, and are likely to have been collagenous as they are in extant calcareous sponges. Extant hexactinellids do not incorporate structural proteins into their spicules and so the Forteau sponge must have employed a substantially different mode of spiculogenesis. Implications for character evolution are explored for a variety of phylogenetic scenarios. Character distributions among extant sponges suggest that the sheathed Forteau spicules are most parsimoniously regarded as autapomorphic. However, the recent recognition of robust organic components to spicules in Eiffelia suggests that spicule sheaths may be widespread among Cambrian sponges, and increasing support for a close relationship between hexactinellids and demosponges invites the serious consideration of homology between these sheaths and the wholly organic spicules of *Darwinella*, a peculiar extant demosponge. Additionally, a link to the sheathed spicules of the problematic Cambrian chancelloriids is considered.

# Just Eye-catching: monocular Crustacea from the Upper Cambrian 'Orsten' of Sweden

### Joachim T. Haug\*, Dieter Waloszek and Andreas Maas

Section for Biosystematic Documentation, University of Ulm, Germany

Goticaris longispinosa and Cambropachycope clarksoni are two euarthropods from the Upper Cambrian of Sweden preserved in typical 3D 'Orsten' manner. The most remarkable structure of the two taxa – and making them look quite similar – is a large single compound eye in front of the head. Both species, described in 1990 by Walossek and Müller, were recognised as derivates of the stem-lineage of Eucrustacea because of their special limb morphology. G. longispinosa was known from at least three growth stages, C. clarksoni only from a single developmental stage. Besides a few almost complete specimens of different developmental stages, over a dozen isolated eyes have been discovered since but could not be identified as belonging to the one or other species. Now, with more specimens and morphometric data obtained from the isolated eyes, almost all specimens could be positively assigned. We also could reconstruct a larval sequence of five successive stages for both taxa, presented here for the first time. These new findings enhance our knowledge about the early evolution of Crustacea significantly.



# Seed plant phylogeny: the root of the problem, or the problem of the root? Jason Hilton<sup>1\*</sup> and Richard M. Bateman<sup>2</sup>

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Despite considerable long-term effort, phylogenetic relationships within seed plants remain contradictory; competing morphological and molecular analyses present a wealth of credible hypotheses. Our recent morphological cladistic analysis of lignophytes (seed plants plus their progymnosperm progenitors) highlights the critical importance of outgroup selection. Restricting outgroups to extant taxa forces inappropriate taxa into key positions for interpreting morphological character-state transitions and/or reconstructing hypothetical ancestors. Even given extinct outgroups, selecting particular progymnosperm outgroups can either support monophyletic seed plants or an early divergence into pycnoxylic and manoxylic taxa permits diphyly. In addition, the supposed consensus of relationships evident among recent molecular phylogenies has been greatly exaggerated. For example, placement of the much-discussed Gnetales varies from sister to extant pines, through sister to extant conifers, to sister to all extant seed-plants. Such phylogenetic lability primarily reflects long-branch problems, which in turn reflect the inability of sequence-based trees to effectively accommodate fossil taxa.

# The importance of being pedunculate: first record of a linguloid with pedicle from the Middle Cambrian Burgess Shale

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Lingulella waptensis Walcott, which is the only linguloid brachiopod (Order Lingulida, Superfamily Linguloidea) in the Middle Cambrian Burgess Shale, is here redescribed. All specimens of *L. waptensis* recorded previously are known from their hard parts only. Here we describe the first record of an exceptionally preserved lingulid brachiopod with pedicle from the Burgess Shale. The pedicle of *L. waptensis* is similar to that of other described linguloid pedicles in that it emerged between the valves and had a central coelomic space. However, it is considerably thinner and more easily deformable as compared with other known Cambrian pedunculate linguloids, and it cannot have been used for burrowing into the substrate. *L. waptensis* most likely lived epifaunally, using the pedicle for anchoring in the muddy substrate, with only a limited ability to adjust its position. The Cambrian record of epibenthic pedunculate brachiopods is reviewed in a phylogenetic context.



# Cranial mechanics of Dicynodontia using Finite Element Analysis and quantitative histology

### Sandra C. Jasinoski<sup>1\*</sup>, Emily Rayfield<sup>1</sup> and Anusuya Chinsamy<sup>2</sup>

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Differences in cranial morphology across Dicynodontia have been correlated with changes in masticatory function, and hence, dietary preference. Cranial specialisations of Lystrosaurus, such as a deepened skull and a patent premaxilla-nasal suture, may have increased the efficiency of its masticatory system allowing it to exploit resistant vegetation. This study quantitatively examines the biomechanical significance of cranial form of Lystrosaurus and Oudenodon, a generalised dicynodont, using Finite Element Analysis (FEA) and bone histology. In FEA, two bite directions were modelled: 1) a vertically directed beak bite at the premaxilla-maxilla suture, and 2) a horizontally directed propalinal shredding at the palatine. In the orthal biting model, the preliminary FEA indicates that overall higher peak compressive stresses accumulate in the Oudenodon skull, suggesting that the Lystrosaurus skull could withstand higher compressive stresses; whereas the horizontal biting model suggests the opposite. Thus, the preliminary FEA suggests that Lystrosaurus was capable of a more powerful vertical bite necessary for feeding on resistant vegetation. Several histological features that correlate with function are quantified including: 1) size and shape of secondary osteons; 2) channel orientation; and 3) cortical bone thickness. These features will be compared with the FEA results, thereby validating the use of this computational analysis.

# Reef-coral diversity is inversely related to coral-reef building in the Caribbean Cenozoic

#### Kenneth G. Johnson

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Study of the stratigraphic distribution of large-scale reef carbonates indicates that the Late Oligocene was the acme of reef building in the Caribbean. This has been known since the early twentieth century. However, analysis of a specimen-based compilation of reef-coral species occurrences indicates that reef-coral diversity was lower on both regional and local scales during the Late Oligocene than in the Miocene or Pliocene. Extensive reef building reappeared in the Caribbean during the Early Pleistocene, contemporaneous with a regional extinction of the diverse Pliocene zooxanthellate coral biota. Therefore, coral reef building and reef-coral diversity are inversely correlated in time. This paradoxical result suggests that the factors promoting the origin and maintenance of reef-coral diversity are either independent of or inimical to factors that encourage the existence of extensive coral reef ecosystems capable of producing thick deposits of carbonate. The consequences of this result must also be considered by reef ecologists working to monitor, understand, and conserve the ecological functioning of diverse coral reef ecosystems in modern oceans.



### Deep-sea food bonanzas (sunken wood and whales): munchies for molluscs Steffen Kiel<sup>1,2\*</sup> and James L. Goedert<sup>3</sup>

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The evolutionary history of invertebrate communities utilizing whale carcases and sunken wood in the deep-sea can be explored using fossil evidence. Twenty-eight wood-fall and six whale-fall communities have now been found in Late Eocene to Early Miocene deepwater strata in Washington State, USA, including the oldest whale-fall community known to date. The Eo-Oligocene whale-fall communities lack those taxa that most heavily rely on sulphide produced by anaerobic breakdown of bone lipids but are very similar in their trophic structure to contemporary wood-falls. This suggests that these earliest whale-fall communities represent a 'chemosymbiotic opportunist stage' and that the 'sulphophilic stage' of modern whale-falls developed during the Early Miocene, resulting from a significant increase in both body size and oil content of bones of some kinds of cetaceans during this time.

# Extraordinary high innovation rate in late Early Devonian cephalopod evolution Björn Kröger

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Late Palaeozoic cephalopod faunas differ drastically from that of the Early Palaeozoic. Taxa such as Ammonoidea, Nautilida, and Bactritida are not known from pre-Devonian strata; instead, a wide variety of brevicones, Tarphyceratida and orthoceridans dominate the Ordovician and Silurian. The Zlichovian origin of ammonoids, which is the hallmark of the change between these two faunas, is well understand. In contrast, non-ammonoid Siluro-Devonian evolution is not well known. A section in the Tafilalt, Morocco, provides a first detailed stratigraphical record of non-ammonoid cephalopods of this critical time. Thousands of specimens were collected bed-by-bed, spanning a Ludfordian-Eifelian interval. No conspicuous trend in standardised richness and evenness can be recognised. However, an evolutionary pulse occurs in the section at the Pragian-Zlichovian: bactritoids appear in the late Pragian, with the earliest occurrence of Ammonoids, and the globally earliest record of a nautilitid, Centroceras, in the Zlichovian. The first occurrences in the Tafilalt are supported by available global data. This led to the general conclusion that Bactritida, Nautilitida, and Ammonoidea nearly simultaneously appear in the Pragian-Zlichovian. However, the appearance of these higher taxa does not reflect enhanced global cephalopod evolutionary rates, nor a specific cephalopod radiation in the Early-Middle Devonian.



### Character acquisition through geological time

### Graeme T. Lloyd

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One approach to investigating the history of life is to reduce the problem to the temporal sequence of acquired morphological characters. Here a method for deriving the tempo of character acquisition from cladistic matrices is outlined. Application of this method to published data (covering both vertebrates and invertebrates) reveals a common pattern of an initial burst of character acquisition at the origin of a clade. Comparison between matrices suggests that this burst varies in length and timing, and hence a common, abiotic explanation seems improbable. Worker bias also seems unlikely, and a linear pattern in clades with a recent origin further supports a biological explanation. Important implications of these results include an abandonment of this mode of evolution as representative of 'living fossils' and the suggestion that some higher taxa may be biologically meaningful.

# Parallel three dimensional finite element analysis of dinosaur track formation P. L. Manning<sup>1\*</sup>, L. Margetts<sup>2</sup>, J. M. Leng<sup>2</sup> and I. M. Smith<sup>3</sup>

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Fossilised tracks and trackways provide palaeontologists with information regarding dinosaur locomotion such as their gait, posture and speed. Current best practice is to interpret trackways as 2D surface features. Using computational geomechanics, this paper demonstrates that subsurface deformation can lead to transmitted or subsurface tracks at different depths, whose size and shape relates to a distorted 3D pressure bulb (failure envelope). The results of parallel 3D finite element simulations are compared with a set of transmitted tracks owned by Amherst College (USA). At Amherst College, palaeontologists have peeled away each layer of solidified sediment to find a track in each one. Each of these tracks has a unique geometry, a different length and angle between digits. If each of these was found in isolation, they would be erroneously interpreted as coming from different species of dinosaur. Significantly, palaeontologists use a simple equation relating the length of the foot and the distance between two tracks (stride) to calculate the dinosaur's speed. As the track length changes with depth, so does the apparent stride. The consequence is a different speed for the trackway at each depth: a clear source of misinterpretation. To simulate the transmission of the track through the soil layers, an elasto-plastic soil model is used together with a fine resolution 3D mesh. The requirements of such a model have a marked impact on the computational cost and the authors describe how existing parallel libraries were extended to build a scalable track simulator.



# Community evolution of micromammals from Langebaanweg and other west coast fossil sites (Mio-pliocene to the Holocene) Cape Province, South Africa

#### **Thalassa Matthews**

Iziko South African Museum, Cape Town, South Africa

The Mio-Pliocene site of Langebaanweg (LBW), which dates to around 5.2 Ma, represents one of the largest collections of Mio-Pliocene fossils in Africa, and contains an extremely rich and diverse range of over 230 vertebrate and invertebrate taxa. LBW also has a rich micromammalian fauna consisting of many murid, chrysochlorid, bathyergid, macroscelid and soricid species, which are of particular interest in that the site represents a time period in which modern genera are found together relict Tertiary taxa. Previous researchers have suggested that there may have been a change in environmental conditions during the time period that the two main fossil-bearing members of the Varswater Formation, that is the Langeberg Quartzose Sand Member (LQSM) and the Muishondfontein Pelletal Phosphate Member (MPPM), were laid down. The presence of enamel hypoplasia on the teeth of several ungulate species has been attributed both to dietary stress (Hendey 1981), and to periods of drought and increased aridity (Franz-Odendaal 2002) during the period of deposition of the MPPM. The LBW micromammals were analysed in order to ascertain whether the micromammalian community reflected the same changes, and also to assess the differences, and similarities, in the micromammal populations of the two members. An analysis of the evolution over time of the west coast micromammalian community is presented.

### Macroecological responses of terrestrial vegetation to environmental change across the Triassic-Jurassic mass extinction boundary in East Greenland Iennifer C. McElwain<sup>1\*</sup> and Peter Wagner<sup>2</sup>

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The Triassic-Jurassic boundary (Tr/J) (200 mya) marks the fourth greatest extinction event in Earth history, yet both the pace and causal mechanism of the extinctions remain the subject of considerable debate. In order to decipher gradual versus catastrophic causal mechanisms of extinction we have investigated changes in the ecological structure of plant communities across the Tr/J boundary by comparing the relative abundance distributions (RADs) of 4,304 macrofossil plant specimens, collected from nine fossil plants beds within Rhaetian-Liassic Kap Stewart Group strata at Astartekløft, East Greenland. Information theory was used to determine which of four ecological models (geometric, log-normal, Zipf and zero sum multinomial) provided the best fit for the RADs of each fossil plant assemblage given the expected numbers of taxa with 1, 2, etc. specimens predicted by the best version of each model at the appropriate sample size. A geometric series provided the 'best fit' for the majority of nine fossil plant beds investigated, suggesting that the majority of Triassic and Jurassic plant communities were organized according to simple "first-come, first-served" partitioning of ecospace. A zero-sum multinomial provided the best fit for the RAD of fossil plants from the Tr/J boundary bed. This model, essentially identical to a log-series, assumes the ecological equivalence of all species in the plant community and that abundances are governed by intrinsic properties such as migration, origination and extinction rates rather than interactions among species. More importantly we find a marked increase in the slope of the geometric modelled RAD moving up-section toward the Tr/J boundary; a trend which implies decreasing numbers of common taxa, the

likely increasing extinction/emigration of ecologically rare taxa with time. The pattern of macroecological change is most consistent with a hypothesis for sharp ecological change in the final 10 meters of rock leading to the Tr/J boundary (defined by a globally registered 2 per mil negative isotopic excursion) rather than gradual or no ecological change. These results support predictions from modern metapopulation theory that ecological rarity increases extinction risk. They also suggest that major ecological changes in Triassic vegetation, and perhaps ecosystem instability, were in place before plant species-level extinction, global temperatures and greenhouse gasses reached their peak at the Tr/J boundary.

Taphonomy of exceptionally preserved tadpoles from the Miocene Libros fauna, Spain: ontogeny, ecology and mass mortality

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Exceptionally preserved larval frogs (Rana pueyoi) are abundant in the Late Miocene Libros fauna of NE Spain. The larvae, hosted within profundal lacustrine laminated mudstones, exhibit variations in developmental stage, orientation with respect to bedding, articulation and the extent of soft tissues. Soft tissues are defined predominantly by a carbonaceous bacterial biofilm; jaw sheaths, however, are organically preserved and the former positions of the brain and nerve cord are defined by calcium carbonate. Based upon the position of eyespots, presence and ultrastructure of jaw sheaths, composition of gut contents and the shape of the body and tail, the Libros larvae are assigned to the benthic lentic ecomorphological guild. This, the first ecomorphological reconstruction of a fossil larval anuran, supports phylogenetic evidence that benthic lentic ecology is a conserved ranid feature. Mass mortality of larvae occurred infrequently during summertime algal bloom-induced dysoxia and during late autumn flood/storm events; the former predominantly affected less developed individuals, and the latter individuals across a broad range of developmental stages. Variations in the taphonomy of the larvae are independent of fine-scale lithological fluctuations; instead, the gross characteristics of the sedimentary environment, the biochemistry of individual tissues and ontogeny are the primary controls upon the quality of preservation.



# Spiral-shaped graphoglyptids from an Early Permian intertidal flat Nicholas J. Minter<sup>1\*</sup>, Luis A. Buatois<sup>2</sup>, Spencer G. Lucas<sup>3</sup>, Simon J. Braddy<sup>1</sup> and Joshua A. Smith<sup>3</sup>

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Spiral-shaped foraging trace fossils, assigned to the graphoglyptid cf. *Spirorhaphe azteca*, are reported from an Early Permian intertidal flat in the Robledo Mountains of southern New Mexico, USA. Remarkably similar spiral-shaped structures are produced in modern intertidal flats by the paraonid polychaete *Paraonis fulgens*, and function as traps to capture mobile microorganisms migrating in the sediment in response to tides. We envisage a similar function for the Early Permian trace fossils. Previous studies have suggested that the lack of *P. fulgens*-type traces from ancient intertidal deposits indicates that such behaviour only evolved geologically recently in such settings. However, this report demonstrates that such specialized foraging behaviour was present in intertidal settings by at least the Early Permian. Graphoglyptids are typical of deep-marine settings, and characteristic of the *Nereites* ichnofacies. This represents their first undoubted occurrence in intertidal facies in the geological record. We postulate that the occurrence of graphoglyptids in deep-marine and intertidal settings is related to the predictability of resources. The scarcity of intertidal graphoglyptids in the geological record is most likely a preservational effect.

### Palaeozoic phytoplankton diversity patterns

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The Palaeozoic phytoplankton principally comprised the acritarchs and the prasinophyte algae, although fossil Zygnemataceae, Hydrodictyaceae and possible Scenedesmacaceae are known. We have documented the timing, extent and nature of the biodiversity fluctuations in these groups from the Cambrian to the Carboniferous. As modern phytoplankton are intimately linked to the Earth's ocean–atmosphere system, our analysis shows how the phytoplankton responded to the significant changes in Earth's climate and palaeoceanography through the studied interval. Furthermore, the relationship between the diversity of the phytoplankton, forming the base of the marine food web, and origination and extinction events in the Palaeozoic metazoans can be explored. Acritarch diversity increased from the Early Cambrian to a peak in the Middle Ordovician Darriwilian Stage. This increase mirrors that of the metazoans in the classic Sepkoski curve. A notable decline in acritarch diversity coincided with the end Ordovician Hirnantian glaciation. Prasinophyte algal diversity also increased from the Early Cambrian, but declined during the Late Cambrian and Ordovician, before increasing rapidly to a maximum in the Late Devonian. A significant decline in acritarch and prasinophyte diversity occurred in



the latest Devonian and Early Carboniferous and this coincides with the closure of the Laurussian-Gondwana seaway and the formation of Pangaea.

Patterns of origination and extinction in the Solent Group: Cerithioidea (Caenogastropoda) reflect wider patterns of molluscan origination and extinction in the Late Eocene to Early Oligocene

#### **Martin Munt**

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The Late Eocene to Early Oligocene Solent Group of the Hampshire Basin was deposited in a mosaic of marginal marine and freshwater settings. These settings were home to a range of both endemic and cosmopolitan cerithioidean (Caenogastropoda) gastropods belonging to the families Potamididae, Melanopsidae, Thairidae and Batillaridae. It has long been recognised that the Middle Eocene to Early Oligocene was marked by apparent pulsed faunal turnover. Major biotic turnovers in both the marine and terrestrial realms, contemporaneous with climatic change, are recorded at the Mid/Late Eocene (Bartonian/ Priabonian) boundary, near the Eocene/Oligocene boundary and in the Early Oligocene (the so-called Grande Coupure). The greatest loss of molluscan diversity has been recognised at the Mid/Late Eocene boundary. Patterns of cerithioidean diversity mapped-out from the Paris Basin indicate major loss in diversity between the Bartonian and Priabonian. However, within the Hampshire Basin it is difficult to determine whether such changes were reflected in cerithioidean diversity which was in any case low during the Bartonian. Four of the five taxa recorded from the (Bartonian) Barton Group range up into the (Priabonian) Solent Group. Of the four taxa which cross the boundary, three are endemic and one cosmopolitan. Allmon (2003) observed that whereas diversity loss within the Atlantic marine realm may have been greater at the end of the Bartonian, taxonomic turnover was greater at the Eocene/Oligocene boundary. New taxa emerged in the Early Oligocene forming a distinctive Oligocene fauna. Within the Solent Group extinction is limited to those potamidids which became extinct before the Eocene/Oligocene boundary. Extinction did not occur within the freshwater Melanopsidae and Thairidae which cross the boundary unaffected. Paralleling the findings of Allmon (2003), a distinctive Oligocene fauna, albeit a unique potamidid fauna, is seen in the Solent Group. The Early Oligocene Grande Coupure (big break) is characterised by extinction and dispersal-related origination. To date there has been no indication that the Grande Coupure is seen in groups other than mammals. The recent constraining of the position of the Grande Coupure by Hooker et al. (2004) to below the Nematura Bed (Hamstead Member, Solent Group: Early Oligocene) facilitates the recognition of its signature within the non-mammalia fauna. Within the Solent basin the early part of the Oligocene saw the emergence of an endemic potamidid fauna. In addition to endemics, the first appearance of an Oligocene cosmopolitan taxon is at the base of the Bembridge Marls (base of the Oligocene). With the return to quasimarine conditions during the deposition of the (post Grande Coupure) Cranmore Member (Solent Group: Early Oligocene), the endemic potamidid fauna is replaced by cosmopolitan potamidids, which is interpreted as Grande Coupure-like dispersal related origination.



### Life history evolution of Tropical American Cupuladriid bryozoans

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Cupuladriids are free-living bryozoans common both today and as fossils in Tropical America. A major component of their success is their ability to produce new colonies asexually via fragmentation as well as sexually via larvae. These alternative strategies raise questions about the evolution of sexual and asexual reproduction. Theories about the maintenance of sex and dispersal predict that asexual propagation should persist in stable environments while sex should be more beneficial in areas of high environmental instability. In contrast, life history theory of growth and recruitment predicts that asexual propagation should be favoured in areas of high productivity versus sexual reproduction in low productivity environments. We tested these alternative predictions for eight species of Cupuladria in the southwestern Caribbean over the past 10 Ma, during which time oceanographic conditions changed as the rising Isthmus closed off the Caribbean from the Pacific. Through time, each species increased its sexual rather than asexual reproduction, and colonies likewise became progressively stronger, squatter, and smaller, all of which are traits that reduce rates of asexual reproduction by fragmentation. These trends are consistent with life history theories about growth and recruitment and contradict models regarding maintenance of sex or dispersal. However, the trends persisted long after the period of major environmental change, suggesting that ongoing changes in community composition were also important driving factors. The results are strong evidence for the importance of environmental change as a driving factor in life history evolution.

## The graptolite synrhabdosome: evidence of cooperation between automobile colonies

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Synrhabdosomes are radial arrays of graptoloid graptolites connected at their midpoint, and represent a unique example of behaviour in the fossil record. They can be considered 'supercolonies' formed by the entanglement of several different colonies. Previous workers regarded synrhabdosomes as short-lived clusters of graptolites held together by soft-tissues, and argued that they represented sexual congregations, feeding frenzies or artefacts of taphonomy. However, detailed examination of field and museum collections reveals that synrhabdosomes were in fact long-lived, taphonomically-robust clusters of individuals held together by a 'nemal knot'. That is, rather than continuing to grow a straight nema as normal graptolites would, synrhabdosome-forming individuals modified their growth pattern and used tangled, possibly bifurcated nemata to attach to each other, forming a synrhabdosome. Synrhabdosomes consist of entirely mature specimens and can not form in earliest astogeny, suggesting that they form from unrelated individuals. This, along with their radial symmetry, shows that graptolites were able to control their relative position, indicating automobility. Though Synrhabdosomes themselves are rare, they were formed by many species throughout the evolutionary history of the graptoloids, allowing simple forms to achieve complex morphologies by cooperation between unrelated colonies.



### Palaeontological significance of material properties of brachiopod shells

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By the end of the Cambrian (~ 500 M.a.), calcium carbonate biomineralisation was predominant among invertebrate organisms secreting hard exoskeletons. This predominance of calcium carbonate (calcite and aragonite) was enhanced throughout the development of diverse biomineral fabrics with the subsequent radiation of numerous shell-bearing taxa at the beginning of the Ordovician. Within each phylum, a wide range of shell ultrastructures was developed reflecting diverse modes of life that require different material properties. However, our knowledge of how biomineral ultrastructure relates to material properties is still limited. Here, we use nanoindentation and electron backscatter diffraction (EBSD), mostly applied in engineering and materials science, to assess in detail the material properties and crystallography respectively of two calcite brachiopods living in the same environment but with different modes of life and shell ultrastructure. Understanding how ultrastructure and crystallography correlate with material properties, enables us to begin to understand why organisms produce such a range of biomineral structures and how these are appropriate to their mode of life.

# The rise and demise of microbialites in the Cambro-Ordovician of Laurentia Robert Raine

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During the Cambro-Ordovician, shallow water carbonate successions were deposited across most of Laurentia, many of which are dominated by microbialites in terms of both rock volume and morphological diversity, with a wide range of fabrics, morphology and inter-relationships. The microbialitic deposits represent a complex interplay of the photic and nutrient requirements of the community that formed them, and are further constrained by salinity, energy levels, sedimentation rate and accommodation space. Ecosystems dominated by microbialites suffered a major decline after the Ordovician, and these ecosystems constitute the last major peak of microbialite abundance (both in Laurentia and worldwide), after a period of domination from the Palaeoproterozoic time onwards. The Ordovician thus represents a major shift within carbonate environments and their associated ecosystems. Nevertheless, at this time, microbialites exhibit one of their greatest levels of disparity in form, associated with their occurrence across a wide range of bathymetries. A number of interacting factors may have been responsible for both the success and the demise of microbial communities during the Cambro-Ordovician. These include metazoan grazing pressure, the Phanerozoic sea-level maximum, competition for ecospace, and the existence of a large continental landmass, Laurentia, which was anchored in the tropics throughout this interval.



# Osteostracan evolution through space and time: a phylogenetic approach Robert S. Sansom

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The Osteostraci (cephalaspids) range from the Early Silurian of Europe to Late Devonian of Siberia and Canada. They share a last common ancestor with jawed vertebrates which represents a crucial stage in vertebrate evolution: the transition from jawless to jawed vertebrates. Our understanding of this episode has been hampered by a lack of consensus over and incomplete knowledge of osteostracan intrarelationships. Previous studies are limited by methodology, taxonomic scope or accuracy of findings. Here novel observations, new taxa and global parsimony techniques are used to construct the first comprehensive phylogeny. Support is established for five main monophyletic orders. The new phylogeny is highly consistent with palaeobiogeography, demonstrating endemism for many clades. Palaeobiogeographic reconstruction demonstrates osteostracan origin in the Norway/Britain province. Application to the stratigraphic record highlights an apparent 'explosion' of diversity in the Mid-Silurian. Sea level is found to play a strong role in Silurian osteostracan diversification patterns, a likely artefact of facies preservation. The new phylogenetic hypothesis impacts not only upon our understanding of the acquisition of many key vertebrate characters but also ideas of palaeobiogeographic evolution across Laurussia and Siberia. Furthermore, the phylogeny has broader impact in studies of macroevolution, development, Palaeozoic stratigraphy and vertebrate microremains.

## Habitat tracking during climate change: evidence from cryptic species in planktic foraminifers

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Recent genetic work (e.g. Darling et al., 1999; de Vargas et al., 2001) revealed a significantly larger diversity in planktic foraminifers than previously detected by morphology alone. Detailed morphological analyses were able to link some of these genotypes to "morphotypes" i.e. morphological subunits of the original "species" (Huber et al., 1997; de Vargas et al., 2001) with different environmental adaptations (Renaud and Schmidt, 2003). We analysed the reaction of these cryptic species to climatic changes in comparison to the traditional "morphological species". We investigated two species: Globorotalia truncatulinoides the most recent planktic foraminifer and Globigerinoides ruber which originated at the beginning of the Neogene. Both G. truncatulinoides (de Vargas et al., 2001) and G. ruber include four cryptic "genetic species" (Darling et al., 1999). We analysed a core from the subtropical gyre of the SE Atlantic spanning the last 1 Ma. The morphology of the foraminifers was quantified using a Fourier analysis of their outline in two orthogonal views, size of the test, and coiling direction. The morphological variations observed through time therefore combine mixing of the different morphotypes in various proportions depending on the environmental context representing habitat tracking and a potential long-term evolution.



### The Formation of Lava Trees

#### Andrew C. Scott1\*, Don Swanson2 and Allan MacIntyre3

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Plant fossils may be very common in volcanic rocks, preserved as compressions, impressions, permineralizations and petrifactions, as well as charcoal. However, few fossil plants have been recovered from basaltic lava flows. It is unclear whether this represents a lack of preservation or a lack of exploration. An understanding of the process of entombment and preservation of plants by modern volcanic activity should lead to better search strategies in ancient sequences. Spectacular examples of *in situ* preservation are the lava trees of Hawaii. However, 'lava tree forests' occur associated with several volcanoes. The Kilauea Volcano is an active inter-plate basaltic shield volcano on the Island of Hawaii in the Pacific. The volcano is clothed in vegetation dominated by the angiosperm tree *Ohia* and tree ferns. Lava eruptions may engulf this forest and surround the trees. The lava is over 1200°C on contact with the trees. The lava solidifies around the trees and the trees may be partially charred, completely charred or destroyed depending on size and moisture content of the trunk. Subsequent degassing of the lava allows the preservation of 'Lava Trees'. We have developed a model of entombment that explains this remarkable preservation.

### The role of Parasites in Macroevolution

### Adolf Seilacher<sup>1\*</sup>, Wolf-Ernst Reif<sup>2</sup> and Peter Wenk<sup>3</sup>

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In contrast to the notion that the world would be better without them, parasite networks probably contribute to the long-term stability of ecosystems. This they do by modulating population curves through series of epidemics and endemics. In addition, heteroxenic parasites balance the populations of the different host species, in which they live during their developmental cycles. They may also increase their own long-term survival by targeting taxonomic groups above the species level (*e.g.* families). This will be shown by modern examples. While pathogens and endoparasites are unlikely to be preserved in the fossil record, they may have been largely responsible for the stasis observed in the evolution of ecosystems and for their incumbency in the face of constant Darwinian change and faunal mixing. Only global catastrophies marked by mass extinctions could have led to the collapse of the omnipresent parasite networks. For such studies it is essential to change focus from the medical effects on the hosts to the vital interests of the parasites themselves.



### Critically evaluating position of ovule attachment in basal seed plants Leyla J. Seyfullah

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In seed plants the position of ovule attachment to the parent plant is an important feature for delimiting and distinguishing taxonomic groups. This talk critically assesses ovule attachment in early seed plants and combines analysis of previous accounts with reinvestigation of key taxa. Results are analysed in a phylogenetic context in which cupulate organisation represents the symplesiomorphic condition but with multi- and uni-ovulate cupules co-occurring at the base of the tree. Other modes of ovule attachment are evaluated, including taxa that lack a cupule and bear ovules terminally on dichotomous branching systems, as well as others with ovules attached directly to fern-like foliage, the latter representing a derived condition within some (but not all) pteridosperm groups. A number of previous accounts of attached ovules are discounted and reinterpreted as superimposition of one (typically ovulate) specimen on top of an underlying (typically foliar) specimen.

#### Brood care in a Silurian ostracod

### David J. Siveter<sup>1\*</sup>, Derek J. Siveter <sup>2, 3</sup>, Mark D. Sutton<sup>4</sup> and Derek E. G. Briggs<sup>5</sup>

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An exceptionally preserved new ostracod crustacean from the Silurian of Herefordshire, UK, preserves eggs and possible juveniles within its carapace, providing an unequivocal and unique view of parental brood care in the invertebrate fossil record. The female fossil is assigned to a new family and superfamily of myodocopids based on its soft-part anatomy. It demonstrates a remarkably conserved egg brooding reproductive strategy within these ostracods over 425 million years. The soft-tissue anatomy urges extreme caution in classifying 'straight-hinged' Palaeozoic ostracods based on the carapace alone and fundamentally questions the nature of the shell-based Palaeozoic ostracod record.

### Poriferan paraphyly and its implications for Precambrian paleobiology Erik A. Sperling<sup>1\*</sup> and Kevin J. Peterson<sup>2</sup>

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Well-supported molecular phylogenies combined with knowledge of modern biology can lead to new inferences about the sequence of character acquisition in early animal evolution, the taxonomic affinity of enigmatic Precambrian and Cambrian fossils, and the Proterozoic earth system in general. In this study we demonstrate, in accord with previous molecular studies, that sponges are paraphyletic with calcisponges more closely related to eumetazoans than they are to demosponges. In addition, our Bayesian analysis finds the Homoscleromorpha, previously grouped with the demosponges, to be even more closely related to eumetazoans than are the calcisponges. Hence there may be at least three separate extant "poriferan" lineages each with their own unique skeleton. Because

spiculation is convergent within "Porifera," differences between skeletonization processes in enigmatic Cambrian taxa such as Chancelloria and modern sponges does not mean that these Problematica are not organized around a poriferan body plan, namely a benthic, sessile organism feeding with a water canal system. The shift from an anoxic and sulfidic deep ocean that characterized the mid-Proterozoic to the well-ventilated Phanerozoic ocean occurs before the evolution of planktonic bilaterian predators, and cannot have been caused by the advent of fecal pellets. The evolution and ecological dominance of sponges provide an alternative mechanism for the drawdown and sequestration of dissolved organic carbon within the sediment.

### Life on land during the Cambrian Period

#### Paul K. Strother

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Palynological preparations from nearshore and estuarine mudstones of Cambrian age from the margins of Laurentia contain abundant non-marine cryptospores. These are sporelike cells, typically packaged as sets of dyads and tetrads, whose only crime is to lack the perfect symmetry of later forms that produced the trilete spores of higher land plants. In all other respects, the Cambrian cryptospores are compatible with an embryophytic derivation. Dyad and tetrad topologies match developmental variation observed in extant bryophyte and lycophyte sporogenesis. Non-tetrahedral forms of cryptospores have a persistent fossil record that extends well into the Silurian. Late Cambrian tetrads and dyads from Wisconsin are morphologically very close to Ordovician forms found elsewhere. Cryptospores are distinct from acritarchs and other kinds of fossil algae. Some cryptospore clusters are associated with organic coverings, others are found with receptacle-like structures. The Cambrian landscape was not one of tiny upright axes, these did not come about until the Silurian. Instead, it was likely populated by thalloid plants of an evolving bryophytic complex that occupied a wide range of mesic habitats.

#### A new look at the 'basal' molluscs

### Mark Sutton1\* and Julia Sigwart2

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The position of the 'primitive' molluscs, the Polyplacophora (chitons) and shell-less vermiform Aplacophora, remains highly contentious despite many morphological, developmental and molecular studies of extant organisms. These groups may represent either a basal molluscan grade, or a clade (Aculifera) sister to the 'higher' molluscs (Conchifera). These incompatible hypotheses make very different predictions about the earliest molluscs. Fossil molluscs and mollusc-like animals from the lower Palaeozoic include a range of exceptionally preserved problematic taxa (e.g. Halkieria, Wiwaxia, Acaenoplax, Odontogriphus) that document character combinations not seen in extant molluscs. Additionally, an array of lower Palaeozoic taxa, traditionally treated as 'palaeoloricate polyplacophorans', are known only from their skeletal elements; these include forms that apparently lacked a foot, and others with complex multi-rowed scleritomes. Many key molluscan fossils have been recently described or redescribed, and hence much new information is now available. A new cladistic analysis incorporating both



Palaeozoic and extant molluscs is presented here. Our results support the monophyly of Aculifera, and suggest that extant aplacophorans and polyplacophorans both derive from multi-valved 'palaeoloricates'; the Palaeoloricata is hence paraphyletic, incorporating stem-group polyplacophorans, aplacophorans and aculiferans. *Wiwaxia* and *Halkieria* are accommodated basally as stem-group aculiferans, but crown-group molluscs.

# New Zealand subantarctic phytoliths and their potential for past vegetation reconstruction

#### Vanessa Thorn

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Phytoliths are microscopic deposits of biogenic opal silica, which accumulate within many plants. This research proves the effectiveness of dispersed phytolith analysis for only the broad reconstruction of past vegetation by investigating modern plants and soil, in this case, from subantarctic Campbell Island, south of New Zealand. Retrospective reconstruction of source vegetation from the Campbell Island soil assemblages indicates a broad grassland association for study sites with different local plant communities, biased by the overrepresentation of grass phytoliths. Highlighted issues include the non-production of phytoliths from key taxa, the occurrence of conservative morphotypes and the differential preservation of various phytolith forms. These results suggest that an understanding of taphonomic biases from the depositional setting and comparison with a thorough modern reference collection are essential for interpreting fossil phytolith assemblages. A case study of phytoliths from Late Miocene lignites within the East Coast Volcanics Formation, also from Campbell Island, is shown to contain a tree/shrubdominated assemblage, different to the modern grass-dominated motif, implying a warmer climate than at present during the Neogene.

# Chitinozoan biozonation and facies analyses of the Llanvirn to Llandovery of the Condroz Inlier (Belgium): implications for the Condroz-Brabant basin evolution Ian Vanmeirhaeghe

Research Unit Palaeontology, Ghent University, Belgium

From the Condroz Inlier, a structurally complex area with Ordovician and Silurian rocks, several key sections are lithostratigraphically studied and a chitinozoan biozonation for the Llanvirn to Llandovery is established. This allowed for a review of the stratigraphy of the Condroz Inlier and a correlation with the contemporaneous succession of the Brabant Massif. In combination with facies analyses from both the Condroz Inlier and Brabant Massif, a basin evolutionary model is proposed. In the early Llanvirn, a uniform deep shelf to upper slope setting occurred in the Condroz-Brabant basin, differentiating in the late Llanvirn, with a deeper Brabant Basin. This differentiation persisted throughout the rest of the Ordovician and Silurian, with the Condroz Inlier inner and outer shelf deposits recording sea-level fluctuations and emersion phases, whereas the Brabant Massif succession predominantly consists of deep shelf to slope and basin deposits, only recording pronounced sea-level changes. The Condroz-Brabant succession is correlated to the sealevel reconstruction curves, established for the Baltoscandian Ordovician and the global Silurian, allowing a good fit for the larger part of the succession. Discrepancies between the Llandovery sea-level curve and the sedimentary succession of the Condroz Inlier are attributed to regional tectonics, probably related to the Avalonia-Baltica collision.



# Evolution of the shell in aculiferan molluscs (Polyplacophora + Aplacophora) Jakob Vinther 1,2

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The living polyplacophorans (chitons) are distinguished by their eight large shell plates and a surrounding girdle with smaller sclerites. Two opposing ideas on how the shell plates of chitons evolved had already emerged by the 1800s: (1) that each shell-plate formed from a single sclerite that simply started continual lateral growth or (2) that each shell plate formed by the merging of several sclerites into one. The Lower–Middle Cambrian sachitids, to which *Halkieria* belongs, are stem-group aculiferans and seem to provide a solution to the problem. The shell of *Maikhanella*, a sachitid, which is known from the Lower Cambrian of China and Mongolia, has been interpreted as a shell plate formed from sclerites (*Siphogonuchites*) and therefore favours the sclerite merging model. The transition from having an epithelium secreting multiple sclerites that grow to a finite size to an epithelium forming a shell plate with continuous lateral growth must have involved a dramatic step. The Upper Palaeozoic multiplacophorans, an extinct group of polyplacophorans, have a very different configuration of shell plates to the modern, eight-plated chiton. The unusual living chiton *Schizoplax brandtii*, however, shows how the present set of eight plates could have evolved from an earlier organisation of two shell-plates as expressed in *Halkieria*.

#### Trouble in t'Toarcian of Tibet

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The Early Jurassic (Toarcian) mass extinction has been intensively studied in western Europe where it is seen to coincide with a major phase of transgression and the spread of anoxic bottom waters. Contemporaneous oceanic sediments from Japanese accreted terranes similarly record the development of anoxic conditions. The interval thus shows strong similarities with the end Permian interval when anoxic waters were also widespread in both shelf and oceanic settings. It is therefore intriguing that the Early Jurassic biotic crisis was a relatively minor event, only eliminating taxa up to the family level, whilst the end-Permian extinction eliminated families, orders and even higher taxa. Evidence from the Lower Jurassic of southern Tibet may help explain this discrepancy. This eastern Tethyan region lay at low southerly palaeolatitudes and contains a record of carbonate ramp deposition. Within the carbonates an abrupt deepening event introduced dysoxic conditions into the region. This coincides with the loss of lithiotid bivalves and several genera of lituolid foraminifera, two of the principal victims of the crisis in equatorial latitudes. The extinction record of Tibet is thus comparable to that seen in Europe. However, biostratigraphic dating using calcareous nannofossils indicates that the extinctions/deepening happened near the end of the Toarcian Stage and not at the beginning as happened in Europe. The Toarcian crisis is therefore seen to be regionally diachronous and not a simultaneous global catastrophe like the end-Permian event.



### Pyritization of soft-tissues: an alternative model

### Philip R. Wilby<sup>1\*</sup>, Alex Page<sup>2</sup> and David A. Riley<sup>2</sup>

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Although pyrite is a common diagenetic mineral, it rarely preserves soft-bodied animals. This has generally been attributed to a delay in its precipitation relative to the decomposition of soft-tissues. Existing models for pyritization suggest that this barrier can only be overcome under exceptional conditions, where the sediment contains unusually high concentrations of reactive iron and very low levels of dispersed organics. Under such conditions, the flux of iron is sufficiently great to ensure that pyrite nucleation is centred upon the carcass. Even so, the process is generally too slow to capture labile tissues such as muscle. Numerous recent discoveries of pyritized muscle preserved in association with phosphatized soft-tissues suggest that an alternative, parallel mechanism may also operate widely, with apatite acting to stabilise labile tissues for subsequent pyritization. Enclosure of the organic tissues by an apatite matrix allows bacterial sulphate reduction to be moderated, ensuring that the carcass forms the locus for pyritization, even where ambient reactive iron is not remarkably high.

### Food, feeding and tooth microwear in ornithopod dinosaurs

#### **Vincent Williams\* and Mark Purnell**

Department of Geology, University of Leicester, UK

How animals exploit and compete for finite food resources is a fundamental aspect of their ecology and represents a major evolutionary pressure, yet it is often difficult to investigate rigorously in fossil taxa. The evolution of herbivory in dinosaurs, for example, has been linked to major adaptive radiations and macroevolutionary trends, but were these driven by the appearance of new ecological niches, by innovations in feeding mechanisms, or both? Currently, models of feeding mechanisms in dinosaurs are based on analyses of functional morphology and whilst this approach generates well-constrained hypotheses, they are difficult to test. Quantitative tooth microwear analysis is a potent tool that has been used to great effect to investigate the diets of extinct mammals but has never been applied to dinosaurs. The lack of a differentiated heterodont dentition in dinosaurs makes comparisons problematic as we cannot look at homologous facets. Also, whilst the microwear on mammals' teeth accumulates over a lifetime, dinosaur teeth were continually shed and replaced; was their functional life long enough for diagnostic microwear textures to form? We have conducted the first quantitative analysis of tooth microwear in dinosaurs. Our results demonstrate that microwear can provide powerful insights into the precise jaw motions of dinosaur feeding and provides a robust test of functional hypotheses.

# **Abstracts of poster presentations**

Viséan megaspore assemblage from Dunbar, East Lothian, Scotland

#### Caroline Arioli<sup>1</sup>, Marco Vecoli<sup>1</sup>, Charles H. Wellman<sup>2</sup>

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Viséan megaspore assemblages were described by Spinner in 1969. They were obtained from two thin coal seams, exposed on the coast three miles east-south-east of Dunbar (East Lothian, Scotland), that are locally assigned to the Lower Limestone Group of the Lower Carboniferous. Further investigations by Spinner and Clayton (1973) in Skaterow, a locality close to Dunbar, reported megaspore assemblages similar in overall composition. This interesting area was re-sampled, the stratigraphy clarified and a third coal seam identified. Rich megaspore assemblages were recovered and subjected to detailed analysis using LM, SEM and TEM. The dominant megaspores recorded in the three studies belong to the genera *Lagenicula*, such as *L. subpilosa* (Ibrahim) forma *major* Dijkstra ex Chaloner, 1954, *Setosisporites*, such as *S. pseudoreticulatus* Spinner, 1969, and *Zonalesporites*, such as *Z. rotatus* (Bartlett) Spinner, 1965. Comparisons with assemblages from other areas contribute further to the correlation of Lower Carboniferous deposits and provide evidence for regional differentiation of the floras.

# Functional morphology of the *Panderodus* apparatus: a derived coniform conodont

#### Howard A. Armstrong<sup>1</sup> and Ivan J. Sansom<sup>2</sup>

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- <sup>2</sup> Earth Sciences, University of Birmingham, UK

Our knowledge of the function of the conodont apparatus, the earliest manifestation of the vertebrate skeleton, is based on functional modelling of ramiform bearing apparatuses. The ozarkodinid apparatus, for example, has been interpreted as comprising rostral, grasping ramiform elements that were exposed to function and a caudal array of slicing and grinding elements. This functional paradigm has been extended to *Panderodus* and infers bilateral occlusion for the paired elements of the rostral (qa, qg and qt) and caudal domains (pf, pt) and a dorso-ventral motion for the symmetrical element (ae element). Growth of the pf element scales to positive allometry whilst that of the q elements scales to isometry or negative allometry. This supports a grasping-tooth model, proposed for more derived taxa, in which the q elements grasped the prey and the p elements were retained within the pharynx to process food particles. The function of the petromyzontid laminae presents a functional anologue for the rostral domain as it incorporates occlusion of the bilateral components and a dorso-ventral located median element; but lacks the rostral-caudal differentiation found in *Panderodus*. Differences in element morphology and apparatus architecture may result from differences in feeding strategy.



### Cambrian-Ordovician brachiopod faunas and biogeography of Iran

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In plate tectonic reconstructions, Iran is interpreted as an assemblage of northern peri-Gondwanan terranes, but existing data are insufficient to define positions relative to the Gondwanan margin and other peri-Gondwanan segments. New collections of brachiopods from Upper Cambrian through Lower-Middle Ordovician from the Tabas Region (Central Iranian Plate) and Damghan area, Alborz Mountains (Alborz Plate) provide important insights into palaeobiogeographical relationships. In summary: Upper Cambrian Billingsella assemblages show affinities to Malyi Karatau Range faunas of Kazakhstan. The lingulide Thysanotos is widespread in late Tremadoc-early Arenig successions of Baltica and some other peri-Gondwanan terranes (e.g. Perunica). Early Ordovician lingulate microbrachiopod assemblages have affinities to Baltica, although trilobite faunas from Eastern Alborz retain strong links with South China and not to Baltica. An essentially West Gondwanan Protambonites assemblage is known from Armorica and Perunica, but also the Uralian Margin of Baltica. Lower Darriwilian orthide-polytichioid faunas are associated with Nicolella, which appears contemporaneously in Burma (Sibumasu) and South Tien Shan, but in late Ordovician in west peri-Gondwana. Yangtzeella in Alborz suggests affinity with South China and the Tauride terrane. Caradoc brachiopods such as Drabovia from the Kerman Region of south-central Iran indicate close relationship with North Africa and Bohemia (Perunica).

# 3D models of dinosaur tracks using Light Detection And Range (LIDAR) imaging

#### Karl T. Bates<sup>1</sup>, Phillip L. Manning<sup>1,2</sup> and David Hodgetts<sup>1</sup>

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The methods currently used to record vertebrate tracks suffer from a significant degree of abstraction and lack the resolution required to interpret fossil tracks comprehensively. In particular, manual methods fail to quantify the complex three-dimensionality of tracks and instead describe them essentially as two-dimensional features. If ichnologists are to interpret fossils tracks correctly then new methods are required to record and analyse the 3D geometry of tracks in the field with minimal abstraction. Terrestrial Light Detection And Range (LIDAR) imaging is a highly accurate method of collecting 3D spatial and geometrical data currently employed in other areas of field geology. Its primary data output is a dense point cloud that represents a precisely sampled replica of an object's surface. An extensive LIDAR survey of the track-bearing surfaces at the Fumanya dinosaur tracksites (SE Pyrenees) was performed in order to evaluate the method as a means of recording and analysing fossil tracks in the field. Using LIDAR data it has been possible to construct digital models of fossil tracks that reproduce their surface geometry with high-fidelity. These models allow the ichnologist to interact directly with individual tracks within the context of their exposure. In addition to traditional 2D measurements (e.g. track length) a range of additional 3D parameters have been measured (e.g. surface area, volume) enabling a robust multivariate approach to track analysis and interpretation. Geometrically precise 3D models generated from LIDAR data will also allow ichnologists to visualise and analyse fossil tracks alongside those generated experimentally in finite-element environments.



High Resolution Light Detection And Range (LIDAR) survey of the Fumanya dinosaur tracksites (SE Pyrenees): Implications for the conservation and interpretation of palaeontological heritage sites

# Karl T. Bates<sup>1</sup>, Phillip L. Manning<sup>1,2</sup>, David Hodgetts<sup>1</sup>, Frank Rarity<sup>1</sup>, Bernat Villa<sup>3</sup>, Oriol Oms<sup>4</sup> and Robert L. Gawthorpe<sup>1</sup>

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Palaeontological heritage sites have the potential to offer exceptional information about palaeobiodiversity and the evolution of life. Increasing political and social awareness of the need to protect palaeontological heritage sites is compelling researchers to consider new methods of reconciling conservation and scientific exploration. Terrestrial LIDAR (LIght Detection And Range) imaging is an accurate and efficient method of collecting quantitative spatial data that is currently under-utilised in palaeontology as both an analytical and a geoconservation tool. In order to assess the value of integrated LIDAR imaging and digital photography as a geoconservation tool, a survey of the Maastrichtian dinosaur tracksites at Fumanya (SE Pyrenees, Catalonia) was undertaken using established groundbased procedures. The unique ichnites at Fumanya constitute one of the most important Cretaceous tracksites in the world but have suffered significant erosion since the early 1980s when they were first exposed by open-air lignite mining. The preliminary LIDAR survey of the Fumanya South site has provided sufficient data to construct a number of high-resolution 3D Digital Outcrop Models (DOM) of the locality. The 3D geometry of individual tracks within the DOM can be viewed and analysed quantitatively, providing the first comprehensive record of the tracksite. By enabling workers to build high-resolution photo-realistic DOMs, integrated LIDAR and digital photography may provide the means to produce a global inventory of palaeontological heritage sites, providing a unique level of access and visualisation.

# Cope's Rule as a control for maximum size in Ordovician-Silurian trilobites Mark A. Bell<sup>1,2</sup>, Simon J. Braddy<sup>2</sup> and Richard A. Fortey<sup>1</sup>

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Cope's Rule (the evolution of organisms towards large size) is tested for the first time, within a phylogenetic framework, on two trilobite families: the Asaphidae (Late Cambrian – Late Ordovician) and Lichidae (Middle Cambrian – Late Silurian), both well known for including giant representatives (*e.g. Isotelus rex* and *Uralichas hispanicus* respectively). The length and width of the cephalon and pygidium, and whole body lengths of individuals from European and Moroccan collections, were analysed. Where required, complete body lengths were reconstructed using formulae derived from disarticulated sclerites in the NHM. An original phylogenetic analysis of 60 genera within Asaphidae was conducted using PAUP, in order to provide the phylogenetic framework to study size variation across this group, firstly via pairwise comparisons of relevant sister taxa and secondly size change from primitive to derived members of each clade. The results indicate that Cope's Rule is an important mechanism in the development of giant size in trilobites, with the derived members of Isotelinae, Asaphinae and Lichidae all attaining larger sizes than the more basal members of each clade.

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# Lower Carboniferous ostracods from Scotland: colonisation of the non-marine realm

#### Carys E. Bennett

Department of Geology, University of Leicester, UK

Ostracods are abundant in the fossil record from Ordovician to recent times, but it was not until the Lower Carboniferous that they colonised freshwater environments. Analysis of ostracod bearing sediments from the Viséan (Mississippian) of Fife, Scotland, examines the nature of this transition. Marine limestones and mudstones, deposited in a shallow marine seaway, pass upward into restricted-marine to non-marine deltaic cycles. These include fluvial sandstones, lacustrine mudstones, lagoonal stromatolitic limestones, pedogenic carbonates, evaporites and coals. This study shows that marine sediments contain a high diversity of bairdiacean, hollinellid, cavellinid and palaeocope ostracods. Bairdia submucronata, Hollinella radiata, Beyrichia radiata and Hollina longispina are solely found in marine sediments, associated with a diverse macrofauna of corals, crinoids, goniatites, gastropods, brachiopods and bivalves. Non-marine and restricted marine sediments are characterised by a low diversity, high abundance of ostracods, dominated by cavellinids (which are eurytopic) and paraparchitaceans (which are mainly non-marine), for example Paraparchites armstrongianus and Shemonaella sp. These ostracods are associated with Naiadites, Curvirimula, Spirorbis, Estheria, fish fragments and plants. An investigation into the diagenetic alteration of the ostracod shells is an important preliminary step before  $\delta^{13}$ C and  $\delta^{18}$ O stable isotope analysis to determine palaeoenvironmental conditions.

# Pliocene to Recent bryogeography of the eastern Atlantic and Mediterranean Sea: natural patterns and human impact

#### Björn Berning<sup>1</sup> and Paul D. Taylor<sup>2</sup>

- <sup>1</sup> Institut für Geologie und Paläontologie, Universität Graz, Austria
- <sup>2</sup> Department of Palaeontology, The Natural History Museum, London, UK

A comparison of cheilostome bryozoan faunas from the Pliocene of the NE Atlantic and the coeval Mediterranean Sea results in a substantial reduction of the hitherto assumed number of shared species. Only six (4%) of the 141 species present in the Coralline Crag Formation of Suffolk (as well as in contemperaneous Dutch and Belgian sediments) also occur in the Mediterranean realm. These regions were thus separated by oceanographic barriers and the exchange of cheilostomes, most of which possess short-lived, non-planktotrophic larvae, was rather by chance (e.g. rafting) than the rule. In contrast, Recent faunas from the same areas share a much greater number of bryozoans (97 species, i.e. 63% of 155 species recorded off SE England), which cannot be explained by any natural oceanographic processes. We therefore propose that human activities have drastically altered bryozoan faunal compositions and geographic species ranges since the beginning of seafaring and with the introduction of extremely durable floating debris. These findings are important for conservation biologists as well as for palaeontologists reconstructing biogeographic pathways who may make use of the restricted geographical ranges of species of cheilostome species.

Catherine E. Burgess and Paul N. Pearson

# posters

# Exceptional Preservation of Eocene Foraminifera from the Southern Ocean

Department of Earth, Ocean and Planetary Sciences, Cardiff University, UK

The isotopic and trace metal composition of the calcium carbonate tests of foraminifera are important palaeoclimatic indicators. However, it is known that alteration of foraminifera following their deposition on the seafloor by dissolution, recrystallisation and addition of diagenetic calcite can alter the isotopic and trace metal composition of the tests leading to incorrect palaeoclimatic interpretations. The temperatures indicated by the oxygen isotopic composition of well preserved foraminifera are more similar to the temperatures obtained from other palaeoenvironmental proxies, than those from poorly preserved foraminifera. This study demonstrates the use of Reflected Light Microscopy (RLM) and high-magnification Scanning Electron Microscopy (SEM) to determine the preservational state of foraminifera from a number of high latitude sites. The value of RLM as a technique for determining preservation in the field where SEM is not available is established and a new Eocene Southern Ocean site containing exceptionally well preserved foraminifera is identified.

### The Animal Ancestors Project

#### Richard Callow, Jonathan Antcliffe, Martin Brasier

Department of Earth Sciences, University of Oxford, UK

The candidates for the earliest members of the animal phyla appear in the fossil record near to the Precambrian–Cambrian boundary. While the timing and correlation of these fossils can now be relatively well constrained by stratigraphy and geochronology, there is no consistent system for the placement of these fossils in the widely disparate animal groups. Many previous papers have attempted to extend the ranges of fossil groups back in time, using loose criteria based upon morphological and/or functional analogy. We are left with a menagerie of enigmatic fossils and no solution to when the animal groups originated. In the Animal Ancestors Project, which is to be published in book form, we propose to establish a suite of criteria for the diagnosis of fossils from each of the major animal phyla. The specimens chosen for testing and for illustration will also be part of a major collection at Oxford, which will be available for inspection. This body of data will empower researchers and students across different disciplines to see why the 'enigmatic' fossils are enigmatic and why the 'acceptable' forms are acceptable, thus allowing us to pin-point the first definitive examples of each animal phylum in the fossil record.

# Biotic response to catastrophic environmental change in the Toarcian (Early Jurassic)

#### B. A. Caswell, A. L. Coe, P. W. Skelton and A. S. Cohen

Department of Earth Sciences, The Open University, UK

Organic-rich mudrocks of early Toarcian age are found globally and are interpreted to represent an Oceanic Anoxic Event. This was a period of considerable environmental change associated with a large C-isotope excursion, major changes in the seawater Os-isotope and Sr-isotope compositions (Kemp *et al.*, 2005), extinction of benthic marine invertebrates and changes in the phytoplankton assemblage. The lower Toarcian benthic fauna was of very low diversity and dominated by 2–3 bivalve species across NW Europe.

Data for this study has been collected from exposures near Whitby, Yorkshire, where *Bositra radiata* (Goldfuss), *Pseudomytiloides dubius* (Sowerby) and *Meleagrinella substriata* (Münster) dominate. The existing species range data (Little and Benton, 1995) has been revised with the range of one species being extended by up to 10 m (*c.* 200,000 years). Size frequency distributions (SFDs) of populations of *P. dubius* and *B. radiata* have been measured at *c.* 100 stratigraphic levels throughout the *Harpoceras falciferum* (Sowerby) Zone. The SFDs show several distinct distribution types which vary through time in a complex pattern. Mean shell size and shell size range are both related to total organic carbon and sulphur.

# Palaeobotany and taphonomy of Jurassic hot spring sinters, southern Patagonia, Argentina

### Alan Channing<sup>1</sup> and Alba Zamuner<sup>2</sup>

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- <sup>2</sup> Facultad de Ciencias Naturales y Museo, Universidad Nacional La Plata, Argentina

The Bahía Laura Group of Santa Cruz province, Patagonia, Argentina, contains a diverse, often well-preserved and important Middle to Late Jurassic, gondwanan flora. To date floras are recorded from the tuff-dominated La Matilde Formation and occur solely in the NE (Cerro Cuadrado–Cerro Madre e Hija) and SE (Gran Bajo de San Julián) of the province. One flora, comprising bennettitaleans and attributed to the ignimbrite-dominated Chon Aike Formation, occurs in the centre of the region (Estancia Bajo Pellegrini). Plant fossils are also reported from numerous hot spring travertine and sinter deposits within Bahía Laura strata of the same area. However, we have investigated these and we find that plant occurrences are rare and preservation too poor to allow taxonomic description. Here, we present an initial report of a well-preserved and relatively diverse plant assemblage from Bahía Laura Group, Chon Aike Formation strata of the Estancia Flecha Negra area, central-western region of the Deseado Massif, Santa Cruz province, Patagonia, Argentina. The locality contains fossiliferous cherts, compression floras and a petrified forest which provide an indication of regional plant diversity during this as yet poorly-represented stratigraphic interval.

### Late Ordovician cool-water carbonates and ocean dynamics

### Lesley Cherns and James R. Wheeley

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

Widespread early-mid Ashgill (late Ordovician) limestones that interrupt fine clastic successions in mid-high palaeolatitudes are interpreted as cool water carbonates formed during an episode of global cooling prior to the end-Ordovician glacial maximum. Gondwanan bryozoan mounds developed during eustatic regression with extension of sea ice and reduced fluvial clastic sediment influx. These correlate with mud mounds in Baltica and Avalonia in formerly offshore ramp environments. In the Welsh Basin, upwelling of cool waters is indicated by local phosphatic carbonates deposited in down-ramp settings, as a result of increased circulation in bottom waters. Generally wider faunal distributions reflect sea level fall and thermohaline circulation overturning the sluggish, salinity-stratified oceans that had restricted faunal dispersal through the greenhouse Ordovician, but also show biofacies control. A global oceanographic model includes oceanic overturn in explaining the limestone deposition during polar ice expansion and sea level fall, and changes in faunal distributions.

# 7

### Early Palaeozoic cooling events: evidence and speculation

Lesley Cherns<sup>1</sup>, James R. Wheeley<sup>1</sup>, Michael G. Bassett<sup>2</sup>, Leonid E. Popov<sup>2</sup>, Robert M. Owens<sup>2</sup>, Mansoureh Ghobadi Pour<sup>3</sup> and Andrei V. Dronov<sup>4</sup>

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The end-Ordovician Hirnantian glaciation allied to marine mass extinction is variously considered either as a short-lived event or as the culmination of a long drawn out climatic shift from early Caradoc through to late Llandovery times. Carbon isotope excursions corroborate sedimentological and palaeontological evidence for repeated rapid global climatic change. Against that record, we review facies and faunal evidence of periodic cooling events that span from at least mid Cambrian through to late Silurian times. Cold climate facies evidence includes diamictites and ice rafted dropstones among the Gondwanan marginal to marine succession, widespread development of high-mid latitude carbonates, and probable permafrost features in Cambrian Baltica. At the pre-Hirnantian 'Boda Event', the development of cool water carbonate facies from high to low latitudes is explained by a model of southern ice sheet expansion that led to oceanographic overturn and promoted faunal migrations. What drove the periodicity of early Palaeozoic climate cooling? We consider the occurrence of cooling episodes against evolving palaeobiogeography and oceanic gateways, bathymetry and atmospheric greenhouse gases, and how these might interface with orbitally controlled rhythms.

### The onset of non-planktotrophy in schizasterid spatangoid sea urchins

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

Department of Earth and Ocean Sciences, University of Liverpool, UK

In a broad study of developmental mode in all sea urchin groups Jeffery (1997, Geology 25: 991–994) found that non-planktotrophic (non-feeding) larvae first evolved immediately prior to the Cretaceous–Tertiary boundary and that non-planktotrophy was adopted almost synchronously in five different orders at this time. However, the smaller scale patterns within orders and at lower taxonomic levels remain poorly known. Important questions include: Are there more switches to non-planktotrophy than previously thought? Are switches scattered through time and space or concentrated in particular stratigraphic horizons or geographical areas? Which factors drive switches to non-planktotrophy? This study addresses these questions by means of an investigation of the Cretaceous representatives of the family Schizasteridae (Echinoidea: Spatangoida). Developmental modes were determined from the adult test by using either morphological or crystallographic criteria and were then mapped onto a new phylogeny of the group. This method allowed the number, direction and timing of the switches in larval mode to be determined. The resulting data were then used to determine the temporal and geographic distribution of switches, and to assess which factors drove these switches.



# The radiolarian record of the equatorial Atlantic during the Paleoecene/Eocene Thermal Maximum (PETM) event

### Taniel Danelian<sup>1</sup>, Johan Renaudie<sup>1</sup> and Marie-Madeleine Blanc-Valleron<sup>2</sup>

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The radiolarian record across the PETM event is practically unknown, either because of hiatuses at the critical interval or because of the absence of this siliceous zooplankton group in complete sections. The recent ODP Leg 207 was successful in recovering the PETM event in all five sites drilled on Demerara Rise, a subsided plateau off the shore of Surinam. Here we present preliminary results from a high-resolution (centimetric) study of the PETM event at Site 1260. Radiolarian preservation was evaluated based on both optical and scanning electron microscopy, combined with XRD studies. The upper Palaeocene chalk generally contains rare and moderately well-preserved radiolarians. The uppermost 17 cm of chalk preceding the PETM event is particularly rich in opal-CT, most of it filling the internal chambers of planktic foraminifera, while radiolarians appear to be particularly affected by dissolution. The 20 cm-thick interval that corresponds to the carbonate dissolution level of the PETM contains common and rather well-preserved radiolarians. The assemblage discovered in the PETM interval appears to be of low diversity and displays several particularities in its taxic composition. Amongst the numerous and diverse members of the family Triospyridae, the presence of species Dorcadospyris platyacantha is worth noting, since it was previously found only in middle latitudes. The apparent absence of Buryella tetradica in the PETM assemblage is also of interest, because the species is common in Upper Palaeocene to Lower Eocene sediments, and was found in the Upper Palaeocene chalk of the studied interval.

### Hydrodynamics and lifestyle in ostracoderms

#### **Ben Davies**

Department of Geology, University of Leicester, UK

Stem gnathostomes, traditionally referred to as ostracoderms, represent a crucial phase of vertebrate evolution during which many of the characters that are now taken as typical vertebrate features appeared for the first time. While recent work has gone a long way to clarifying relationships and patterns of character acquisition, understanding of the ecology and biomechanics of these early fishes has lagged behind. Very little is known, for example, about how they swam. A major gap in our understanding of ostracoderm locomotion is how they manoeuvred. This is particularly problematic in forms without pectoral fins. We have used models suspended in a wind tunnel to investigate the hydrodynamic properties of three successful ostracoderm body forms. The subjects studied were the cyathaspid Anglaspis, the pteraspidiform Errivaspis and the cephalaspid Ateleaspis. Forces acting on the models were measured using the labVIEW software package. The software records pitching moments drag and lift at different angles of attack and velocity. These measurements make it possible to build up a picture of the hydrodynamic behaviour of the subjects. In additional experimental work, the Finite Volume software package FLUENT has been used to produce a more detailed interpretation of ostracoderm hydrodynamics. The solver provides a highly visual interpretation of physical processes, helping to identify factors influencing lift and drag. The comparison between experimental and numerical data provides corroboration of conclusions. Another issue crucial to the locomotion of Ostracoderms is, understanding the range of movement of the postcranial

region. Examination of dermal plates from the post-cranial region of the heterostracan *Loricopteraspis dairydinglensis* has allowed us to determine the possible range of articulation between scales and, by extension, the maximum range of movement of the tail during an undulatory swimming cycle. Trace fossils of *Undichnia trisculata*, attributed to the cephalaspid *Zenaspis*, have also allowed us to infer the mode of movement of the trace maker across the substrate and the nature of its undulatory cycle. The data suggest that instability played a role in manoeuvring in some groups. The software was also used to investigate the effects of lift and drag on the three taxa, and the implications for how they moved in their ecosystems. By comparing the experimental work to the work using computer fluid dynamics it was possible to achieve a wider understanding of the locomotory cycle of these early fishes. This work will lead to better understanding of the development of locomotion in early vertebrates and its evolutionary importance.

# Controls on trace fossil diversity in the Lower Cambrian Eriboll and An t-Sròn formations, northwest Scottish Highlands

### Neil S. Davies<sup>1</sup>, Robert J. Raine<sup>1</sup> and Liam G. Herringshaw<sup>1,2</sup>

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The Lower Cambrian Eriboll Formation of the northwest Scottish Highlands is well known for the high-density, low-diversity assemblage of vertical burrows (*Skolithos* and *Monocraterion*) that make up its upper Pipe Rock Member. However, very little ichnological work has been conducted within the overlying An t-Sròn Formation (*Cruziana* ichnofacies), which succeeds the Eriboll Formation conformably in all outcrop areas. This study presents a full description and analysis of the ichnofauna of the Fucoid Member and Salterella Grit Member of the An t-Sròn Formation, along with new observations on the distribution of vertical trace fossils within the Eriboll Formation. A palaeoenvironmental model is proposed that explains the controls on the diversification of the ichnofauna upwards through the two formations. It is suggested that the Pipe Rock Member represents opportunistic colonization of very shallow, laterally extensive event deposits of sediment within a shallow marine environment; the more diverse communities present within the *Cruziana* ichnofacies of the An t-Sròn Formation are interpreted as having been situated further offshore, in a deeper water setting beyond the maximum distal extent of this sedimentation.

# New perspectives on the palaeoecology and palaeogeographical distribution of Ordovician fish from Gondwana

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The Ordovician is a significant period in the evolution of fish, during which the clade underwent prominent and apparently stepwise diversification events, with the development of numerous groups of both jawed and jawless fish. However, as the majority of the existing research regarding Ordovician vertebrates and their habitats has had a significant

Laurentian bias, recent field-based research has been undertaken at a number of known Gondwanan vertebrate localities in order to provide new perspectives on early fish from the southern hemisphere. The preliminary results of the palaeoecological and palaeogeographic aspects of this investigation are shown herein. Ichnological and sedimentological data are presented from the vertebrate localities that enable well-resolved reconstructions of the habitats of a number of Ordovician fish, such as those of Sacabambaspis from the Anzaldo Formation of Bolivia and the Sepulturas Formation of Argentina, and Arandaspis and other pteraspidomorphs from the Larapinta Group of central Australia. Data from these and other localities suggest that early Ordovician fish were constrained to shoreface habitats within the shallow marine realm, and it is argued that this narrow palaeoecological range may be used as a prospecting tool to search for other Ordovician vertebrate-bearing horizons. In addition, the recent discovery of fish-bearing localities in the Middle East demonstrates that the arandaspids occupied the fringes of the entire Gondwanan continent, and were not as palaeogeographically restricted as previously thought. These new data have implications for models that attempt to define global vertebrate dispersal during the Ordovician and could be used to redress uncertainties that may have arisen from the Laurentian bias of existing data.

Ichnology and sedimentology of the Llanvirnian Stairway Sandstone, Northern Territory, Australia: Implications for the understanding of early arandaspid habitats

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The Larapinta Group consists of an almost complete Middle Ordovician succession of shallow marine, mixed clastic and carbonate sediments, with little evidence of prolonged unconformity, which infilled the Amadeus Basin of central Australia. The youngest four formations of the group - the Arenigian Horn Valley Siltstone, Llanvirnian Stairway Sandstone, Llanvirnian-Caradocian Stokes Formation and Caradocian-? Ashgillian Carmichael Sandstone – are significant, in that they contain some of the oldest known arandaspid vertebrate fossils from Gondwana. The most diverse assemblage of microremains is found within the Stokes Formation (Apedolepsis, Arandaspis, Areyongalepis, Sacabambaspis, Porophoraspis), whilst the Stairway Sandstone is the only formation to bear articulated specimens (of Arandaspis). The other two formations contain poorly preserved microremains. This poster presents new data regarding the extremely diverse ichnofauna and sedimentology of the Stairway Sandstone formation, and discusses the implications that these have for the understanding of the habitats of the early arandaspids. Microvertebrate remains are found throughout the Stairway Sandstone, in a variety of shallow marine habitats which have been determined using ichnofacies analysis. However, the articulated remains are only found in the uppermost unit of the Stairway Sandstone, within a pauperized ichnofacies of suspension-feeder burrows and hosted in sandstones typical of rapid, 'event' deposition. Analysis of this uppermost unit indicates that the preservation of these articulated specimens was significantly controlled by the characteristic taphonomic conditions of an environment of sporadic high sediment supply. Comparisons are drawn with other known articulated arandaspid localities from Gondwana where similar conditions are known to have prevailed.

### The neoichnology of terrestrial arthropods

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A comprehensive neoichnological study was conducted to investigate the effect of substrate conditions on the morphology and preservation potential of arthropod trackways. Trackways were made using a range of modern arthropods on substrates of various grain size and moisture content, in protocols simulating subaerial and transitional subaqueous-subaerial depositional environments. General morphological trends, of increased definition of individual tracks and loss of tracks within series, are highlighted as "dry to dampground" and "soft to firmground" surface moisture taphoseries. Heavier arthropods can produce trackways across a broader moisture, and grain size, range, whilst different arthropods can produce similar trackways under certain conditions. Undertrack fallout was investigated using cockroaches, and the resultant undertrack taphoseries mimics the surface moisture taphoseries. Previous hypotheses of the factors that influence trackway survivorship were also investigated. Increasing concentrations of clay minerals exponentially increase the survivorship of trackways subjected to an air current, whereas increasing surface moisture has a linear effect, and a combination of the two provides excellent conditions for trackway survivorship. The results of this study can be used to aid ichnotaxonomic revisions, whilst also facilitating the identification of trace fossil producers and highlighting potential biases in palaeoecological reconstructions based on trace fossils.

# On the beach: palaeoecological significance of clasts from the Dutch and Welsh coasts

#### Stephen K. Donovan

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Rare limestone clasts from the beach at Marloes Sands, southwest Wales, include slender, straight to sinuous borings crosscutting younger, clavate borings. The former were produced by 'worms'; the latter preserve shells of Gastrochaena dubia. Calcareous linings to bivalve borings, part of the hard parts of the producing mollusc, extend into many slender borings. The chance association of the two morphologies of borings has led to the lining becoming intimately associated with both. The modified linings of the bivalve borings have a similar morphology to the crypt of certain clavagellid bivalves, presenting an analogue for the morphology of a pre-clavagellid, boring ancestor. Ensis americanus is a burrower in sandy, shallow water substrates off the Dutch coast. Three articulated shells with broken valves, from the strandline at Zandvoort, Noord-Holland, have dense skeletozoan infestations of Balanus crenatus on the outer and inner surfaces of all valves. Such infestations must have occurred after death of the bivalve, decomposition of the soft tissues and disinterment of the shells. Infestations are perhaps less than a year old, testifying to the post-mortem persistence of the ligament and the density of skeletozoan infestation after a geologically brief duration. Such specimens (balanuliths) would be a palaeoecological conundrum if fossilized.



# Palaeoecological implications of rare predatory borings in Pleistocene brachiopods from Antillean fore-reef palaeoenvironments

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Brachiopods, though relatively rare, occur in a variety of settings associated with the Pleistocene fore-reef deposits of Jamaica and Barbados. Skeletozoans infesting the brachiopod shells include calcareous worm tubes, bryozoans, the sponge domicile *Entobia* isp. and predatory drillholes (*Oichnus* ispp.). *Tichosina* sp. cf. *T. bartletti* (Dall) was large, smooth and probably free living, whereas *Terebratulina* sp. cf. *T. palmeri* Cooper and *Argyrotheca* sp. cf. *A. barrettiana* (Davidson) were micromorphic, plicate and attached; samples of the latter species and the thecideidinean *Lacazella* sp. cf. *L. caribbeanensis* Cooper were small. *Tichosina* shells were commonly infested by episkeletozoans, but were not bored by predators; this supports the view that *Tichosina* preferred open-marine, deeper-water environments where predation was rare and hard substrates were at a premium. About 3% of Jamaican *Terebratulina* shells were perforated by *Oichnus* ispp.; this is a similar order of magnitude to most post-Palaeozoic brachiopod faunas reported in the literature. Some dense infestations exist in which an order of magnitude more shells are bored; these are termed predatory gastropod 'feeding frenzies' herein. These are local in occurrence and have yet to be explained.

# A new arthropod from the Early Devonian Rhynie chert, Aberdeenshire (Scotland), with a remarkable filtering device in the mouthparts

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A new arthropod is described from the Early Devonian Rhynie cherts, Aberdeenshire, Scotland, UK. Although an incomplete thin section preparation, this enigmatic fossil differs substantially in overall shape and in various morphological details from previous named discoveries at Rhynie. A remarkable feature is what appears to be a very thick cuticle, albeit with a curious spongiform texture and ducts running through it. Secondly, associated with the mouth is a unique, elongate, steeply-rising structure comprising filamentous or platelet-like projections. This 'hairy throat' probably acted as some sort of post-oral (?) filtering device and implies a terrestrial animal; a liquid-feeder that practised preoral digestion. Affinities of this new fossil remain equivocal, but preoral digestion implies an arachnid. Indeed the overall outline present in the thin section and, perhaps, the filtering device show some intriguing similarities to spiders (Araneae).



### New skeletal and dental material of Mississippian chondrichthyans from Derbyshire, UK

### Mike Edge<sup>1</sup>, Jenny Clack<sup>1</sup> and John Beck<sup>2</sup>

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The Carboniferous Limestone of Derbyshire around Bakewell is well known for isolated chondrichthyan teeth and scales, however anatomically preserved material is very rare. Recently the authors have discovered articulated skeletal material including lower jaw and shoulder girdle elements, and other prismatic cartilage structures associated with teeth and/or skin denticles from at least two genera. The material comes from two localities near Eyam: Bleaklow Quarry and a spoil heap from an 18th century lead mine. Stratigraphically these derive from the Eyam Limestone, either the Brigantian Visean P, zone or the Namurian Pendleian E<sub>1</sub>, zone. Identity of many of the prismatic cartilage structures is uncertain but includes cranial and branchial cartilages. Preliminary studies have identified teeth associated with two of these. One is a tooth provisionally identified as Protacrodus aequalis, previously known only from the early Tournaisian of the South Urals of Russia: our specimen is the first record of this species in Derbyshire, extending its range geographically and stratigraphically. The other could be either Denea fournieri, a stethacanthid recorded previously in the area, or another stethacanthid. Bleaklow quarry specimens include a stethacanthid-like pectoral girdle. Potentially, the new specimens should clarify the anatomy and systematics of several chondrichthyans previously known mainly from tooth morphologies, and provide insight into wider basal chondrichthyan phylogeny.

### The British Lower Silurian (Llandovery) Crinoidea

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Crinoids are one of the most important shelly groups of the Palaeozoic. Current research on British Llandovery crinoids, including their disarticulated columnals, provides new information on their stratigraphy, biodiversity and overall morphological trends. Only about a third as many nominal crinoid species are known from the Llandovery as the Wenlock; indeed, the well-known and diverse crinoids of the Wenlock at Dudley give an impression of a lag in recovery after the late Ordovician extinction. However, in part, the rare preservation of complete Llandovery crinoids represents a taphonomic artefact. Llandovery crinoid columnals have largely been ignored hitherto, but are widespread, and can provide data for biodiversity and palaeoecologic studies that would otherwise be unavailable. New material has been collected from the Welsh Borderland, southwest Wales and Llandovery, and the Girvan district and North Esk Inlier. Llandovery columnal associations are less diverse than those known from the Ashgill, further supporting the idea of a lag period of recovery immediately after the end Ordovician extinction. However, they also demonstrate a greater diversity of crinoids than otherwise recognised. Although many of the distinctive Ordovician columnal morphologies disappeared, it is anticipated that the more distinctive Llandovery stems can be attributed appropriately to the correct species.



### Description and paleoecology of Miocene rhodolites (Kozjansko, Slovenia) Luka Gale

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Recent and fossil rhodolites are bulbous forms, created by undetached encrusting red algae. They have been proven useful in paleoecological studies. External and internal features of Badenian rhodolites from two locations, Dekmanca and Spodnje Selce, from Kozjansko were obtained through measuring, slicing and making thin sections. Material was altered during early and late diagenesis, but remains highly useful. Concerning their shape, rhodolites were described as spheroidal, ellipsoidal, discoidal or spindle-like. Their surface can be bumpy and/or smooth, reflecting growth forms inside. These were described as straight laminae, wavy laminae or columnar and often show progressive stabilisation of a rhodolite, as well as several cycles of growth, caused by (relative) changes in water energy. Centres of the rhodolites were assigned to different lithic grains, allochems or they appear to be empty spaces, later filled with blocky calcite. Apart from red algae, rhodolites also contain several other organisms and numerous geopetal textures. They were affected by boring organisms and abrasion. Besides previously known genera Sporolithon, Lithothamnion and Mesophyllum, genus Lithophyllum was distinguished and proved to be of major importance. Ratios between these four genera, external and internal properties of fossil rhodolites were used to estimate depth at the time of their growth.

#### Mussel shell microstructural studies

#### Luciana Génio<sup>1</sup>, Steffen Kiel<sup>1</sup>, Crispin Little<sup>1</sup>, John Grahame<sup>2</sup> and Marina Ribeiro Cunha<sup>3</sup>

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The bivalve family Mytilidae has representative genera and species in both recent and fossil deep-sea chemosynthetic communities. The phylogenetic relationships among these taxa, and their relation to other mytilids are, however, not yet fully resolved. Molecular phylogenetic data suggest that modern mytilid genera from hydrothermal vents, cold seeps, sunken whales, and wood form one monophyletic group, and should be included in the subfamily Bathymodiolinae. This hypothesis remains untested using morphological data. Such studies will be necessary to resolve current problems within mytilid systematics and to improve the taxonomic identification of the fossil species. Our research aims to identify phylogenetic relationships of the Mytilidae using early ontogenetic shells and shell microstructure characters. Different structures may occur in the outer shell, which can be entirely aragonitic or composed of an outer calcitic sublayer and an inner aragonitic sublayer. Preliminary results indicate that mytilids inhabiting chemosynthetic environments show considerable differences among shell microstructural details, as well as in larval and juvenile shell morphology. Future investigation will evaluate whether those characters can indeed be used for phylogenetic analyses.



### Reedocalymeninae and associated trilobites from the Ordovician of Iran and Central Asia

### Mansoureh Ghobadi Pour<sup>1</sup>, Robert Owens<sup>2</sup> and Leonid Popov<sup>2</sup>

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Calymenid trilobites belonging to the subfamily Reedocalymeninae were distributed widely across the upper and mid shelf biofacies of Gondwana and peri-Gondwana during the Ordovician, and provide useful palaeogeographical information. In the Middle Ordovician of Iran this subfamily is represented by two genera, Neseuretus and Neseuretinus. The former is known from the Lashkarak Formation (lower Darriwilian [=upper Arenig/lower Llanvirn]) of the Alborz Mountains, in which its appearance coincides with the termination of carbonate sedimentation, an abrupt decline of faunal diversity and, probably, with a considerable cooling of the surface waters. Fortey and Morris (1982) showed that the Neseuretus biofacies is usually associated with inshore epicratonic deposits in high latitude Gondwana, and pointed out its remarkably low diversity. Neseuretinus is abundant in the upper part of the Shirgesht Formation (upper Darriwilian [=upper Llanvirn]) of central Iran, where it occurs within a mid shelf (BA 4) trilobite assemblage of medium diversity that includes Leiomegalaspides, Ovalocephalus and Radnoria among others. This association, including Neseuretinus, is closely similar to contemporaneous trilobite faunas from Burma and Uzbekistan. Vietnamia sulcata (Kolobova) from the Chashmankalon and Archalyk beds (lower to middle Ashgill) of the Zerafshan Range, Uzbekistan, is probably the youngest known species of Reedocalymeninae. It occurs in an assemblage dominated by brachiopods and corals (e.g. Agetolites) that is interpreted as BA 3. Another species of this genus from central Asia, V. pamirica (Balashova), occurs in the upper Caradoc of central Pamir, Tajikistan; it is probably conspecific with Sarrabesia teichmuelleri Hammann and Leone, from the Upper Ordovician of Sardinia.

### Gerastos (Class Trilobita) from the Lower and Middle Devonian of southern Morocco

#### S. Gibb and B. D. E. Chatterton

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"The characters do not give the genus, but the genus gives the characters" (Darwin, 1859).

Recent collections from Lower and Middle Devonian strata of Morocco have uncovered twelve new species/subspecies of the trilobite Gerastos. Copious, exceptionally wellpreserved, articulated specimens from the Tindouf, Ma'der and Tafilalt basins, have been discovered. These new taxa are valuable for regional biostratigraphy. Cladistic analysis of the best preserved Moroccan and European Devonian species of Gerastos, together with the type species of Proetus, Longiproetus, Devonoproetus, Rhenocynproetus, and Dohmiella, leads to the conclusion that all of these genera but Proetus nest within Gerastos and are therefore junior subjective synonyms. *Proetus* species, on the whole, are older and more conservative in form than Gerastos and that genus was probably ancestral to Gerastos. During the Devonian, the trilobita probably suffered a greater reduction in diversity during the Middle Devonian than during the better-known Frasnian/Famennian Mass Extinction events. Thus there was decoupling between the timing of disappearances of many trilobite

families during the Devonian and the well-known Mass Extinctions. Certain morphological features that evolved and/or were lost through time in *Gerastos* assist in shedding light on the success of the Proetida beyond the Devonian. For example, within *Gerastos*, a reduction in ornamentation, especially upon the anterior-most glabella and around the margins, together with a reduction in or loss of the genal spines and an increased ratio of glabellar to cephalon width (tr.) ( $k/\partial$ - $\partial$ ), could demonstrate increasingly cryptic behaviour, through a burrowing lifestyle. Proetids have comparatively conservative morphologies, similar to many Cambrian Ptychopariida, supporting the suggestion that they were generalists. Perhaps the successful Proetida were generalists that were also capable of hiding from comparatively new groups of large actively radiating mobile predators (fishes and ammonoids) during the Devonian. In contrast, more specialized odontopleurids, lichids and corynexochids entered an 'arms race' that they subsequently did not win.

# The potential use of molecular palaeontology in the exploration of prehistoric animal-microbe symbiosis

#### Fiona L. Gill and Richard D. Pancost

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Biomarkers are organic molecules that can be unambiguously assigned to groups of organisms, on the basis of their unique chemical structures and/or stable isotopic signature. Many prokaryotic biomarkers can be recognised in the fossil record, and could potentially be recovered from macrofossils or coprolites. In such materials, they could be used to reconstruct the microbial assemblages symbiotically associated with ancient animals. Two examples of modern macrofauna-microbe associations include cold seep bivalves with chemosymbiotic bacteria and cellulose-digesting methanogenic archaea in ruminant mammals. In both cases, previous work has shown the occurrence of the microbes and their corresponding biomarkers in the tissues or dung of the animal. We aim to investigate the potential of extending this biomarker approach to track biochemical processes such as chemosymbiosis and methanogenesis in the fossil record, on the scale of individual organisms. Our geochemical analyses of body fossils and coprolites will be interpreted with reference to a suite of equivalent modern samples. Although symbiotic associations between microbes and macrofauna in the geological record are often inferred on the basis of uniformitarianism, ecology and preservational features, the biomarker approach will provide a critical complementary means of demonstrating the presence of symbiotic microbes. This has the potential to provide insights into larger questions such as the evolution of nutritional and digestive strategies through time.

# The Ordovician–Silurian pentameroid seas of North Greenland: tropical incumbents rule the waves

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Key Ordovician–Silurian localities in Peary Land, North Greenland, are dominated by thick horizons of pentameroid brachiopods within a mosaic of inner-shelf, shallow-water carbonate environments. Upper Ordovician environments were locally dominated by

Proconchidium whereas the lower Silurian preserves sequences containing abundant Veridita, Virgiana and Sulcipentamerus; most taxa probably lived in co-supportive clusters relying on their strong musculature to help facilitate articulation, and on their posteriorly-thickened shells to increase stability on the substrate. Where present, the pentameroids are abundant, occurring in a variety of shell concentrations to the exclusion of most other benthos. Tropical environments and faunas associated with the Laurentian midcontinent were quite different from those of the margins; the latter had stronger links with Avalonian and Baltic faunas, although the late Ordovician Proconchidium fauna can be traced westwards to Baffin Island still within Laurentia. The successions in Peary Land confirm the overwhelming abundance of the virgianid brachiopods during the early Silurian and their supremacy in shallow-water, tropical environments. The pentameroid brachiopods formed incumbent communities through the late Ordovician and early Silurian in the tropical belt and may have initiated phases of incumbent replacement in the shallow-water facies of adjacent provinces following the end Ordovician extinction events.

# Latitudinal floral extinction at the Palaeocene–Eocene boundary Guy J. Harrington

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The Palaeocene–Eocene thermal maximum (PETM) at ≈55.8 Ma is characterised by rapid global warming from the tropics to the poles caused by the release of greenhouse gases at rates that are similar to present and forecast estimates of anthropogenic fossil fuel emissions. Long-term impacts on plant taxonomic richness and extinction rates are currently unclear. Using information from literature sources from North and South American pollen records and from raw data from the eastern US Gulf Coast and western interior USA, I show that long-term Palaeocene–Eocene extinction intensity varies by latitude. Plant extinction is greatest in low latitude paratropical vegetation types (>20%), rather than in warm-temperate high latitudes (2%) or in arctic biomes (0%). Extinction susceptibility is linked strongly with geographic range of plant taxa. These results show that even under greenhouse climates, diverse vegetation types with narrow geographic ranges are most prone to extinction and confirm contemporary concerns for the future survival of wet, tropical biomes in a warming world.

# Reinvestigation of the flora of the early Oligocene Insect Limestone, Isle of Wight Peta Hayes<sup>1</sup> and Margaret Collinson<sup>2</sup>

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The early Oligocene Insect Limestone is a horizon of thin lenticular limestones near the base of the Bembridge Marls Member on the Isle of Wight. Although famous for its insect fauna, the diverse flora is also of great significance. Much of our knowledge of this flora is based on the A'Court Smith collections deposited in the Natural History Museum, London, and monographed by Reid and Chandler in 1926. However, many taxa are yet to be fully described and named, some identifications need revisiting and many specimens labelled Insect Limestone are actually preserved within a different lithology. Reinvestigation of museum collections and the collection of new material is leading to a revised floral list. In addition, Low Vacuum Scanning Electron Microscopy is providing improved illustration of diagnostic characters of delicate reproductive structures exceptionally preserved within the



fine-grained limestone. Detailed study has removed palms and figs, for example, from the floral list and confirmed that trees of the walnut family were a rare but consistent element of a bulrush-dominated swamp vegetation. These fossils provide important evidence for reconstructing a community existing just prior to the onset of the Oi-1 glaciation that marks the transition from a greenhouse to an icehouse world.

# Silicified Upper Cambrian (Sunwaptan) trilobites from the St. Charles Formation in the Bear River Range of southeastern Idaho

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Previously unreported silicified trilobite faunas occur in a narrow stratigraphic interval of the Upper Cambrian (Sunwaptan) St. Charles Formation in the Bear River Range of southeastern Idaho. The faunas occur in four closely spaced rudstones and trilobite packstones indicating deposition in a shallow subtidal setting above storm wave base. At least 23 species are represented, included two undescribed genera and several undescribed species. The faunas are notable for their high trilobite abundance and pervasive silicification. Most coeval faunas have been described on the basis of small numbers of "crack-out" specimens, and the new material reveals many details of anatomy, including knowledge of most exoskeletal sclerites. The four trilobite-yielding beds contain markedly different taxon-abundance profiles, yet most species are shared between them. This suggests multiple, taphonomically-controlled samples of a similar underlying distribution, though true ecological variation cannot be discounted. Because the rocks can be physically cracked, to yield trilobites in traditional mechanical fashion, a comparison of "crack-out" versus silicified taxon-abundance profiles reveals strong bias in mechanical sampling toward large, smooth taxa.

#### Nitrogen and Carbon Isotopes: a New Tool for Palaeontologists?

### Jo Hellawell, Chris Nicholas and Robbie Goodhue

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The trophic level of organisms within an ecosystem can be distinguished on the basis of their nitrogen and organic carbon isotope ratios, due to the internal isotopic fractionation of each organism at every stage of the food web. These isotopic fractionations have been used successfully by various authors to model trophic structure in present day and Neogene ecosystems. In this current study  $\delta^{15}N$  and  $\delta^{13}C_{\rm org}$  are being used to investigate the community structure and palaeoenvironmental changes within a much older fossil ecosystem. The Early Eocene fish of Fossil Lake in the Green River Formation of SW Wyoming are part of an exceptionally well-preserved diverse aquatic community. Fluorapatite skeletal material of fossil fish specimens analysed from throughout the stratigraphic succession indicate that isotopic signatures can be used to define the trophic structure of extinct communities and for chemostratigraphic investigations. However, the pathways taken by nitrogen and carbon isotopes during organic matter degradation are still poorly understood. Experiments are now underway to determine whether the isotopic ratios of fish are affected during death, burial and early diagenesis. We hope to clarify this



using modern fish in order to understand any taphonomic changes that may have occurred in the Fossil Lake.

### New chitinozoans from the historical Hirnantian type area, Bala, Wales.

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The "Hirnantian" was originally introduced by Bancroft (1933) to name the highest Ordovician beds in the Bala area and was formally attributed regional stage status in the Ashgill Series by Ingham and Wright (1970). Recently it has been elevated to an international stage in the global stratigraphical chart and designated the uppermost stage of the Upper Ordovician Series. A GSSP for the stage has since been defined in Wangjiawan, China. The actual type locality for two of the core elements of the Hirnantia fauna is a small abandoned quarry [SH951296] on the western slopes of Cwm Hirnant. There, the Hirnant Limestone Member of the Foel-y-Ddinas Mudstone Formation yielded a new, surprisingly well-preserved chitinozoan fauna, attributed to the Spinachitina taugourdeaui zone, which allows a tight correlation with the Hirnantian of the Baltica and Laurentia palaeocontinents. Chitinozoans from the nearby Rawtheyan-Hirnanatian Bwlch-yr-Hwch section were biostratigraphically less significant; the chitinozoan assemblage from the Caradoc Cymerig Limestone Member at Gelli-Grin belongs to the Spinchitina?cervicornis zone, and is identical to the one recovered from the Burrellian in Onny Valley, Welsh Borderland (Vandenbroucke, 2005). A Silurian assemblage higher up section, discovered in the Cwm-yr-Aethnen Formation, is attributed to the globally recognised Eisenackitina dolioliformis zone.

### Bags and pipes: Ediacaran-type preservation in the Lower Cambrian of Northwest Scotland

#### Liam G. Herringshaw<sup>1,2</sup>, Alice E. L. Humphreys<sup>1,3</sup>, M. Paul Smith<sup>1</sup> and Robert J. Raine<sup>1</sup>

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The Pipe Rock Member of the Eriboll Formation (Lower Cambrian) of Northwest Scotland is celebrated for its distinctive Skolithos ichnofauna. However, body fossils were unknown from the unit until Campbell and Paul (1983) described an assemblage of pentaradial organisms from a locality near Inchnadamph, Sutherland. Seilacher and Goldring (1996) named them Spatangopsis scotica, a new example of the putative cnidarian clade Psammocorallia, and the fossils display a preservation most like that of Ediacaran taxa, but despite this they have been little-studied and are poorly understood. Re-examination of the Scottish specimens and examples of the type species S. costata Torell, from the Mickwitzia Sandstone of Västergötland, Sweden, has provided much new information on their palaeobiology and zoological affinities. Unlike those of the type species, the radial septa of S. scotica are partitioned into distinct chambers that appear to extend from the centre of the star-shaped, bag-like body to the external surface. Specimens which have split along the septal plane indicate S. scotica had a greater rigidity than S. costata, but there is no other evidence for skeletonization in either taxon. Spatangopsis was most probably an early cnidarian, but the 'sand coral' hypothesis of Seilacher remains controversial.



# Deconfounding patterns in the occurrence of homoplasy and limitations of the homoplasy metric

### Jennifer Hoyal Cuthill, Philip Donoghue and Simon Braddy

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A considerable body of work has been devoted to the identification and quantification of homoplasy, but it has proved extremely difficult to deconfound trends in the occurrence of homoplasy and limitations of the homoplasy metric. We present the most comprehensive meta-analysis of homoplasy levels among morphological characters yet undertaken. A battery of homoplasy metrics are employed to quantify the effects on homoplasy from both matrix parameters and data partitions. The principal finding of this study is that the average number of character states has an important role in determining the proportion of possible homoplasy that is expressed. Consideration of the number of character states reveals a more complex picture of homoplasy distribution: involving multiple effects from a number of covarying matrix parameters. Biases among average numbers of states are shown to correlate with elevated homoplasy levels among some taxonomic groups. A formula for the relationship between maximum homoplasy possible, the number of taxa and the number of character states is presented. The relationships between the proportion of maximum homoplasy expressed, the maximum possible and the number of character states among real data are quantified. Two correction methods are proposed to remove the correlation between these variables and the retention index.

### Mammalian diets as indicators of palaeoenvironmental change: Eocene–Oligocene ungulates of Europe

### Sarah C. Joomun<sup>1, 2</sup>, Jeremy J. Hooker<sup>2</sup> and Margaret E. Collinson<sup>1</sup>

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The 'Grande Coupure' was a major faunal turnover which affected the endemic mammal fauna of Europe, most significantly the perissodactyls and artiodactyls (ungulates), during the earliest Oligocene. There was a climatic change from greenhouse to icehouse conditions during the Late Eocene and Early Oligocene, and the Grande Coupure was coincident with the first major glaciation in Antarctica (Oi-1). Possible causes of the Grande Coupure are climatic deterioration at the start of the Oligocene or competition following the dispersal into Europe of Asian taxa. The feeding preferences of ungulates can be used as an indicator of the palaeoenvironment in which they lived, as they only eat plant material. Diet can be determined by studying the tooth morphology, mesowear and microwear. La Débruge is a highly fossiliferous, pre-Grande Coupure mammal site from the Late Eocene (MP18) of France. It has yielded a large number of ungulates including Palaeotherium and Plagiolophus (perissodactyls, family Palaeotheriidae). Palaeotherium became extinct at the Grande Coupure and Plagiolophus survived the Grande Coupure. In preparation for an in-depth comparative study, material from La Débruge has been used in order to assess intra- and inter-generic variation in the dental wear. The implications of these results will be discussed.

# osters

# Perisphinctes Ravine – a key Jurassic-Cretaceous boundary succession in Kuhn Ø, NE Greenland

### Simon Kelly<sup>1</sup>, Bill Braham<sup>2</sup>, John Gregory<sup>3</sup>, Peter Doyle<sup>4</sup>, and Dominic Strogen<sup>1</sup>

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During CASP fieldwork in NE Greenland, a major biostratigraphical reference section spanning the Jurassic-Cretaceous boundary was documented from Perisphinctes Ravine, eastern Kuhn Ø. A continuously exposed section extends for some 220m from the Bernbjerg Formation (Early Volgian-Ryazanian) up into the Mid Cretaceous Sandy Shales (Valanginian-?Hauterivian). Well-preserved macrofaunas, mainly ammonites and bivalves, were collected in the field from concretionary horizons, and belemnites from the mudstones. Microfossil and palynological samples obtained throughout the section are currently undergoing analysis. Biostratigraphic and palaeoenvironmental data will be displayed in an integrated table using Stratabugs. This section contains important correlations between the different biozonation schemes applicable in eastern Greenland. In the lower part of the section, dark Volgian-Ryazanian mudstones contain pectinatitid, dorsoplanitid and chetaitid ammonites together with buchiid bivalves. Calcareous mudstones of Late Ryazanian-Valanginian age are rich in buchiids and belemnites with a few ammonites. Later Valanginian-? Hauterivian red-beds and dark mudstones are characterised by belemnite faunas. This section will provide the basis for more detailed Late Jurassic and Early Cretaceous macropalaeontological, micropalaeontological and palynological correlations with other Boreal and Sub-Boreal regions, such as Arctic Canada, NW Europe, Svalbard, Russian Platform and Siberia.

### Using bryozoan zooid size to infer North Atlantic sea temperatures for the Pliocene world

#### Tanya Knowles<sup>1</sup>, Beth Okamura<sup>1</sup>, Paul D. Taylor<sup>2</sup>, Mark Williams<sup>3</sup> Alan Haywood<sup>4</sup>

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The mid Pliocene (3.29–2.97 Ma) was a time of broadly global warmth and higher sea levels. It represents the last time in Earth history when the level of atmospheric CO<sub>2</sub> was similar to today (*ca.* 380 ppm) and as such, it may provide a comparative world for future global warming. The Mean Annual Range of Temperature (MART) experienced by a bryozoan colony can be estimated utilising the inverse relationship between zooid size in cheilostome bryozoans and water temperature at the time of budding (O'Dea and Okamura, 2000). This technique, first calibrated from living bryozoans, has been successfully applied to fossil bryozoans from the Crag deposits in East Anglia, and in this study it is additionally being applied to fossil bryozoan material from Pliocene rocks in Virginia, North Carolina, Florida, Costa Rica and Panama. These fossil data, across a range of latitudes, may provide information about sea surface temperatures that can be used to test climate scenarios from computer-based General Circulation Models for the Pliocene world.

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# A novel contemporary fluvial ichnocoenose, unionid bivalves and the *Scoyenia–Mermia* ichnofacies transition

#### Andrew M. W. Lawfield and Ron K. Pickerill

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The last two decades have seen a dramatic expansion of interest in continental ichnofacies models. Despite this resurgence since the original erection of the Seilacherian Scoyenia ichnofacies, the finer details of freshwater ichnology remain poorly constrained by actualistic observation. Observations were undertaken on a modern fluvial trace assemblage, within the Saint John River, Atlantic Canada. The invertebrate trace-making assemblage was dominated by the unionid bivalves Anodonta and Lampsilis, together with a less abundant gastropods component. The molluscan generated trace assemblage comprises forms comparable to the ichnogenera Curvolithus, Helminthopsis, Gordia, Spirophycus and Lockeia, found within a sand softground substrate. These elements are traditionally associated with the Mermia ichnofacies, which is characteristic of permanently subaqueous settings, and is generally considered to indicate a lacustrine depositional environment. However the presence of vertebrate tracks as a part of the emersion assemblage would indicate a Scoyenia ichnofacies setting. Neither of these observed assemblages conform with the occurrence of the assemblage within a high energy, active channel which if the guidelines of some recent literature are followed suggests that it should be placed within the Skolithos ichnofacies.

Morphology of the stem chelicerate *Leanchoilia illecebrosa* (Hou, 1987) from the Lower Cambrian Chengjiang biota from Yunnan, China, reconsidered

Yu Liu, Xianguang Hou, Jan Bergström, Dieter Waloszek and Andreas Maas Section for Biosystematic Documentation, University of Ulm, Ulm, Germany

We restudied Leanchoilia illecebrosa (Hou, 1987), the second most abundant Chengjiang euarthropod on the basis of >500 new specimens. This permits us to present new observations particularly on appendage morphology, and to discuss previous interpretations within the taxon Leanchoilia Walcott, 1912 and, briefly, the relations with the similar Alalcomenaeus Simonetta, 1970. It appears that none of the Chengjiang species described subsequent to L. illecebrosa (Hou, 1987) can be positively identified as a separate taxon. Still, there remains some unexplained variation in the large material. New observations include: 1) confluent globular stalked compound eyes; 2) three short spines along outer tergopleural margins; 3) a prominent basipod with spinous inner edge; 4) the articulation between basipod and the two rami; 5) an ample, annulated body-basipod articulation membrane; 6) up to nine endopodal podomeres, the first eight bearing spinules laterodistally each, the endopod tip carrying a long spine flanked by thinner spines medially and laterally; 7) one spine at the inner distal edge of each endopod podomere; 8) an exopod comprising two portions, a sub-triangular one proximally and a leaf-shaped one distally carrying long setae marginally; and 9) a partial connection between the proximal endopodal podomeres and the distal exopod portion.

## Ultraviolet B radiation and extinction: evidence from experimental investigations Barry Lomax, David Beerling, Katie Field, Janice Lake and Charles Wellman

Department of Animal and Plant Sciences, University of Sheffield, UK

Since the discovery of the annual austral Winter-Spring 'ozone hole' the biological effects of increasing UV-B flux at the Earth's surface have attracted a substantial research effort. Some 20 years later palaeobotanical evidence in the form of mutated tetrads of lycopsid spores and mutated gymnosperm pollen suggests that the stratospheric ozone (O<sub>3</sub>) layer may have collapsed globally at the Permo-Triassic boundary, culminating in the Earth's biota being exposed to prolonged periods of intense UV-B radiation. Indirect evidence from mechanistic models predicts that the stratospheric O<sub>3</sub> layer may have been periodically depleted, through a variety of physical phenomena both terrestrial and extraterrestrial that have previously been linked to mass extinction events. However, at present little is known about how this important environmental variable has shaped the evolution of the terrestrial biosphere or how plants respond to chronic UV-B exposure as predicted to have occurred during some intervals of mass extinction. In this poster we begin to address this important issue via the exposure of the laboratory model species Arabidopsis thaliana to a high flux of UV-B radiation to assess how UV-B radiation alters morphological features of the plant epidermis, which are readily preserved in the leaf fossil record.

### Evidence of frugivory in terrestrial chelonians of the Scenic Member, Brule Formation, South Dakota

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The Scenic Member has yielded several well-preserved tortoise shells referable to the genera Hesperotestudo, Gopherus and Stylemys. During preparation two specimens (Stylemys nebrascensis and cf. Stylemys sp.) were found to contain fossilized hackberry seeds (Celtis sp.). Taphonomic evidence suggests that the internal contents of the shells were not subject to extensive disturbance during burial or fossilization. Sedimentological evidence and seed dimensions indicate that abiotic transport of seeds into the shells was unlikely. Ecological studies on the living relatives of both Celtis and Stylemys provide evidence of a frugivoredisperser relationship between these taxa in Recent ecosystems. These lines of evidence led to the conclusion that the seeds are preserved stomach contents. With the exception of some unidentified Campanian coprolites which may be assigned to turtles, this is the earliest evidence of chelonian frugivory and implies a long co-evolutionary relationship between the genus *Celtis* and vertebrate dispersal agents.



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

### J.E.A. Marshall<sup>1</sup>, T.R. Astin<sup>2</sup>, J.F. Brown<sup>3</sup>, E. Mark-Kurik<sup>4</sup> and J. Lazauskiene<sup>5</sup>

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The Kačák Event is a late Eifelian (Mid Devonian) episode of marine dysoxia and associated extinctions that has been widely recognised in the shelf seas that surrounded the Old Red Sandstone continent. It was contemporary with the lacustrine Orcadian Basin in Scotland. This basin contains the distinctive Achanarras horizon that contains a well-known fish fauna. The Achanarras lake was wide and deep, and would have been filled by rainfall from a monsoon system at an insolation maximum. Faunal elements within the lake are in common with the Kernavè Member in Estonia and this level can also be conodont-dated as late Eifelian *eiflius* or *ensensis* zone. Therefore the group of lacustrine flooding climatic events that occur at and above the Achanarras level can be correlated with the marine Kačák Event (*sensu lato*) and both can be regarded as having a common climatic cause and driven by an insolation maximum. A reconstruction of the Orcadian Basin drainage system and a water balance model based on the calcium flux within the lake shows that a very significant volume of water would have been seasonally discharged to the Rheic Ocean and would have caused an additional environmental effect.

### Body size of giant Patagonian dinosaurs

#### Gerardo V. Mazzetta

Royal Cornwall Museum, UK

Regression analyses on limb bone and vertebra measurements were used to estimate the body mass, as a measure of body size, of giant sauropods and theropods from the mid-Cretaceous (Albian to Cenomanian) of Patagonia. The titanosaurian sauropod *Argentinosaurus huinculensis* weighed up to 73 tonnes, and, consequently, is the largest terrestrial animal whose body mass has been rigorously determined. Another titanosaur, *Antarctosaurus giganteus*, was the second largest, weighing about 68 tonnes, while *Antarctosaurus wichmannianus* reached 35 tonnes. The holotype specimen of the carcharodontosaurid theropod *Giganotosaurus carolinii* (MUCPv-CH-1) was approximately as massive as the average-sized *Tyrannosaurus rex*, and only slightly smaller than "Sue", the largest specimen hitherto known. Nonetheless, a new dentary of *Giganotosaurus* (MUCPv-95) is 8% longer than that of the holotype. Assuming geometric similarity, that particular individual would have had a body mass in excess of 8 tonnes and therefore would have been the largest theropod ever unearthed. The results suggest that some southern South American dinosaurian taxa seem to represent size maxima in dinosaur evolution.

# Preservation and erosion of theropod tracks in eolian deposits; examples from the Middle Jurassic Entrade Sandstone, Utah, USA

### Jesper Milàn¹ and David B. Loope²

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The Middle Jurassic Entrada Sandstone, exposed near the town of Escalante, southern Utah, comprises large-scale cross-bedded eolian deposits that are interbedded with horizontally laminated sand sheets and thin sets of eolian cross-strata, representing periods with a moister climate. The flat-bedded units contain numerous tracks and trackways from small to large sized theropod dinosaurs, as well as rare sauropod trackways. Due to the finely laminated nature of the flat-bedded deposits, the tracks are today exposed in several different, distinct erosional states, allowing detailed studies of track and undertrack formation in eolian deposits. This gives a unique opportunity to record the changes in track and undertrack morphology that occur with depth along each subjacent horizon below the true track. From this study it becomes evident that the deformation around and below a theropod track of 40 cm length, extends as much as 20 cm outward around the track. Further, it is of vital importance to know the range of morphologies that deeply eroded tracks can display, when studying tracks and trackways preserved under less than optimal conditions.

# Traces of behaviour: a sideways walking prosauropod and a crouching theropod who stood up and walked away

#### Jesper Milàn<sup>1</sup>, David B. Loope<sup>2</sup> and Richard G. Bromley<sup>1</sup>

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Dinosaur tracks and trackways are common in the eolian cross-strata of the Lower Jurassic Navajo Sandstone, exposed at the Coyotes Buttes locality on the border between Arizona and Utah. Tracks and trackways of small theropod dinosaurs are particularly abundant along a single horizon, but tracks of crocodilians and prosauropods occur less frequently. Among the tracks and trackways are two distinct trackways showing evidence of individual behaviour of the trackmaker. A prosauropod trackway can be followed for several meters up the sloping front of an ancient dune face, and interestingly the trackway shows the animal to progress sideways up the dune slope in the first half of the trackway before it changes orientation and progresses head-on up the dune. A trace of a crouching small theropod is unique, having impressions of all the limbs, the ischial callosity, the tail and tracks leading both to and away from the crouching site.



# Palaeoecology of an Early Permian playa lake trace fossil assemblage from Castle Peak, Texas, USA

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The Early Permian Choza Formation of the Clear Fork Group at Castle Peak in Texas, USA, contains a diverse and remarkably abundant trace fossil assemblage comprising exquisitely preserved arthropod trackways (*Diplichnites*, *Lithographus* and cf. *Kouphichnium*), striated trails (*Cruziana*) and isolated resting traces (*Rusophycus*), surface or shallow subsurface grazing trails or burrows (*Gordia*, *Helminthoidichnites* and *Treptichnus*), backfilled deposit-feeding burrows (*Planolites*), meniscate backfilled burrows (*Taenidium*), horizontal branching networks and tetrapod trackways (*Dromopus*, *Erpetopus*, *Varanopus* and cf. *Amphisauropus*). Trace fossils formed in, and around the margins of, an ephemeral lake within an alluvial plain, and provide evidence of temporary communities, comprising notostracans, euthycarcinoids, myriapods, insects, reptiles and rare amphibians.

The trace fossil assemblage is typical of the *Scoyenia* ichnofacies, and is similar to other assemblages from a range of different transitional subaqueous to subaerial settings. Such diverse trace fossil assemblages probably reflect relatively long-lived ephemeral water bodies, whereas more impoverished examples probably represent shorter-lived ephemeral water bodies. Assemblages with abundant delicate arthropod trackways probably reflect low energy conditions conducive to the presence of an abundant vagile epifauna and the preservation of their trackways, whereas assemblages with open vertical burrows tend to lack arthropod trackways and probably reflect higher energy conditions.

# Early Devonian plant taphofacies from Tredomen Quarry, Brecon Beacons Jennifer Morris

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The Late Silurian-Early Devonian is a key time interval for the evolution of vascular plants, but ecological and evolutionary studies are hampered by the lack of megafossils from Old Red Sandstone terrestrial red bed deposits. A better understanding of these environments and plant taphonomy will help distinguish between ecological/evolutionary patterns and taphonomic effects. Tredomen Quarry (Brecon Beacons) is an increasingly important site for understanding Old Red Sandstone environments and ecosystems. Already known for its trace fossils, trigonotarbid and fish specimens, the quarry contains abundant plant fossils. Borehole drilling has provided a +100m record of Old Red Sandstone, exhibiting the cyclic perennial-ephemeral sedimentation of the St. Maughans Formation, the Bishops Frome Limestone calcrete horizon and the pedified red mudstones of the Raglan Mudstone Formation. Palynomorph assemblages from the top of the quarry indicate an early Lochkovian age (MN spore biozone). Assemblages from the borehole indicate an upper Přídolí age (pre-MN), despite being above the Bishops Frome Limestone. Three facies types have been recognised, based on megafossil assemblages and sedimentology. Facies one includes rhyniophytoids Salopella, Uskiella and Cooksonia cf. caledonica, occurring in green, fine-grained sandstones. In facies two, Prototaxites, hairline hyphae, and small branching axes (occasionally fertile) occur in green siltstone lenses. The third facies of

basal fine-grained, green sandstones includes 'tea leaves' plant debris, *Prototaxites*, poorly-preserved rhyniophytoids, plus well-preserved fish. Although taphonomy is responsible for the restriction of plant material to reduced, perennial fluvial deposits, the presence of different plant taphofacies within these deposits could reflect ecological variations.

Faunal gradients and biogeographic patterns in the Oligo-Miocene of the western Indo-Pacific: insights from the Arabian Peninsula

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The "Terminal Tethyan Event" (TEE), the collision of the African–Arabian plates with Eurasia, caused the disconnection of two major Paleogene biogeographic realms, the Atlantic and Pacific. Marine benthic invertebrate taxa, showing a wide geographic distribution until the Eocene, diminished during the Oligocene and finally became restricted to the Atlantic, Mediterranean and Indo-Pacific realms during the Early Miocene. Our project aims at documenting the faunal differentiation in corals, molluscs, echinoderms, bryozoans and larger foraminifers of the western Indo-Pacific during the final phase of the TEE. First results from Oman show that a Mediterranean affinity was still present, as evidenced, for instance, by the occurrence of tridacnids of western origin in the Fars Group (Warak and Ghubbarah Formations). An independent evolution of the Indo-Pacific is therefore likely to have started only after closure of the seaways during the Early Miocene.

### A multi-generational herd of the basal ceratopsian dinosaur *Psittacosaurus* Zhao Qi¹, Paul M. Barrett² and David A. Eberth³

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The Lujiatun Beds of the Yixian Formation (Lower Cretaceous: Barremian) have yielded a spectacular Lower Cretaceous terrestrial biome that includes three-dimensionally preserved, fully articulated dinosaur skeletons. Here, we describe a remarkable accumulation of the basal ceratopsian dinosaur *Psittacosaurus*, comprising an associated group of six complete individuals. The close apposition of the skeletons, their completeness, articulation and lack of mixing indicate that they were buried simultaneously and that this does not represent an attritional deposit. Petrographical analysis indicates that these individuals were probably entombed by a mudflow. Use of Developmental Mass Extrapolation permits reconstruction of the age profile of the group: the smallest individual was approximately 12 months old at the time of death, whereas the largest was around three years old. This suggests that the group was formed of individuals from at least three different clutches that lived together in a small stable herd that included several age classes. This represents the first evidence for post-nestling gregarious behaviour in early ceratopsians and indicates that the advanced intraspecific social behaviours inferred for more derived members of the clade emerged near to the origin of the group.



# A re-evaluation of carpoid systematic position using three-dimensional reconstruction techniques

#### Imran A. Rahman and Mark D. Sutton

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Carpoids are an extinct group of Palaeozoic marine deuterostomes. Extant deuterostomes are classified into three phyla (chordates, echinoderms and hemichordates), but allying the carpoids with any one of these groups has proved highly controversial, as they possess a mixture of characters not seen in any extant organisms. Three-dimensional virtual models of the species *Ctenocystis utahensis*, *Placocystites forbesianus* and *Lagynocystis pyramidalis* have been produced in an attempt to evaluate alternative hypotheses of carpoid affinity. These were constructed using X-ray microtomography (XMT) and the SPIERS software suite. Study of these "virtual fossils" has allowed the visualisation of features inside the fossils that were previously unknown or poorly understood: in *Ctenocystis* a cavity was identified inside a large anterior plate; in *Placocystites* a series of rods and hooks were observed within the main body cavity; and in *Lagynocystis* a large external opening was recognised adjacent to an internal comb-like structure. These features have important implications for functional interpretations of the animals, and consequently may help test models of carpoid systematic position.

# Validating the Finite Element method whilst exploring avian biomechanics and evolution

#### **Emily Rayfield**

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Finite Element Analysis can reconstruct stress and strain in a structure during function. It is used to assess the mechanical behaviour of extinct organisms, but one questions remains: how well do our Finite Element model results reflect reality? To address this we can phylogenetically and functionally bracket extinct animal FE-models with data from living animals detailing: (a) how well FE-models replicate experimentally-recorded in-vivo/vitro bone strain; and (b) which parameters matter the most for accuracy. Here I present the first FE-model of a bird skull (Ostrich: Struthio camelus), with a view towards: (1) validating 'in-silico' model strain against in-vitro strain data; and (2) furthering our understanding of the biomechanics and evolution of the avian cranium. When loadings are applied to the FE-skull model based on preliminary pecking forces recorded in-vivo, and biting forces calculated from musculoskeletal architecture, FE-model results show that the behaviour of the skull is fundamentally different during pecking versus biting; and FE-model strain does replicate what is understood so far about avian cranial mechanics and morphology. Furthermore, the results suggest a fundamental shift in M. pterygoideus adductor muscle function from bite force production to jaw stabilisation during avian evolution that may distinguish specific ecomorphotypes in extinct taxa.



# The exceptional preservation of silicified arthropods in the Miocene Barstow Formation, southern California

### David A. Riley and Alex Page

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The exceptionally-preserved silicified arthropods of the Barstow Formation have not been previously subjected to detailed SEM study. This has revealed micron-scale morphological detail including compound eyes, hairs, claws and setae, wing veins, and surface ornamentation of insect cuticle, as well as preservation of bacteria and microbial borings. We have re-described *Schistomerus californense*, *Dasyhelea australis antiqua*, and ?ceratopogonid midges, which are amongst the most commonly recovered faunal elements. We recognise two morphologies of *Dasyhelea australis antiqua*, including a pre-pupa stage that had not previously been distinguished. This work represents a significant advance on previous studies, illustrating the fauna in far greater detail. Silicification is heavily biased towards the preservation of the most sclerotised anatomical features, occurring as coating and void fill that casts the waxy layer of the epicuticle. The waxy layer may serve as a template for silicification, possibly forming hydrogen bonds with a silicic acid precursor. The silicification of soft-bodied arthropods in the Barstow Formation exhibits an equivalent quality of preservation to the phosphatisated Upper Cambrian Orsten fauna.

# Scaling bite forces in predatory animals: how does *T. rex* compare with modern predators?

#### Manabu Sakamoto

Department of Earth Sciences, University of Bristol, UK

Scaling of bite force with body size in extant predators is investigated to extrapolate expected values in large predators, such as theropod dinosaurs. A regression analysis of bite force to body mass was performed in extant predators and was observed to scale similarly to area with volume in isometric bodies. Bite force in theropods can be expected to scale along this geometric similarity. Forces predicted in this way are significantly higher than previous estimates but are still disproportionately low for the colossal sizes attained by theropods. It is shown that muscle-driven bite force is progressively weaker relative to increase in body mass. Bite force need not increase in proportion to body size, as larger animals would need less effort to bite through resistant materials: material properties of soft tissue vary little among vertebrates and bone can be crushed with forces already exerted by extant predators. Therefore, bite force may not need to be maximised.

Foraminifera from the Lower Khuzestan Plain, south-western Iran: Holocene coastal evolution with a Cretaceous signature

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Foraminifera were analysed from various depths in 23 sediment-cores raised along a northwest–southeast transect in the Lower Khuzestan Plain of south-western Iran for reconstructing the Holocene coastline of the northern Persian Gulf. Two main fossil

foraminiferal associations were identified, those of *Ammonia beccarii* (Linné) and *Heterohelix navarroensis* (Ehrenberg). The *A. beccarii* association bore similarity to a modern inter-tidal foraminifer association of *A. beccarii* – *Elphidium* sp. 1 from the study area. The *H. navarroensis* association identified reworked Cretaceous sediment in the Holocene fluvio-coastal deposits. The former association defined the landward extent of coastal environments during the Holocene, constrained by AMS radiocarbon age dates, whereas the latter association defined the degree of reworking of older sediment in the study area. Although the *A. beccarii* association showed a higher species diversity ( $\alpha$ ) compared to the *H. navarroensis* association, the  $\alpha$  value was highest for the palimpsest association of *A. beccarii* – *H. navarroensis*.

### Irish Fossil Chitons (Mollusca: Polyplacophora)

#### Julia Sigwart<sup>1,2</sup>

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- <sup>2</sup> University College Dublin, School of Biology and Environmental Science, Dublin, Ireland

Three species of fossil polyplacophoran molluscs are known from Ireland. Two species were originally described in the 19th Century: *Helminthochiton giffithi*, and *Pterochiton thomondiensis*, and an articulated specimen representing a third indeterminate species has been described recently for the first time. Previous work on the evolutionary context of these species has relied on published illustrations and descriptions without examination of the type material. In particular, *H. griffithi* is a taxonomically important species, as the type of a family that includes four fossil genera from the Ordovician and Devonian; however, inaccessibility of the unique holotype has resulted in mis-interpretation of the preservation and anatomy by authors working from copies of copies of the original illustrations. *P. thomondiensis* is an interesting record for a genus known from the Carboniferous of Ireland, Belgium and dubiously from North America. As chitons are considered rare in the fossil record, these specimens represent an interesting and important aspect of Irish palaeobiology.

# Waterloo Bay, Larne, Northern Ireland: A potential Global Stratotype Section and Point for the base of the Jurassic System

#### Michael J. Simms<sup>1</sup> and Andrew J. Jeram<sup>2</sup>

- <sup>1</sup> Department of Geology, Ulster Museum, Botanic Gardens, Belfast, Northern Ireland <sup>2</sup> Mullaghdubh House, 27 Gobbins Path, Islandmagee, Co. Antrim, Northern Ireland
- Many stratotypes for geological Stage and System boundaries are already designated, but that for the base of the Jurassic Period the best known of all geological periods has yet to be selected from candidates in southern England, Austria and the Americas. A foreshore section at Waterloo Bay, Larne, on the east coast of Northern Ireland, exposes a succession from the upper Mercia Mudstone Group (Triassic, Norian) through to the lower Lias Group (Jurassic, Sinemurian). Never previously studied in detail, we have established that the Triassic–Jurassic boundary section here is superior in many respects to that at St. Audrie's Bay, SW Britain, long cited as one of the candidate GSSPs. The base Lilstock Formation to top Planorbis Subzone interval at Larne is significantly thicker, and deposition demonstrably more continuous, than anywhere else in NW Europe. Clear sedimentary cycles enable correlation across the UK with significant potential also for global correlation,

an important aspect of any proposed GSSP. A rich and diverse fauna is present, with ammonites particularly well represented and well preserved compared with other UK sites. Within the Planorbis Subzone (basal Lias Group) clearly definable biohorizons can be recognised for *Psiloceras erugatum*, *Neophyllites imitans*, *N. antecedens*, *Psiloceras planorbis/sampsoni* and *P. plicatulum*. The site would make an ideal stratotype for the first three of these, for which no surface stratotypes currently exist, in addition to its potential as the base Jurassic GSSP.

# Graptolites and mudrocks track ocean change: the *convolutus* Zone (Silurian; Llandovery; Aeronian) of Wales and Scotland

### Andrea Snelling, Alex Page and Jan Zalasiewicz

Department of Geology, University of Leicester, UK

Early Palaeozoic oceans are characterized by intervals of extensive anoxia, marked by deposition of graptolitic mudrocks, potentially representing a significant reservoir for the drawdown of atmospheric CO<sub>2</sub>. Globally synchronous anoxic events may be related to deglacial transgressions (Page et al. in press), and tracking the onset and extent of anoxia provides an opportunity for investigating Early Palaeozoic oceanography, with regard to the carbon cycle and palaeoclimate. The convolutus Zone strata in central Wales show distinctive, alternating units of laminated and bioturbated facies, representing anoxic and oxic depositional conditions respectively. Detailed correlation of the graptolite assemblages and sedimentology is being undertaken to establish the nature of these events. Comparison with successions from the Lake District and Scotland provides the opportunity to track such events across Iapetus Ocean. The aim of this study is to chart the ocean redox conditions in 4D across the Welsh Basin, examining whether there is local diachroneity within anoxic facies development, and to compare the graptolite assemblages and lithofacies with the more open-ocean settings of Scotland. This should establish whether variations in the sedimentary anoxia are influenced by local, regional or whole ocean conditions, and highlight the potential role of graptolitic mudrocks in drawing down atmospheric CO<sub>2</sub>.

# Palaeoecology of a unique Late Cretaceous rocky shore community from Skåne, Sweden

#### Anne Mehlin Sørensen and Finn Surlyk

Geological Institute, University of Copenhagen, Denmark

During Late Cretaceous time the global sea-level was approximately 150 m higher than today and the Earth experienced greenhouse conditions. Large areas of southern Sweden were transgressed from the south and an archipelago was formed with low islands and peninsulas. On the island Ivö, a Campanian high-diversity rocky shore ecosystem was developed. The well-preserved calcitic fauna, the bioimmurations on many of the encrusting specimens, and impressions of the aragonitic fauna, give a great opportunity to reconstruct the ecology of this rocky shore environment. Furthermore, fauna assemblages representing different nearshore environments are found close to Ivö. One assemblage represents a high-energy, shallow marine sandy environment with a diverse fauna, and another is interpreted as a shallow mangrove-like siliciclastic environment with a low diversity fauna dominated by oysters. These contemporaneous scenarios allow the study of single species distribution and to evaluate their environmental tolerance within a set of highly different nearshore environments.



# Morphology, ontogeny and ecology of the Palaeozoic whole plant fern Oligocarpia (Sphenopteris) gothanii Halle

#### Liadan G. Stevens

University of Birmingham, UK

Detailed morphological investigations have been undertaken on the rare whole plant Oligocarpia (Sphenopteris) gothanii in the Halle collection of Permian fossil plants from China. Multiple specimens have been examined, including a variety of whole plants of different sizes that are shown to represent different ontogenetic stages preserved within an individual species. Developmental patterns have been identified and include changes to growth architecture and habit with age, and changes from vegetative to sexual reproduction strategies within its life cycle. This reinvestigation has allowed taxonomic and systematic emendation of the plant to be undertaken, and details have been expanded to represent the whole plant morphology thus presenting information comparable to living species. Ecological perspectives are provided by the floral associations in which Oligocarpia occurs, and co-occurrences with the bryophyte Thallites infers a wetland habit.

# A bone bed without bones: the Middle Cambrian 'fragment limestone' of Scania, Sweden

### Michael Streng<sup>1</sup>, Gerd Geyer<sup>2</sup> and Graham E. Budd<sup>1</sup>

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- <sup>2</sup> Institute of Palaeontology, Würzburg University, Germany

The Middle Cambrian 'fragment limestone' of southeastern Scania (S. Sweden) is a greenish-gray wacke- to packstone layer that varies in thickness from 2 to 20 cm, overlying the Gislöv Formation (*sensu stricto*) with an erosive contact. It is extremely rich and diverse in small phosphatic-shelled fossils: 16 different taxa have been identified thus far, among which the phosphatic shelled brachiopods are the most common (seven taxa). Other faunal elements are paraconodonts (two taxa), palaeoscolecids (two taxa), phosphatocopids (at least two taxa), *Microdyction* sp., *Lapworthella* sp., and *Hyolithellus* sp., and undeterminable trilobite hash. Petrographic features of the fragment limestone such as phosphorite nodules, pyrite and authigenic glauconite, scattered quartz grains, the high content of phosphatic-shelled organisms, as well as signs of stratigraphic mixture (reworking), presence of intraclasts, and an erosive sole, indicate a genesis similar to classical bone beds such as the Muschelkalk Grenzbonebed of South Germany. The fragment limestone is considered here to be a condensation deposit (Konzentratlagerstätte) in which phosphatic-shelled organisms have been enriched by long-term sedimentary reworking and winnowing of finer material.



# Biomechanical analysis of the biting performance in the sabre-tooth cat *Smilodon fatalis*

### Elizabeth Sweet, Manabu Sakamoto and Mike Benton

Department of Earth Sciences, University of Bristol, UK

The extraordinary canines of the sabre-tooth cat *Smilodon fatalis* have led many workers to speculate on their function. Many hypotheses have been proposed, but two are plausible; the stab bite versus the shear bite. The refined stab hypothesis proposed a combined action of the head and neck depressor musculature, aided by the inertia of the jumping body to provide the necessary force for stabbing. In the 'canine-shear bite' hypothesis the mandible played an active role in the attack process, providing anchorage for the head depression of the upper canines. Despite careful anatomical studies they have not been quantitatively tested nor the situation resolved. The biting performance of *S. fatalis* is assessed using an adaptation of the dry skull method. This in conjunction with detailed studies of muscle scarring in the mastoid region provides a good approach to assess the 'canine-shear bite' hypothesis. Osteological correlates on dried skulls are used to recreate muscles and lever mechanics used to calculate bite force. Although the dry skull method underestimates bite force, comparative analysis ensures consistency; relative rather than absolute bite forces are of interest. Initial findings support the 'canine-shear bite' hypothesis. The resultant implications for sabre function and bite adaptation are discussed.

### Functional analysis of an exceptionally preserved eye of an Eocene fly

### Gengo Tanaka<sup>1</sup>, David J. Siveter<sup>2</sup> and Andrew R. Parker<sup>3</sup>

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- <sup>2</sup> Department of Geology, University of Leicester, UK
- <sup>3</sup> Department of Zoology, The Natural History Museum, London, UK

Here we report on an exceptionally preserved dolichopodid fly eye from the Eocene of Russia, which provides a rare view of a fossilised visual organ including soft parts, and facilitates reconstruction of its anatomy and optical function. Evidence from its morphology (long distance between the basal part of the crystalline cone and the basement membrane) and estimation of the diameter of an optical receptor (based on the formula of Land and Nilsson, 2002) suggest that the fossil fly eye has typical neural superposition optical features like some diurnal extant flies and mosquitoes. The highest preserved fidelity of detail in the eye is the presence of the eye grating structure (Parker *et al.*, 1998), consisting of ridges and sulci, like a human fingerprint, on each corneal lens surface. Wave optical analysis based on computer-aided 'characteristic matrix method' strongly supports previous notions (Parker *et al.*, 1998) that the structure acts as an antireflective layer. Detailed observations of the corneal lens surface of 108 Recent fly species (26 families) and the result of the character-state distribution on the phylogenetic tree (Grimaldi and Engel, 2005) indicate that the fly eye grating structure shows convergent evolution, which also reflects functional demands rather than phylogenetic constraints of this structure.



# The importance of including fossil taxa in complete supertrees: an investigation into diversification rate changes within the Cercopithecoidea

#### James E. Tarver

Department of Earth Sciences, University of Bristol, UK

Analysis of diversification rate shifts were conducted on a complete phylogeny of the Cercopithecoidea (hominids, gibbons and Old World monkeys) consisting of 287 taxa (including 154 extant and 133 fossil taxa) and on a pruned phylogeny consisting solely of extant taxa. The results for the complete phylogeny show seven statistically significant shifts in the diversification rate, whilst only three are recorded in the neontological tree. Importantly two of these undetected shifts occurred at the base of the tree within the stem group and have subsequently affected all extant taxa. An analysis based purely on extant taxa would conclude that it is only certain lineages within the Cercopthecoidea such as the Macaques that have undergone significant shifts in their diversification rates. However, these results show that the crown group was affected by a diversification rate shift approximately 22 million years ago. An earlier shift in the rate of diversification was also detected approximately 33 million years ago, but this is attributable to a gap in the fossil record. Therefore, fossil taxa should not be omitted from supertrees as they can have a strong impact on our understanding of the patterns and process of macroevolution.

# 'Kokemushi Paradise': an extraordinary occurrence of cobble-encrusters in the Pleistocene of Japan

#### Paul D. Taylor<sup>1</sup>, Piotr Kuklinski<sup>1</sup> and Shunsuke F. Mawatari<sup>2</sup>

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- <sup>2</sup> Division of Biological Sciences, Graduate School of Science, Hokkaido University, Sapporo, Japan

A locality discovered recently in the Pleistocene Setana Formation of northern Japan contains a rich fauna of cobble-encrusting sclerobionts dominated by bryozoans ('Kokemushi' in Japanese). About 10 metres of sandy and shelly gravel are exposed in a small working quarry at Kuromatsunai, southwestern Hokkaido. Both the lithic clasts and shells of calcitic bivalves here are invariably encrusted, some also forming attachment surfaces for bushy stylasterid corals whose broken branches are found in the sediment matrix along with the ramose bryozoan Myriapora. Often the surface of the clasts is totally covered by encrusters. Bryozoans are particularly diverse and number at least 50 species, most being heavily-calcified ascophoran cheilostomes. They are accompanied by barnacles, spirorbid worms and cemented bivalves. Analysis of the depositional palaeoenvironment is pending but faunal evidence indicates a fast flow regime, possibly in a tidal channel. Such is the abundance, diversity and quality of preservation of the Kuromatsunai fauna that it offers unprecedented opportunities for investigations of hard substrate palaeoecology. These include: the relationship of encruster diversity to clast size, shape and composition; interspecific overgrowth patterns between different species of encrusters; and ecological succession.

# 5 **)**

# Tracking changes in the eurypterid faunas of New York State Erik O. Tetlie

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New York State has the most comprehensive eurypterid-bearing sequences in the world, spanning from the Late Wenlock through to the Lockhovian. The sequence has five distinct eurypterid biozones, evidently determined by changing environment. From oldest to youngest, these are: Rhinocarcinosoma biozone, Hughmilleria biozone, Waeringopterus biozone, Eurypterus biozone and Erieopterus biozone, after the dominant eurypterid genus at each stratigraphic level. In addition to these five major biozones, several smallscale lateral and horizontal trends are evident. The most obvious changes in overall fauna in the Eurypterus biozone is related to water depth. In intertidal environments of the Williamsville Formation, the fauna is dominated by *Eurypterus* (ca 69% of total fauna), with very minor occurrences of a large number of other taxa, e.g. Acutiramus (2.1%), Paracarcinosoma (1.5%), Dolichopterus (1.2%) and phyllocarid crustaceans (3.5%). However, further east, in the middle of the gulf that was covering eastern North America, the same horizon contains less than 5% Eurypterus, and is dominated by Paracarcinosoma (58%) and phyllocarids (25%). Other horizontal and vertical trends in the faunal composition, size distribution and completeness of the fossils within the Eurypterus biozone will also be explored.

# Exceptionally preserved marrellomorph arthropod specimens from the Lower Ordovician of Morocco

#### **Peter Van Roy**

Ghent University, Belgium

The Marrellomorpha are a small clade of generally rare Palaeozoic arthropods. The group represents a distinct high-level body plan, characterized by the possession of a conspicuously spinose cephalic shield and a simple, undifferentiated trunk composed of a relatively high number of somites. Because of their generalized morphology, the marrellomorphs consistently plot close to the base of the Euarthropoda in cladistic analyses. Nevertheless, the exact systematic position of Marrellomorpha remains elusive. Genera belonging to the Marrellomorpha are Marrella from the Middle Cambrian, Furca from the Caradoc (Upper Ordovician) and Mimetaster from the Emsian (Lower Devonian). The Emsian (Lower Devonian) Vachonisia is often considered to be a marrellomorph too, but its position and affinities are best regarded as uncertain. Of all marrellomorphs, the genus Furca is by far the most incompletely known: its two described species, F. bohemica and F. pilosa, together are represented by just 25 poorly preserved isolated cephalic shields from the Bohemian Caradoc (Upper Ordovician), leaving some doubts about their marrellomorph affinity. Recently, several exceptionally well-preserved specimens belonging to a new species of the genus Furca were collected from the Arenig (Lower Ordovician) of the Upper Fezouata Formation near Zagora, south-eastern Morocco. The new material reveals hitherto unknown details of the trunk and appendages, and unequivocally establishes the marrellomorph affinity of the genus Furca. Additionally, the Moroccan fossils considerably extend the range of Furca down into the Lower Ordovician.



# Chitinozoans and acritarchs from earliest Tremadocian strata in southern Tunisia Marco Vecoli<sup>1</sup>, Claudia V. Rubinstein<sup>2</sup>, G. Susana de la Puente<sup>2</sup> and Thomas Servais<sup>3</sup>

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- <sup>3</sup> Paleontologie Sciences de la Terre, USTL, France

Although there is a general agreement on the earliest Ordovician as the time of origin for chitinozoans, their biostratigraphic utility in early and middle Tremadocian strata is problematical. Gondwanan Tremadocian chitinozoan biozones are not sufficiently constrained by independent chronostratigraphical evidence, and recent investigations highlight inconsistencies between graptolite, acritarch and chitinozoan biostratigraphic correlation. We report a chitinozoan assemblage from the early Tremadocian strata of borehole Tt-1 in southern Tunisia, occurring together with abundant and well-preserved acritarch suites. The acritarchs indicate a basal Tremadocian age, demonstrated by the occurrence of index taxa such as Acanthodiacrodium angustum, Ooidium rossicum, Vulcanisphaera africana, Saharidia fragilis. This age attribution is confirmed by the co-occurrence of brachiopods and phyllocarid crustaceans. Enigmatic microfossils such as Virgatasporites and Attritasporites are also present, for which a non-marine origin is inferred. Chitinozoans are poorly preserved and occur in low abundance and low taxonomic diversity. Nonetheless, a preliminary systematic assessment of the microfauna permits the identification at the generic level of specimens of Lagenochitina sp. and Eremochitina sp. A similar and age-equivalent chitinozoan suite was described from the Algerian Sahara by Combaz (1967). The present data show that biostratigraphically significant chitinozoans occur since the lowermost Tremadocian in the peri-Gondwanan palaeogeographic domain.

# Ultrastructure of calcareous annelid tubes: taxonomic and phylogenetic implications

#### **Olev Vinn**

Institute of Geology, University of Tartu, Tartu, Estonia

Among annelids calcareous tubes are known in serpulid, cirratulid and sabellid polychaetes. Only the tubes of serpulids are exclusively calcareous. They possess a variety of fabrics of tube ultrastructure which can be taxon specific and used in the taxonomy of worms. Diversity of tube ultrastructures in the Cenozoic fossil serpulids is very similar to the Recent serpulids. In general the tube ultrastructure is very well preserved in the Cenozoic serpulids and can be directly compared with the tube structures of extant serpulids. Diagenetically altered tubes can be easily distinguished from the well-preserved serpulid tubes. Species of Subfamily Serpulinae are characterized by multilayered tubes and presence of fibrillolamellar stuctures. Genus *Ditrupa* (Eocene–Recent) has the unique tube ultrastructure. Sabellid nature of *Glomerula* (Jurassic–Recent) follows from its microlamellar tube wall and spherultic prismatic ultrastrure.



# Histology, apparatus architecture and homologies of *Coelocerodontus*: implications for conodont intrarelationships

#### **Sarah Vinnel**

Department of Earth Sciences, University of Bristol, UK

Conodont interrelationships are now well understood, with almost all workers agreeing on a chordate affinity for the group, and recent phylogenetic analyses placing them as stem-group Gnathostomata. However, little is known about the early evolution of these primitive vertebrates. The majority of conodonts are known only as disarticulated remains from which multielement taxonomy can be derived. The key to resolving conodont intrarelationships lies within multi-element reconstructions of both the apparatus compositions and architectures of primitive coniform euconodonts and more derived groups. Rare fused clusters, as well as some discrete elements, of *Coelocerodontus bicostatus* from the Tremadoc of Sweden have been re-examined. Synchrotron technology has allowed a 3-D model of a cluster to be rendered, permitting detailed information about element morphologies and internal structure of the cluster to be recovered. The information gained from this model was used to interpret other clusters imaged only using the SEM. This facilitated the elucidation of the apparatus composition and architecture of *Coelocerodontus*. Together with histological investigations and phylogenetic analyses further insights have been made into the intrarelationships of the group Conodonta.

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

### Clare H. White<sup>1,2</sup>, Brian R. Rosen<sup>2</sup> and Dan W. J. Bosence<sup>1</sup>

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*Acropora* is the most diverse, widespread and abundant of today's tropical reef corals, with its centre of diversity in the Indo-West Pacific (IWP). Counterintuitively, it was absent from IWP until the late Paleogene, but common in the Paleogene to early Neogene in Europe and the Mediterranean (Eur–Med), including high palaeolatitude (48°N) occurrences in the Eocene of southern England and northern France. It subsequently disappeared from Eur–Med in response to mid-Cenozoic climatic cooling. *Acropora* is therefore a potential exemplar coral for understanding the origins and history of the modern reef coral fauna, especially (and topically) in relation to climatic changes. This poster summarises our further work in progress on: (1) palaeoenvironmental and palaeoclimatic aspects, concentrating on the effects of Eocene climatic warming, and based on an assessment of preservational state, diagenesis, and stable isotopic composition (δ¹8O and δ¹3C) in apparently unaltered, but fragmented, specimens of *Acropora*, and associated corals from the Eocene of the Paris and Hampshire Basins (NHM collection), and (2) stratigraphic distribution, based on extraction from the Paleobiology Database (<http://paleodb.org/>) of all *Acropora* records to date, plotted on 'Boucotgrams' (named for Art Boucot).



### Understanding the Roman mosaic artisan, using microfossils

### Ian P. Wilkinson¹, Mark Williams², Jeremy Young³, Graham Lott¹, Samantha Cook⁴ and Mike Fulford⁵

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Excavation of Roman Calleva Atrebatum, modern Silchester, southern England, has revealed a number of 1st to 4th century AD mosaics. Chalk tesserae in these mosaics yield microfossils of ostracods, foraminifera and coccoliths that indicate a provenance in the youngest Cretaceous chalk of the English downlands. This poses a geoarchaeological conundrum: the highest chalk in southern England, which is exposed in the Dorchester–Swanage–Portsdown district, is normally soft, marly and unsuitable for building. It seems that the Roman tesserae manufacturers of the town had found a source of indurated chalk or hardground, on the upper surface of the Chalk Group, which they probably imported from Dorset, a source of other lithologies used in the mosaics.

#### Frozen in time: fossils from the Antarctic

### Lucy A. Wilson, A. J. Tate and J. A. Crame

British Antarctic Survey, Cambridge, UK

Antarctica is a vast continent with a complex geological history yielding a rich and diverse fossil record yet, due to its extreme and hostile climate today, this fauna and flora is still incompletely known. The British Antarctic Survey, based in Cambridge, houses one of the largest collections of Antarctic fossils anywhere in the world, ranging from Cambrian trilobites to Cenozoic molluscs, plus many spectacular plant fossils. High-resolution images have been made of the Type and Figured collection and, together with taxonomic, stratigraphic and locality data, are now easily accessible via the Internet (<a href="http://www.antarctica.ac.uk/Resources/GSD/fossils/">http://www.antarctica.ac.uk/Resources/GSD/fossils/</a>). Up to 1,000 types, including over 150 holotypes, are held within the collection, which is particularly rich in Mesozoic taxa from the Antarctic Peninsula. Given the central locality of the Antarctic in the Gondwanan supercontinent this collection is of high significance for taxonomic and biogeographical studies in the Southern Hemisphere. We provide an overview of Antarctic fossil material, which is now available online, and point to some key problems that it may help to solve.



# The Palaeontology and Stratigraphy of the Upper Greensand (Upper Albian) around Devizes, Wiltshire

M. A. Woods, K. A. Booth, A. R. Farrant, P. M. Hopson and A. J. Newell British Geological Survey, Keyworth, Nottingham, UK

The Upper Greensand near Devizes is famous for its rich fossil faunas, with many museums having examples amongst their collections. However, little has been published about the local stratigraphy since the work of Jukes-Browne (1895, 1905) and Jukes-Browne and Hill (1900). New work by the British Geological Survey (BGS) has involved the re-examination of some of Jukes-Browne and Hill's original localities and the logging of new sections. A programme of cored boreholes is also planned. Early results of this work include the rediscovery of the Potterne Rock, from which Jukes-Browne and Hill locally recorded a rich ammonite fauna. There is a distinct succession of lithologies that are not entirely comparable with the Upper Greensand succession to the south-west, in the Shaftesbury and Wincanton districts (Bristow et al., 1995,1999), and the fossil evidence also suggests significant intraformational thickness changes of biozones compared to the successions recorded by Bristow et al.. It is hoped that subsequent work will allow the Devizes Upper Greensand succession to be formally classified into members, and reveal the exact nature of the relationship between the Potterne Rock and the broadly coeval oyster-rich 'Ragstone' seen in the Upper Greensand of the Shaftesbury, Wincanton and part of the Salisbury districts.

# Vermiform Fossils from The Lower Cambrian Chengjiang Lagerstätte, China Ma Xiaoya<sup>1,2</sup>

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Extant worm-like phyla range from less derived to more complex animals, inhabit all kinds of environments with different modes of life, and have a great morphological and ecological diversity. In recent years, numerous zoologists have paid attention to these worms, but phylogenetic study is still primarily based on morphological and molecular research on extant animal species, with fossil evidence given relatively sparse attention. The world-famous Chengjiang Lagerstätte exceptionally preserves numerous soft-bodied worm-like fossils, which are likely to be a crucial key in answering important questions about the origin and evolution of worm-like animals. The earliest fossil representatives of eight worm-like phyla have been found in the Chengjiang biota; however, some of these are still being assessed, and other enigmatic worm-like fossils have yet to be studied in detail and classified. My on-going PhD will address aspects of the palaeobiology and phylogeny of such vermiform fossils.



### The Lyme Regis Fossil Festivals

### Jeremy R. Young, Jacqueline Skipper and Alastair MacGowan

Palaeontology Department, The Natural History Museum, London, UK

Following designation of the Jurassic Coast of Devon and Dorset as a UNESCO World Heritage site the NHM has developed an active collaboration with the Jurassic Coast team. The most spectacular outcome of this has been the running of Fossil Festivals at Lyme Regis in Easter 2005 and May 2006. The festivals were organised by the Lyme Regis Development Trust and funded by the Heritage Lottery Fund. Other participants included the Lyme Regis Museum, Charmouth Heritage Centre, British Geological Survey, RockWatch, the community of professional fossil collectors and preparators from Lyme Regis, and artists and street theatre acts from across the country. The NHM contribution was centred on a fossil roadshow providing identification of specimens but also included very popular participatory activities - making fossil casts, discovering microfossils, practising fossil preparation skills (using dog-biscuits embedded in clay), and identifying shark teeth picked out of Eocene sands. These were run by a rather large team from the Palaeontology and Learning Departments, with numerous other friends and associates. The festivals were remarkably well-attended and enjoyable. We feel this a real contribution to sustaining palaeontology in the UK and hope you can join us at the next festival, planned for 4-6 May 2007.