

# PALAEONTOLOGY NEWSLETTER



The Newsletter for members of the Palaeontological Association  
Number 39 1998

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**Deadline for copy for Issue No. 40 is 26th February 1999.**

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*Newsletter Editor:* DR S. RIGBY, Dept of Geology and Geophysics, Grant Institute, West Mains Road, Edinburgh EH9 3JW (co-opted)

*Marketing Manager:* DR A. KING, English Nature, Northminster House, Peterborough PE1 1UA

*Publicity Officer:* DR M.A. PURNELL, Department of Geology, University of Leicester, University Road, Leicester LE1 7RH

#### *Editors:*

DR D.M. UNWIN, Geology Department, University of Bristol, Wills Memorial Building, Queens Road, Bristol BS8 1RJ

DR R. WOOD, Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ

DR D.A.T. HARPER, Department of Geology, University College, Galway, Ireland

DR A.R. HEMSLEY, Department of Earth Sciences, University of Wales College of Cardiff, Cardiff CF1 3YE

DR J. CLACK, (University of Cambridge)

DR B.M. COX, British Geological Survey, Keyworth, Nottingham NG12 5GG

DR D.K. LOYDELL (Technical Editor), Dept of Geology, University of Portsmouth, Burnaby Building, Burnaby Road, Portsmouth PO1 3QL

*Newsletter Reporter:* DR P. PEARSON, Geology Dept, University of Bristol, Wills Memorial Building, Queen's Road, Bristol BS8 1RJ

*Other Members:* DR M.J. SIMMS, Department of Geology, Ulster Museum, Botanic Gardens, Belfast BT9 5AB

MR F.W.J. BRYANT, 27 The Crescent, Maidenhead, Berkshire SL6 6AA

**Front cover:** Median section through *Iteria cabaretiana* (d'Orbigny); a nerineoidean gastropod from the Upper Kimmeridgian of the Jura (France). Graphics by Mark Purnell, after a drawing by Mike Barker from an acetate peel. Text graphics by Mark Purnell and Lori Snyder.

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(The Palaeontological Association is a Registered Charity)

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### **Reminder**

The deadline for copy for Issue no 40 of the *Newsletter* is  
**26th February 1999**

## ASSOCIATION MEETINGS PROGRAMME

### **Annual Meeting**

University of Portsmouth; 16-19 December 1998

*The Abstracts are reproduced in the supplement in the centre of this Newsletter.*

Further details are available from Dr David Loydell or Dr Mike Barker (fax +44 (0)1705 842244), and on the Association's Web site.

### **1999 Lyell Meeting**

*(see opposite page)*

#### **Post Conference Field Excursion**

Wednesday 3rd – Saturday 6th March

Organism – Environment Feedback in Mesozoic Carbonate Platforms, Lusitanian Basin, Portugal.

Leaders: Gary Aillud, Matthew Watkinson (University of Plymouth) and Reinhold Leinfelder (University of Munich)

For further information please contact Gary Aillud or Matthew Watkinson, Department of Geological Sciences, University of Plymouth, Drake Circus, Plymouth, PL4 8AA, UK (tel 01752 233100, fax: 01752 233117, e-mail [gailrud@plymouth.ac.uk](mailto:gailrud@plymouth.ac.uk) or [mpwatkinson@plymouth.ac.uk](mailto:mpwatkinson@plymouth.ac.uk))

### **Progressive Palaeontology '99**

University of Bristol; Wednesday 28 April 1999

An informal one day conference in the Department of Earth Sciences, University of Bristol, mainly intended for research students (and supervisors) to get together and present short talks or posters about their work, but all are welcome to attend. First year postgraduates are especially encouraged to tell us about their projects. Details are available from Trevor Cotton, Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol, BS8 1RJ (tel 0117 9545411, fax 0117 9253385, e-mail [trevor.cotton@bristol.ac.uk](mailto:trevor.cotton@bristol.ac.uk)), or on the conference website at <http://palaeo.gly.bris.ac.uk/PP99/home.htm>

### **Annual Address & AGM**

University of Leeds; Wednesday 12 May 1999

Dr P. R. Crane FRS (Field Museum, Chicago)

Palaeontological evidence for the early evolution of flowers.

## The 1999 Lyell Meeting

### ORGANISM – ENVIRONMENT FEEDBACKS IN CARBONATE PLATFORMS AND REEFS

1st - 2nd March, 1999  
The Geological Society,  
Burlington House, Piccadilly

#### Aims and themes of the meeting

This international meeting aims to bring together palaeobiologists, ecologists and sedimentologists to address questions on how interactions between organisms and environments have generated the variety of carbonate platform facies and geometries seen in the ancient and modern record. All hierarchical levels of interaction are to be considered, ranging from that between organismal growth and ambient conditions, via growth fabric development in response to climate and the provision of accommodation space, to the interplay of global and evolutionary change. Themes will include:

- Ecology and palaeoecology of benthic faunas, particularly factors influencing growth fabric genesis
- Processes and rates of skeletal growth, bioerosion and sediment production
- Taphonomy of reef fabrics and sediments
- Sequence stratigraphy of carbonate systems and its bearing on reefal development within them
- Regional to global environmental change and associated patterns of evolution and extinction
- Contribution of carbonate-carbon burial in the global carbon cycle budget and climate feedbacks

#### Keynote addresses

Keynote speakers include Peter Glynn (Miami, USA), Wolfgang Schlager (Amsterdam, Netherlands), Wolf-Christian Dullo (Kiel, Germany), and Jean-Pierre Masse (Marseilles, France)

#### Call for papers

Oral and poster presentations addressing these themes are invited. Papers dealing with patterns and processes, concepts and dynamics are particularly welcome. Abstracts (no longer than 400 words) should be sent to Enzo Insalaco by 1st October 1998.

#### Convenors

Dr. Enzo Insalaco (The University of Birmingham)  
Dr. Peter Skelton (The Open University)  
Dr. Tim Palmer (The University of Wales, Aberystwyth)

#### Sponsors

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For further information contact Enzo Insalaco, School of Earth Sciences, The University of Birmingham, Edgbaston, Birmingham B15 2TT, UK (tel 0121 414 6163, e-mail [e.insalaco@bham.ac.uk](mailto:e.insalaco@bham.ac.uk)).

## NEWS

### W.J. Arkell (1904-1958)

The Oxford University Museum of Natural History, in collaboration with the Bath-based National Cataloguing Unit for the Archives of Contemporary Scientists, is compiling a catalogue of the archives and manuscripts of W.J. Arkell, author, among much else, of *The Jurassic System in Great Britain* (1933), *The Jurassic Geology of the World* (1956), and co-author of the Ammonoidea volume of the *Treatise*.

If members of the Palaeontological Association hold correspondence with Arkell among their papers, and wish to have it incorporated into the catalogue and deposited with the archives already held permanently in the Oxford University Museum, would they please contact W.J. Kennedy at Geological Collections, University Museum of Natural History, Parks Road, Oxford OX1 3PW, U.K. (tel 01865 272956, e-mail Jim.Kennedy@earth.ox.ac.uk).

*Jim Kennedy,  
University Museum of Natural History, Oxford*

### Rockwatch

Dear PalAss Members,

I have just been appointed as National Rockwatch Officer, and having attended a PalAss Meeting in Dublin, remembered the depth of knowledge and enthusiasm on show and wondered if you could help me? Perhaps I should start by providing you with some background information on Rockwatch.

Since Sir David Attenborough formally launched Rockwatch in 1991 the club has helped thousands of young people from all over the country (aged between eight and 16) to pursue an interest in geology. Some have even used Rockwatch as a launch pad into a career in geology. Rockwatch now has a national membership of 3,000 and numbers are growing all the time.

Special events for members have given young people the chance to meet inspirational experts. American palaeontologist Jack Horner joined Chris Packham and 300 Rockwatchers at "A Dinosaur Delight" held at Oxford University Museum. "A Four Billion Year Adventure" in Cambridge was hosted by Simon Conway Morris.

Rockhound Challenge, run by Rockwatch, is the only national competition for young geologists. It has recently been extended to provide classes for "rock artists" and "rock reporters" as well as for young people with geological collections of their own. Rockhound Challenge winners have gone on to promote Rockwatch to a wider audience, appearing in their local press, on BBC's "Blue Peter" and, in one case, on a special ITV programme, "Dinosaur Trail".

Undoubtedly, Rockwatch provides the best forum for involving young people in exploring and expanding their interest in geology.

Rockwatch is going from strength to strength, so what are the plans for taking Rockwatch into the new Millennium? Well, the emphasis will be on continuing to make geology relevant in everyday life and

giving young people the opportunity to take part in events and get their hands on rocks. This is where PalAss members might like to help. We need people with the expertise to lead events for us. My thanks go out to those of you already involved, but if other PalAss members were able to participate, it would swell the number of events available for young people across the British Isles. You can have a lot of fun with these events and they do not need to be long or complicated, a two hour walk in the countryside to find out how the hills were formed, a stroll around a city to take in the building stones, or an indoor fossil roadshow. It is important not to undervalue what may be regarded as 'bread and butter' geology. Once you have one event under your belt and you get the bug, it soon leads to more, so go on, give it a go, you might even enjoy it!

We have produced guidance for event leaders and we hope to be compiling a further booklet describing a range of geology-based activities effective at engaging young people. To that end, if you have 'tried and tested' activities, please let me know.

Please telephone for a leaders' support pack and in return for contributing, leaders can benefit from free insurance and Rockwatch membership. The deadline for our Winter/Spring Events List is the 20th November 1998. I look forward to hearing from you. Best Wishes.

*Duncan Friend*

*(National Rockwatch Officer, tel 01522 574538)*

## **New International Working Group: Gondwanan Biogenic Structures**

During the recent Gondwana-10 meeting in Cape Town it was proposed that a working group should be formed to facilitate communication between ichnologists working on Gondwanan trace fossils. The primary aim of this working group is to correlate the environmental and stratigraphic distribution of ichnotaxa between the Gondwanan continental fragments and to attempt to recognise which ichnotaxa (if any) are endemic.

A newsletter will act as the primary means of communication between the working group members. This will be distributed over the Internet, although a limited number of hard copies will be produced for those without Internet access. This newsletter will contain contact information, contributors' current research, articles, announcements and a 'debate' section. The newsletter will also act as a forum for reporting, and discussing, the activities of the Subcommittee on Gondwanan Stratigraphy (SGS), of which I was elected a voting member.

If anyone would like to become a member of this new working group and contribute to the newsletter, please send your contributions (in English and via e-mail preferably) to Dr. Simon Braddy (S.J.Braddy@bris.ac.uk). Please structure your contribution as follows:

Name, address, e-mail address, phone, fax, outline of current research relating to Gondwanan ichnology, a list of your recent references relating to Gondwanan ichnology, any short articles you care to submit, and any suggestions for the first debate (endemic ichnotaxa?).

*Simon J. Braddy*

*Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol, BS8 1RJ, UK.*

## Fossils

I have some fossils from an area that was once covered with water. The fossils that I have were at one time covered with sand, and the sand minerals went into the rock making sort of a sand rock. If you would like to see it please write to me at Larry J Provencial, P.O. Box 583, Osceola, WI 54020.

## Palaeontology Thesis

Last October Miguel V. Pardo Alonso, from the Dept. Geología, Univ. de Valencia (Spain), presented the Thesis: "Geología del Devonico meridional de la Zona Centroiberica". Miguel did a good job studying the geology (lots of mapping), stratigraphy, palaeontology (brachiopods) of the Devonian of the Southern part of the Central Iberian Zone of Spain (the Herrera del Duque, Almaden and Guadalmez synclines and in the northern limb of the Pedroches syncline). The new doctor, based on the stratigraphy, fossil content and structure of the Devonian series established ten formations, three of which were informally included in a group; a complex, consisting mainly of volcano-sedimentary materials, was also distinguished in Almaden.

The Silurian/Devonian boundary was tentatively placed at the top of the Doradillo Fm., below beds with Lower Lochkovian fossils, the first fossils of this age reported from the area. The Devonian/Carboniferous boundary was located in the Casa de la Vega Fm., between two calcareous levels with conodonts, the first one of upper Famennian age and the second level of upper Tournaisian age. The Frasnian biozonation proposed in previous works was revised, redefining most of the biozones.

In the Devonian, the Lochkovian, Pragian (with tentative assignments to lower, middle and upper subdivisions), Emsian (lower and upper Emsian), uppermost Givetian, Frasnian and Famennian (lower and upper Famennian) were palaeontologically characterized in the studied zone, but the uppermost Emsian, the Eifelian and most of the Givetian, if not all, are lacking. This hiatus, which corresponds to the Middle Devonian gap of previous authors, occurs between the Herrera and Abulagar Fms. Regarding the type of materials constituting these formations, Miguel suggested that the gap could be due to an emersion, possibly of a tectonic origin.

The biostratigraphic study was based on different invertebrate marine fossils and conodonts, but focusing on brachiopods because they are ubiquitous, abundant and diverse, and relatively well preserved. From a systematic point of view, sixty taxa of brachiopods were revised or described, belonging to 37 different genera; from these a new genus and seven new species were proposed. The proposed datation and biozonation will allow future correlations in the zone, and the detailed geological maps (1:25.000) produced will help the understanding of the complicated regional geology.

*Fernando Alvarez*  
*Departamento de Geología*  
*Universidad de Oviedo*  
*Oviedo*

*Tel: + 34 98 510 31 38*

*Fax: + 34 98 510 31 03*

*e-mail: fernando@asturias.geol.uniovi.es*



## **Society of Avian Palaeontology and Evolution (SAPE)**

I have the deep sorrow to announce that two of the most famous members of the SAPE died recently.

N.I. Burchak-Abramovich, from Tbilisi, Georgia, died in October 1997, at the age of 97.

Hildegarde Howard, from Laguna Hills, California, died on 28th February 1998, a few weeks before her 97th birthday.

These two people dedicated their lives to Avian Palaeontology, over three-quarters of a century. They were the elders to whom we owe so much.

I hope that all SAPE members have received the first circular for the 5th International Meeting of the Society of Avian Palaeontology and Evolution, which will be held in Beijing in June 2000. People who have not received this circular can contact the Organising Committee, 5th International Meeting of Society of Avian Palaeontology and Evolution, PO Box 643, Beijing 100044, China, tel 86-10-68354669/86-10-68935168, fax 86-10-68337001, e-mail [ivppkj@public.bta.net.cn](mailto:ivppkj@public.bta.net.cn)

*Cécile Mourer-Chauviré*  
(Secretary, SAPE)

## **New Publication from Palaeontographica Canadiana**

*Palaeontographica Canadiana* is a monograph series of major contributions to Canadian paleontology that is dominantly, but not exclusively, systematic in content. The series is sponsored jointly by the Canadian Society of Petroleum Geologists (CSPG) and the Geological Association of Canada (GAC).

Taxonomie des petits foraminifères du Carbonifère supérieur-Permien inférieur du bassin de Sverdrup, Arctique canadien. Sylvie Pinard et Bernard Mamet. 1998. *Palaeontographica Canadiana* No. 15, 251 pp., 42 pls. ISBN 0-919216-63-3. CSPG price \$64 CAN\$ + \$3.75 CAN\$ shipping + GST in Canada, \$64 CAN\$ +\$7.50 CAN\$ shipping in USA. Elsewhere, contact CSPG. GAC price \$72.50 CAN\$ in Canada, \$72.50 US\$ elsewhere (appropriate taxes and shipping charges included).

### **Summaire/Summary**

Les fusulines constituent l'outil de corréation le plus employé pour la stratigraphie du Carbonifère supérieur et du Permien inférieur. Les divisions de cet intervalle géologique se basent essentiellement sur ces organismes. Les géologues ont jusqu'à présent négligé l'emploi des «petits» foraminifères qui pourtant ont une valeur biostratigraphique comme le démontre cette étude. Une quarantaine de coupes stratigraphiques ont été étudiées et 170 taxa répartis parmi 58 genres sont présent. La plupart de ceux-ci ont été décrits de niveaux équivalents tant en Amérique du Nord qu'en Eurasie. Toutefois, dix-sept formes semblent inédites. Quinze assemblages (peut-être 16) sont reconnus. Les implications pour l'interprétation du paléoclimat et de la paléogéographie sont brièvement discutée.

The foraminiferal stratigraphy of the Late Carboniferous-Early Permian is commonly based on fusulines that provide a reliable zonal framework. Up to now, geologists have neglected smaller foraminifers although they have some biostratigraphic value, as this study will demonstrate. More than forty strati-

graphic sections have been studied, and 170 taxa that belong to 58 genera are present. Most of the taxa have been previously recorded in North America or Eurasia, but 17 are new. Fifteen (maybe 16) biostratigraphic assemblages are recognized. Paleoclimatic and paleogeographic implications are briefly discussed.

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Submitted by A.D. McCracken, Editor of *Palaeontographica Canadiana*, c/o Geological Survey of  
Canada, 3303-33rd st. NW Calgary, Alberta, Canada T2L 2A7

Phone: (403) 292-7130

Fax: (403) 292-6014

E-mail: [mccracken@gsc.nrcan.gc.ca](mailto:mccracken@gsc.nrcan.gc.ca)

## SPOTTED IN THE NATIONAL PRESS

The Times 18th June, 1998      Science Editor Nigel Hawkes

**How T-Rex Ground Down his Victims.** The discovery by Dr. Karen Chin of the US Geological Survey in Menlo Park, California, of between 30% and 50% of the content of 18 inch long by 6 inch wide coprolite consisted of bone fragments suggests that *Tyrannosaurus rex*'s feeding habit did not consist of bolting food but of chewing and munching bones before swallowing the food.

The Times 24th June, 1998      Science Editor Nigel Hawkes

**Feathered Dinosaurs Lift Theory of Bird's Origin.** Two turkey-sized feathered dinosaurs found in Liaoning Province, Northeastern China appear to add weight to the argument that birds are descended from dinosaurs. The fossils are similar in shape to the slender carnosaurus such as *Velociraptors*. The probability is that the feathers were not used for flight. It is suggested that the feathers could have been for camouflage, display, insulation or species recognition.

The Times 7th July 1998      Science Editor Nigel Hawkes

**Debut of Swift and Deadly Dinosaur.** Evidence of a not previously known dinosaur, discovered by an unnamed collector, brings the Isle of Wight again to the public's notice. This time it is a creature some 15 feet long, sharp toothed, fast, and equipped with deadly claws bearing some resemblance to *Velociraptor*. The fossil is around 120 million years old, and from the bones is estimated to have had a tail up to twice its body length. (When are we going to get a dinosaur museum on the Isle of Wight?)

The Sunday Times 27th September 1998      Reporter Steve Farrar

***Tyrannosaurus rex* had the Jaw Power to Crush a Tank.** According to Mason Meers of Florida Gulf Coast University, the bite of *Tyrannosaurus rex* is some ten times more powerful than was previously thought. Enough to chew steel bars or rip a car apart. This latest research should fuel debate as to whether the creature fed off carrion after the soft parts had been earlier predated and had to crush the bones, or was this huge power required to rip off chunks of meat by a twisting motion of the head.

*Jim Bryant*

*27 The Crescent, Maidenhead, Berkshire SL6 6AA*

Please send palaeo-articles from the national press to Jim.

## TREASURES OF TWELVE COUNTIES

As a new era of peace dawns in Northern Ireland all aspects of life are slowly returning to normal. As part of this process, the geological surveys of Northern Ireland and Ireland have joined forces to launch a new cross-border initiative called *Landscapes from Stone*, aimed at promoting the geology of the twelve counties most affected by the troubles (Antrim, Armagh, Cavan, Derry, Donegal, Down, Fermanagh, Leitrim, Louth, Monaghan, Sligo and Tyrone). The northern part of Ireland was once a popular destination for geological tourism, especially organised parties from schools and universities in Britain and elsewhere. One of the objectives of the Landscapes from Stone project is to revitalise this trade, which is of course beneficial to all involved.

I was one of the lucky individuals asked to participate in a familiarisation field trip to the area held at the beginning of October. Sixteen British universities were represented, and I must say we all had a very pleasant time being shown round the sites. Anyone who has been on a geology field trip will appreciate the rare pleasure accorded to one of our hosts (Dr Patrick McKeever of the Geological Survey of Northern Ireland) who on one occasion was able to force sixteen geological field trip leaders out of the minibus into the driving rain. But on the whole we were lucky with the weather and the trip was a revelation.

Geologically, the north of Ireland is in many ways similar to Scotland, from the Dalradian metasediments through to the Tertiary igneous rocks. My purpose here is to mention some of the palaeontological highlights of our trip, although I have no doubt that what we saw in a few days is just the tip of the iceberg, and many of the association's members will know a lot more about the palaeontology of the north than I do.

On the Antrim coast near the famous Giant's Causeway, we were shown spectacular outcrops of Chalk (that's one up on Scotland!). The Chalk is in fact a hard limestone because it is capped by a thick pile of basaltic lavas. I observed a variety of fossils that one might expect in the Chalk, but was alerted by my colleague Paul Wignall of Leeds University to a bed containing abundant belemnites, which are quite rare in the British Chalk. Before continuing these investigations, we were rushed off to see Jurassic mudstones of the area which are in places baked hard by proximity to the igneous rocks. Being black and fine grained, these are difficult to tell apart from the basalts themselves, but contain well preserved ammonites, and were once thought to be conclusive proof of the Neptunian theory that basalt is a sedimentary rock.

Further along the coast is an impressive Carboniferous succession with a few thin coal seams. This is the "Ballycastle Coalfield". Between the coals are a number of marine bands with abundant crinoids, bivalves and brachiopods of various orders. The strata are arranged in coarsening upward cycles, and provide a particularly clear example of a pattern of deltaic sedimentation that is common in the British Carboniferous (and elsewhere). The area provides an excellent opportunity for examining fossil ecology in relation to changing sedimentary environments.

For truly wonderful fossils however, the prize must go to the Carboniferous limestones of the western counties, in which one can find a wide variety of corals, bryozoans, brachiopods, echinoids, crinoids and sponges. Nothing I have seen in the British Carboniferous has prepared me for the amazing coralliferous succession at Streedagh Point in County Sligo (G637 508). Here there are vast bedding planes strewn with large mounds that turn out to be *Lithostrotion* colonies, and between them are literally thousands of large solitary rugose corals up to half a metre in length (*Siphonophyllia gigantea*).

Many of these have peculiarly twisted shapes because they were repeatedly exhumed from the mud during their long lifetimes and their growth disrupted. The site is well worth a visit, although the fossils are uncollectable and should be left where they are.

I recommend the north of Ireland to anyone who has not had the pleasure of visiting before. You will be assured a friendly welcome wherever you go and the pleasure of fossil hunting in some beautiful and unspoilt scenery. Further details of the *Landscapes From Stone* project can be obtained from Mr Enda Gallacher of the Geological Survey of Ireland, Haddington Road, Dublin 4, Ireland.

*Dr Paul Pearson*  
*Department of Earth Sciences,*  
*University of Bristol, Queen's Rd, Bristol BS8 1RJ, UK*

tel: 0117-9288176

e-mail: paul.pearson@bristol.ac.uk

URL: <http://palaeo.gly.bris.ac.uk/personnel/Pearson.html>

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**Department of Geology and Geophysics,  
University of Edinburgh**

Applications are invited for a two-month contract position, covering for Dr S Rigby whilst she is on maternity leave. The successful candidate should have a Ph.D. and some lecturing experience. He/she will be required to teach palaeontology at all levels, from first year outside courses to honours specialisms. Total teaching commitment will be in the region of 25 hours. The starting date is 12th January 1999. Salary will be in the range £16,655-£21,815 (per annum, pro rata), depending on qualifications and experience.

Informal enquiries for the post may be made to Sue Rigby (+44 (0)131 650 8543, e-mail [Sue.Rigby@ed.ac.uk](mailto:Sue.Rigby@ed.ac.uk)). Applications, in the form of a C.V. and the names of two referees, should be sent to Prof E. Clarkson, Department of Geology and Geophysics, West Mains Road, Edinburgh EH9 3JW, Scotland, UK.

**Closing date for applications is 4th December 1998.**

# Palaeo-Comment

## *The possible lifestyle of a Late Ordovician eurypterid*

In 1995, Braddy *et al.* described the new species of the genus *Onychopterella* from the Late Ordovician Table Mountain Group (Soom Shale) in South Africa. Other than alluding to observations made by Kjellesvig-Waering (1958) and Clarke and Ruedemann (1912), no greater attempts were made to address the possible lifestyle of this creature, despite the unique aspects of its morphology. Further, it is worth noting that the other eurypterids which Braddy *et al.* and the other above sources compare to *Onychopterella* show enough anatomical differences from *O. augusti* to render them somewhat ineffective for the purposes of making a lifestyle comparison. I believe that an investigation into the possible lifestyle of this eurypterid is warranted, and after reviewing the comprehensive account of its morphology, I have noted several features which may provide clues as to how it may have lived in its environment.

The body of *O. augusti* emphasizes a flattened form with a wide preabdomen and a very prominent, extended doublure (see Braddy *et al.* 1995 for a complete description). The wide preabdominal region seems reminiscent of the condition in carcinosomatids, but the passing similarity should not imply a similar lifestyle. In *Carcinosoma* the postabdomen sharply begins, and continues along its entire length, as a long, narrow structure, but in *O. augusti* the preabdomen and postabdomen are more confluent, gently tapering distally. While the body of forms similar to *Carcinosoma* are associated with a nektonic or nektobenthic lifestyle (c.f. Copeland and Bolton 1985) the body of *O. augusti* is different enough to warrant an alternative interpretation.

As reconstructed, appendages II and III are so remarkably abbreviate and gracile (in contrast to forms such as *Eurypterus*, with stocky, spinose anterior appendages), that neither protrude significantly beyond the anterior outer margin of the prosoma. Appendage IV is not only abbreviate, but directed posterolaterally, in contrast to the orientation of the same appendage in many other nektonic or nektobenthic eurypterids (pers. obs.). All limb-like appendages of such eurypterids tend to protrude beyond the outer margin of the prosoma. In the more primitive condition of *O. augusti* appendages II-IV are not differentiated into walking and balancing limbs. Braddy *et al.* have documented that appendages V and VI were posteriorly directed to assist the eurypterid in maintaining its balance on the substrate. It is also worth noting that both of these appendages seem much more powerfully built than the others.

Appendage spines obviously had grasping and anchoring functions in life. As reconstructed, the relative lack of spines and slimness of Appendages II-IV (in contrast to the corresponding appendages of *Eurypterus* and other similar forms) would have possibly restricted the predatory capabilities of *O. augusti*. Its appendages do not seem to have been suitable for seizing and grappling with struggling prey, or for rending open the remains of hardbodied organisms. The small gnathobases (Clarke and Ruedemann 1912) seem to support this contention. Braddy *et al.* indicate that in the Soom Shale the remains of *O. augusti* are found 'in association with *Orbiculoidea* and infrequent lingulid brachiopods, orthoconic nautiloids, naraoid trilobites (Fortey and Theron 1995), conodonts (Theron *et al.* 1990), and various enigmatic organisms'. I do not believe that *O. augusti* was equipped to snatch nektonic organisms, like conodonts, from the water column. Any predatory habits present must have been directed towards devouring small, soft-bodied organisms from the mud. Braddy *et al.* do list worms as a possibility. The claw-like arrangement of spines on the distalmost podomere of appendage VI seems especially effective for 'grasping' the substrate, anchoring the limb in the substrate for optimum leverage. This 'grasp' could

have helped the eurypterid keep its 'footing' to maintain its balance. My view is complemented by the suggestion of Braddy *et al.* that the telson could have provided propulsive leverage from the posterior.

In accordance with the available evidence, it is possible that *Onychopterella augusti* was adapted to an infaunal, deposit-feeding existence. According to Braddy *et al.*, and Waterston *et al.* (1985), the spiral structure in the digestive tract is consistent with an organism ingesting a high volume of sediment with the hope of extracting a maximum amount of nourishment. The anatomical evidence may indicate that the eurypterid could have used its telson and posteriorly directed appendages V and VI to provide forward, propulsive leverage while the prominent doublure would slice through the substrate. Their reduction in size prevents appendages II-VI from interrupting the steady, forward movement of the eurypterid while preserving the sleek, 'leading-edge' of the eurypterid's anterior profile, accentuating the doublure, and enabling it to dig without having large, overtly spinose anterior limbs in the way. As reconstructed, the few spines present on appendages II-IV are notably directed posteriorly – their orientation could actually have been useful for pushing aside some mud. The flat, wide body seems appropriately shovel-like for plowing (c.f. Clarke and Ruedemann 1912).

It is certainly possible that the proposed infaunal adaptations may have served other purposes. At any given time, *O. augusti* could have behaved as an ambush predator by burying itself under a fine veil of sediment and lunging at slow, soft-bodied, passing prey. Burial could also have been an effective predator-avoidance strategy, but this seems unlikely given that Braddy *et al.* allege that *O. augusti* was a top predator in its ecosystem. It is more likely that the eurypterid spent its time foraging by ingesting sediment food particles, and devouring any slow, soft-bodied organisms disturbed by its fossorial activities.

In proposing that *Onychopterella augusti* had infaunal, deposit-feeding adaptations, I am suggesting a possible lifestyle not traditionally postulated for eurypterids. I feel that the morphology of this creature is sufficiently different to warrant a lifestyle hypothesis that breaks from tradition.

Jeffrey Minicucci  
Toronto, Ontario, Canada

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## *Palaeo*-Reply XCIX

It is commendable that both Mike Bassett and John Cope wish to defend the reputation of Trueman against the claims I made in my *Palaeo*-Comment in *Newsletter* 37 (see *Newsletter* 38, pp. 17-19) but I am obliged in response to enlarge upon what I wrote.

The “amazing slur” on Trueman’s reputation as a scientist (Bassett’s words) concerns the remark that he had concocted his *Gryphaea* story. I take exception to Cope’s suggestion that my recollection of L.R. Cox’s remark was faulty. Such was the impression made upon me by this remark that it became deeply etched in my memory; I remember clearly both the exact words and the circumstances in which they were uttered. (I have kept quiet about this matter for over forty years, but with both the individuals concerned being long dead I see no harm now in bringing it into the public domain). I was taken aback that an eminent palaeontologist of renowned mild temper should utter such a condemnatory remark, and I asked him to give his reasons.

The essence of his reply was twofold: that his own collecting in the Lower Lias led him to believe that there was no evolutionary relationship between Hettangian *Liostraea* and the succeeding *Gryphaea*; and that there was no “Trueman collection” as one might have expected it in the form of at least hundreds of specimens arranged in precise stratigraphical order, so that the evolutionary story could be checked independently. My subsequent investigations confirmed this. There was nothing in the Cardiff museum, and I now understand from Bassett that no material was transferred there until 1970. For my investigations in the old Swansea Geology Department I depended on the kind assistance offered by the person I knew best, Dick Owen. There was indeed, as Bassett points out, a rich bivalve collection, but from my point of view the key material I was looking for was not there. Cox was quite right, there was no collection of a large number of Hettangian and Sinemurian *Liostraea* and *Gryphaea* precisely specified according to stratigraphic horizon, of the degree of refinement required to test Trueman’s ideas. Accordingly I was obliged to rely entirely on my own collecting.

May I take this opportunity of stating that I consider that Trueman was a distinguished scientist who did imaginative and stimulating work in a number of fields – one thinks in particular of his seminal research on ammonoid functional morphology – but in the case of *Gryphaea* evolution he allowed his imagination to run away with him, and must have been rather astonished that one of his less thorough pieces of work should bring him such fame. However, bearing in mind that “stimulating” often means “stimulating to disagreement”, and that this is one of the ways science proceeds best, I am as happy as anyone to acknowledge my debt to Trueman for stimulating in me a subsequently lifelong interest in evolutionary palaeobiology.

*Tony Hallam*  
*University of Birmingham*





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**Abstracts and Posters**

## ABSTRACTS

### **The apparatus architecture of prioniodontids**

Stephanie Barrett

Geology Department, University of Leicester, University Road, Leicester LE1 7RH, UK

e-mail: SFB4@leicester.ac.uk

Conodonts are among the most prolific fossils of the Palaeozoic, but it has taken more than 130 years to understand the phylogenetic position of the group, and the form and function of its fossilized feeding apparatus.

Prioniodontids were the first conodonts to develop a complex, integrated feeding apparatus. They dominated the early Ordovician radiation of conodonts, before the ozarkodinids and prioniodinids diversified. Until recently the reconstruction of the feeding apparatuses of all three of these important conodont orders relied mainly on natural assemblages of the ozarkodinids. The reliability of this approach is questionable, but in the absence of direct information it served as a working hypothesis.

In 1990, fossilized bedding plane assemblages of *Promissum pulchrum*, a late Ordovician prioniodontid, were described. These were the first natural assemblages to provide information about the architecture of prioniodontid feeding apparatus, and showed significant differences from the ozarkodinid plan. The recent discovery of natural assemblages of *Phragmodus inflexus*, a mid Ordovician prioniodontid with an apparatus comparable with the ozarkodinid plan, has added new, contradictory evidence.

Work is now in progress to try and determine whether the feeding apparatus of *Phragmodus* or that of *Promissum pulchrum* is most appropriate for reconstructing the feeding apparatuses of other prioniodontids. This work will assess whether *Promissum pulchrum* is an atypical prioniodontid, or whether prioniodontids, as currently conceived, are polyphyletic.

### **Parasitism on graptolites**

Denis E. B. Bates (1) and David K. Loydell (2)

(1) Institute of Geography and Earth Sciences, University of Wales, Aberystwyth, Ceredigion SY23 3DB, UK

(2) School of Earth, Environmental and Physical Sciences, University of Portsmouth, Burnaby Building, Burnaby Road, Portsmouth PO1 3QL, UK

e-mail deb@aber.ac.uk, David.Loydell@port.ac.uk

We present here spectacular evidence of parasitism on a planktic graptoloid, in the form of tubular periderm outgrowths on an Ordovician biserial from the Viola Limestone of Oklahoma. Such parasitic outgrowths must have had a major influence on the hydrodynamics of the rhabdosome, in terms of both its overall morphology and its weight distribution. We will also illustrate various other evidence for parasitism on graptolites, indicating that these most conspicuous components of the Palaeozoic plankton were host to a variety of parasitic organisms.

**The skin of chancelloriids**

Stefan Bengtson (1) and Hou Xianguang (2)

(1) Department of Palaeozoology, Swedish Museum of Natural History, Box 50007,  
SE-104 05 Stockholm, Sweden

(2) ?

e-mail: Stefan.Bengtson@nrm.se

Chancelloriids are Cambrian organisms characterized by a sack-like body covered with composite star-shaped sclerites in a manner reminiscent of cacti. When first described from the Burgess Shale by Charles Walcott, they were interpreted as sponges. Later they have been reinterpreted as close relatives of the Cambrian halkieriids, based on the similar construction of the sclerites, which appear to have been formed by partial mineralization of a soft cuticle. Recent challenges to this interpretation are based on claims that chancelloriid sclerites were fully or partly formed from the outside. On this basis, relationships with sponges and ascidians, respectively, have been proposed.

Specimens of chancelloriids from the famous Lower Cambrian Chengjiang biota of Yunnan Province, China, preserve exquisite details of the flexible cuticle between the sclerites. The cuticle has a regular rhombic pattern, apparently reflecting the bases of spine-like processes. No structures resembling ostia, such as would be expected in a sponge, have been observed. Nor does the rhombic pattern resemble the cellular pattern in a sponge pinacoderm or the flattened, imbricating, spicular processes of some sponges. There is no evidence of the cuticle covering the sclerites, as has been claimed in support of the ascidian model. The skin of the Chengjiang chancelloriids was an integrated unit consisting of a flexible bristly cuticle with regularly placed batteries of sharp calcareous spines.

**Is the Palaeozoic fossil record worse than the post-Palaeozoic?**

Michael Benton, Matthew Wills and Becky Hitchin

Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road,  
Bristol BS8 1RJ, UK

e-mail: mike.benton@bristol.ac.uk, R.Hitchin@bristol.ac.uk

Some palaeoecological evidence suggests that the fossil record does not necessarily deteriorate backwards in time. This common assumption has been queried by studies of shell beds, but it is hard to make such studies comprehensive and global. The postulated deterioration has been tested in a different way, using comparisons of phylogeny and stratigraphy. A large number of cladograms and molecular trees were divided into those with Palaeozoic, and those with post-Palaeozoic, originations. There is no major difference between the two sets in terms of congruence of the fossil record with postulated phylogeny, and hence no evidence for deterioration.

**Ordovician cephalopods and inarticulate brachiopods from the Carnic Alps of Austria**

Olga K. Bogolepova

Department of Historical Geology and Palaeontology, Institute of Earth Sciences, Uppsala  
University, Norbyvägen 22, S-752 36 Uppsala, Sweden

e-mail: olga.bogolepova@pal.uu.se

Recent study in the Austrian Carnic Alps reveals a new fossil record of cephalopods and lingulate minute brachiopods. From the upper Ordovician Uggwa Limestone six species of ortho- and tarphycerid cephalopods (*Arionoceratidae* gen. et sp. indet., *Geisonoceras* sp., *Lituites?* sp., *Michelinoceras* sp. 1, *Michelinoceras* sp. 2) and three species of inarticulate brachiopods (*Acrotretella tenuis* sp. nov.,

*Lingulella* sp. and *Roweella?* sp.) are described. The faunal affinities of the described fauna will be discussed with respect to the latitudinal setting of the Proto-Alps during the Ordovician.

### **Permian Polaroids: snap-shots of ancient environments and animal activities**

Simon Braddy\*

Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol BS8 1RJ, UK

e-mail S.J.Braddy@bristol.ac.uk

Ichnological evidence is particularly significant when deducing the biomechanics and behaviour of extinct animals. Many trace fossils are 'snap shots' of the activities of extinct animals and provide insights on the palaeoenvironment of the time. This theme is illustrated by two Permian ichnoassemblages.

The late Permian Ganfontein palaeosurface (near Fraserburg, Karoo, South Africa) represents a crevasse splay formed after a flooding event on a vast alluvial plain. Spectacular sedimentary structures indicate that shallow pools were left after the flood, their margins preserving the activities of the animals living on the flood plain. The traces include *Bradysaurus* and dinocephalian trackways, sinuous fish trails, the trackways of freshwater crustaceans (*Umfolozia*, *Tasmanadia*), scorpions (*Paleohelcura*, *Siskemia*) and beetles (*Permichnium*), and beaded worm trails.

The Lower Permian Robledo Mountains ichnofauna (New Mexico, USA), regarded as the most abundant and diverse assemblage of Permian terrestrial trace fossils in the world, represents a marginal marine setting including tidal flats, non-marine red beds and freshwater conditions. The vertebrate traces include temnospondyl amphibian, araeoscolid, ?diadectid and pelycosaur trackways (the latter of biomechanical significance) and enigmatic sidewinding snake-like (?aistopod) trails. The invertebrate traces include 14 ichnogenera of arthropod trackways, recording the activities of myriapods, arachnids, eurypterids, xiphosurans, crustaceans and several different types of insects, and various new undescribed arthropod resting traces.

### **A re-interpretation of the braincase of the Devonian tetrapod *Ichthyostega stensioei***

Jenny A. Clack (1) and Per E. Ahlberg (2)

(1) University Museum of Zoology, Downing Street, Cambridge CB2 3EJ, UK

(2) Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

e-mail: jac18@hermes.cam.ac.uk

Re-examination of the braincase of the Upper Devonian tetrapod *Ichthyostega* has produced a radical new interpretation and the first identification of a stapes. Earlier descriptions were unable to interpret the braincase elements of *Ichthyostega* in terms comparable to those recognized in other early tetrapods or sarcopterygian fishes. However, our study has identified most conventional braincase parts in a structure which, apart from a few primitive features, is highly specialized in its morphology and organization. The otic region is extremely narrow, and to each side of it lies a large open chamber free of bony structures except for the inflated but lightly ossified stapes. It is not clear whether this chamber would have housed air, water, fatty tissue or muscle, although air or water are most likely, since the chamber was probably associated with the spiracular system. The contents in life would have determined whether the chambers were concerned with hearing, sound production, buoyancy, gas exchange or some other function in the living animal. At present, it is not possible to attribute a function, except

that aerial sound reception seems one of the least likely. In its peculiar and extremely specialized braincase morphology, *Ichthyostega* may be an instance of the phenomenon of ‘early diversification, later stabilization’ which has been seen in the evolution of other tetrapod and also invertebrate features. Other features of its anatomy are still considered primitive, and it remains phylogenetically near the base of the tetrapod tree.

### **Relationships of Cambrian conodonts**

Karen Cochrane\*

School of Earth Sciences, The University of Birmingham, Edgbaston, Birmingham B15 2TT, UK  
email: k.d.cochrane@bham.ac.uk

A histological study of the Late Cambrian-early Ordovician *Proconodontus* euconodont lineage has revealed that the elements comprise a lamellar crown of enamel overlying a basal body composed of spherulitic atubular dentine or, in some cases, globular calcified cartilage, and confirms their vertebrate affinity. This is concordant with studies of later euconodonts, and further emphasises the diversity of tissues that are found in euconodont basal bodies. A generally accepted hypothesis of euconodont origins is that euconodonts evolved via the paraconodonts from the protoconodonts during the Mid-Late Cambrian. In order to test part of this hypothesis, the histology of *Prooneotodus rotundatus*, a paraconodont, has been compared with the morphologically similar euconodont genus *Proconodontus*, and the results will be presented. A second euconodont lineage incorporating *Teridontus* appears to be unrelated to the *Proconodontus* lineage, and raises the possibility that euconodonts, as currently defined, are polyphyletic. Protoconodont and paraconodont relationships are even more uncertain. Protoconodonts are generally considered to be a sister group of the Chaetognatha (arrow-worms) on both anatomical and histological grounds. Since chaetognaths and vertebrates are not closely related, the protoconodont-paraconodont-euconodont evolutionary model is not reconcilable with the vertebrate affinity of euconodonts.

### **Taphonomy of a microvertebrate assemblage from a Lower Triassic fissure deposit at Czatkowice, Crakow Uplands, Poland**

Liz Cook and Clive Trueman

Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol BS8 1RJ, UK

e-mail: Liz.Cook@bristol.ac.uk, c.n.trueman@bristol.ac.uk

In 1978 a bone-bearing fissure fill deposit was discovered preserved in Carboniferous Limestone at Czatkowice Quarry, Poland. These Lower Triassic sediments preserve a diverse and taxonomically significant microvertebrate fauna and include taxa adapted to fully aquatic, amphibious, and fully terrestrial life styles. These animals lived in the vicinity of ephemeral pools found in the dune fields that covered large areas of Poland during the early Triassic. Analysis of the microvertebrate remains follows the techniques of two major research areas: the fossils have been classified using the ‘traditional’ taphonomic weathering, abrasion and fragmentation indices, and geochemical techniques such as ICPMS analysis of uranium, thorium and Rare Earth Elements (REEs), and XRD analysis of the mineralogical composition of the bones. A combination of these methods has allowed taphonomic and diagenetic pathways for the assemblage to be constructed.

**The origin of heterodont bivalves**

John C. W. Cope

Department of Earth Sciences, Cardiff University, P. O. Box 914, Cardiff CF1 3YE, UK

e-mail: CopeJCW@cardiff.ac.uk

Heterodont bivalves are today the most diverse of the seven bivalve subclasses, but their origins are obscure. The most fundamental bivalve radiations occurred in the early Ordovician, following the evolution of the filibranch gill. Because Arenig faunas contain representatives of most bivalve subclasses, it is clear that the principal radiations must have occurred before this, yet so far there are only some nine or ten species known from the Tremadoc Series. Some workers avoid the problem of differentiating between the Palaeoheterodonta and the Heterodonta by combining the two in a subclass Heteroconchia, but as shown by Cope (*Palaeontology*, **40**, 713–746), the shell microstructure of the two groups suggests that they have been long separated. In the absence of shell microstructural evidence, other criteria for distinction must be employed. Analysis of dentition suggests that some long-accepted palaeoheterodonts are in fact heterodonts, and that even in the early Ordovician heterodonts were already present. This implies that all modern bivalve subclasses (with the possible earlier exception of Lipodonta) arose from palaeotaxodont ancestors within a 5–10 million year interval in the earliest Ordovician.

**Re-investigation of classic Scottish Middle Old Red Sandstone fish-bearing nodule localities**

R. G. Davidson (1) and Nigel H. Trewin (2)

(1) 35, Millside Road, Peterculter, Aberdeen AB14 0WG, UK

(2) Department of Geology &amp; Petroleum Geology, University of Aberdeen, Meston Building, Kings College, Aberdeen AB24 3UE, UK

Classic nineteenth century 'nodule bed' Devonian fish sites adjacent to the Moray Firth are being re-investigated. Excavations have taken place at Tynet Burn with more recent field work at Edderton and Gamrie. Detailed logging of both fish and sedimentology is yielding considerably enhanced information on preservation, faunal distribution and palaeoenvironments.

The nodule beds are approximately equivalent in age and the fish assemblage consists of placoderms, acanthodians, an actinopterygian, porolepiforms, osteolepiforms and a dipnoan. The assemblage is typical of the 'Achanarras Fauna' of Givetian age which is widespread in the Orcadian basin, representing a time of generally high lake levels. However, it is apparent that minor lake level fluctuations are superimposed on the general trend.

The localities are interpreted as near shore lacustrine environments. At the Tynet Burn locality during an early stage in diagenesis, synchronous with concretion formation, chemotrophic bacteria invaded open fractures and partially oxidized the fish remains. This event was responsible for the characteristic vibrant red to purple colours of Tynet Burn fossils and took place at a time of low lake level when the fish bed was subjected to oxidation in the vadose zone. Comparisons between the occurrence of fish at different localities is yielding new information on the possible modes of life of fish genera.

**Conodont affinity, chordate phylogeny and the origin of the vertebrate dermal skeleton**

Philip C. J. Donoghue (1), Peter L. Forey (2) and Richard J. Aldridge (3)

(1) School of Earth Sciences, University of Birmingham, Birmingham B15 2TT, UK

(2) Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

(3) Department of Geology, University of Leicester, University Road, Leicester LE1 7RH, UK

e-mail: P.C.J.Donoghue@bham.ac.uk, ral2@leicester.ac.uk

For much of the past 140 years the affinity of conodonts has been one of the most vigorous and poorly constrained subjects of debate in systematic palaeontology. Prior to the discovery of soft tissue remains in association with the characteristic feeding elements, conodonts had been attributed to three kingdoms and almost every major animal phylum. The elucidation of conodont anatomy has led to almost universal acceptance of chordate affinity, but despite this systematic constraint, the debate has become even more controversial. Conodonts have been interleaved with many of the primitive jawless vertebrates and every permutation amongst the invertebrate chordates has been postulated. However, although most hypotheses have been couched in cladistic terminology or expressed in the form of a cladogram, not one is the result of a formal cladistic analysis. Instead, each hypothesis represents either the result of hanging conodonts off a pre-existing cladogram by pre-established synapomorphies, or else classifying conodonts according to unsubstantiated *a priori* assumptions of character polarity in chordate phylogeny. This is unfortunate as conodonts clearly have an important contribution to make to our understanding of chordate evolution, or else they would not evoke so much controversy.

Our analysis suggests that the systematic position of conodonts lies at the critical point in chordate relationships, between the extant jawless vertebrates which lack any form of mineralised dermal skeleton, and the familiar groups of extinct jawless vertebrates which possessed a well developed mineralized dermal skeleton in the form of scales and plates. These results corroborate recent hypotheses for the origin of the vertebrate skeleton and provide a refined understanding of chordate phylogeny. The effects of alternative codings for contentious characters are discussed, along with their implications for relationships.

**Fossils, palaeodepth and tectonics: Miocene evolution of Carriacou, The Grenadines, Lesser Antilles**

Stephen K. Donovan (1) and David A. T. Harper (2)

(1) Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

(2) Geological Museum, University of Copenhagen, Øster Voldgade 5-7, DK-1350 Copenhagen, Denmark

e-mail: Stephen.Donovan@nhm.ac.uk, dharper@savik.geomus.ku.dk

The stratigraphical succession of Carriacou consists of an Eocene–Miocene sequence of volcanics, volcanoclastics and subordinate limestones. Previous interpretations of the fossiliferous Miocene succession suggested that they were laid down in a uniformly shallow water setting. The implication from this is that uplift during and after the Miocene has been minimal.

Preliminary analyses of selected fossil groups suggests that this simple interpretation is incorrect. Volcaniclastic units contain abundant fossils that commonly occur in deeper-water environments in the tropical western Atlantic at the present day, including pteropods, brachiopods and stalked crinoids. Shell concentrations in the Belmont and Grand Bay formations are packed with numerous shells of at

least three taxa of large terebratulide brachiopod, including some in situ 'nests' of gregarious individuals. Columnals of isocrinids are locally common, with rare columnals of a gracile bourgueticrinid. These data suggest at least a deeper water shelf environment, supported by the rare occurrence of the trace fossil *Zoophycos*. The Middle Miocene Carriacou Formation rests unconformably on the volcanoclastic units.

A revised mid Tertiary geological history of Carriacou suggests early–mid Miocene deposition on the deeper water island shelf. This succession was uplifted in the early mid Miocene, with later mid Miocene limestone deposition in a shallower water setting.

#### **A Cambrian pantopod larva from Orsten and its significance for chelicerate phylogeny**

Jason A. Dunlop\* (1), Dieter Walossek (2) and Klaus J. Müller (3)

(1) Institut für Systematische Zoologie, Museum für Naturkunde der Humboldt-Universität Berlin, Invalidenstraße 43, D-10115 Berlin, Germany

(2) Sektion für Biosystematische Dokumentation, Universität Ulm, Helmholtzstrasse 20, 89081 Ulm, Germany (3) An den Eichen 8, 53125 Bonn-Röttgen, Germany

e-mail: Jason.Dunlop@rz.hu-berlin.de

Pantopods (or pycnogonids) are the odd-looking arthropods which hide in zoology textbooks as a class of the Chelicerata. Their relationships remain controversial. Authors who studied the group often interpreted them as unrelated to chelicerates, or any other arthropod group. Reinterpretation of the few Devonian pantopods may solve 'problems' of their appendage number and reduction of the opisthosoma. An Upper Cambrian fossil from the most prolific Orsten Lagerstätte in the Kinnekulle area, Västergötland, Sweden, was proposed by Müller and Walossek (1986) as a larval chelicerate with possible pantopod affinities. This fossil has rudimentary appendages in front of a chelate appendage pair, followed by two pairs of gnathobasic limbs with a single ramus. We confirm its earlier interpretation as a pantopod protonymph and, following Walossek and Müller (1997), argue that it supports two important hypotheses. Firstly, arthropods originally had a head with four appendage pairs (a pair of antennae and three pairs of biramous limbs) and Chelicerata have lost appendage 1, the antennae, during their evolution, making the chelicerae the 2nd head appendage. Secondly, Pantopoda are sister group to all other Chelicerata, on the synapomorphy of chelicerae, but retain as plesiomorphies remnants of the antennae and an anamorphic ontogeny starting with a head larva, with the autapomorphy for the chelicerate stem species being a more advanced pattern of development.

Müller, K.J. and Walossek, D. 1986. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **77**, 157–179.

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**Construction and ecology of late Palaeozoic algal reefs**

Graham Forsythe\*

Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ, UK

e-mail: gtwf2@esc.cam.ac.uk

Late Carboniferous to Early Permian reefs in south-western USA are generally considered to be ecologically simple communities, constructed predominantly by leaf-like 'phylloid' algae, sphinctozoan sponges and various problematica (*Tubiphytes* and *Archaeolithoporella*). Lack of recognized framework builders in these reefs and high proportions of micrite have led to a sediment-baffling (mainly by phylloid algae) interpretation for reef construction.

Detailed ecological study of the biota, however, reveals novel construction mechanisms within late Palaeozoic reefs, most notably interaction between biological growth mechanisms and early marine cementation. Phylloid algae, sponges, *Tubiphytes* and *Archaeolithoporella* have complex patterns of mutual encrustation, both *in-vivo* and post-mortem, and these control the basic structure of the reefs. Phylloid algal thalli are shown to have currently undescribed growth forms and are capable of supporting primary reef voids with associated cryptic biota. Large volumes of early marine cement, together with putative microbial micrite, are instrumental in stabilizing the reef framework to produce positive topographic relief. This active growth of reef frameworks in the late Palaeozoic contrasts with the passive mechanisms of sediment trapping previously proposed.

**Some palaeobiological aspects of the European Jurassic Trigoniidae**

Andrew O. Francis

School of Earth Sciences, The University of Birmingham, Edgbaston, Birmingham B15 2TT, UK

e-mail: A.O.francis@bham.ac.uk

During the Jurassic and Early Cretaceous, the Trigoniidae were among the dominant members of the shallow burrowing bivalve infauna. The family is characterized by its large and peculiar dentition along with a strong and elaborate external ornament, which has lent itself well to a thorough morphological analysis. Through the use of biometric methods, natural species groupings have been identified. Severe taxonomic splitting by previous workers has been recognized and thus, for each genus within the European Jurassic, the number of species is reduced to a handful. Ascending the Jurassic, trends within *Myophorella* include a gradual size increase along with a reduction in the density of tubercle spacing upon the valve exterior. Morphological differences within this genus have also justified its division into two subgenera: *Myophorella* and *Promyophorella*, a division rejected by previous workers. The lack of a continuous record of trigoniids in the European Jurassic has made it difficult to ascertain the particular mode of speciation. There is no evidence for gradualism; a punctuated equilibrium model appears to be a more likely alternative.

The occurrence of trigoniids within the Jurassic appears to be confined to certain stratigraphical horizons. Combined with the fact that some species occur only locally this suggests that their distribution was environmentally controlled. Through field work in Dorset and the Cotswolds the assumption that trigoniids occupied coarse-grained sediments in somewhat unstable environments would appear, for most species, to be correct. However, it has been observed that some inhabited highly argillaceous sediments in quiet water settings.

***Jamoytius kerwoodi* White: an unimaginative interpretation**

Kim Freedman

Geology Department, University of Leicester, University Road, Leicester LE1 7RH, UK

e-mail: kaf3@leicester.ac.uk

The anatomy and affinities of *Jamoytius kerwoodi* White have long been controversial. Its preservation as a flattened organic film makes the interpretation of features equivocal when solely based on comparison of their shapes. For such problematical fossils, a methodology emphasizing taphonomy and incorporating three-dimensional modelling allows features to be identified more rigorously by providing evidence of their composition and three-dimensional architecture. A comparator, moreover, must be carefully chosen. A small number of least equivocal features should initially be used to place the organism within a phylogenetic context, within which the other features can be identified. Applying this technique to *Jamoytius* indicates that it is an agnathan vertebrate. Its preserved features include W-shaped phosphatic scales, more than ten pairs of branchial openings, optic capsules, a round ventral mouth, a terminal nasohypophysial opening and continuous ventrolateral fin folds. A cladistic analysis shows *Jamoytius* as the most primitive vertebrate that possesses scales and ventrolateral fin folds. In this context, discussions about the origins of dermal armour and paired appendages should consider *Jamoytius*. The evidence from *Jamoytius* indicates that vertebrate paired appendages may be primitively continuous, and it may support the suggestion that the armour of the agnathans derives from trunk neural crest.

**Middle Jurassic benthic associations and palaeoenvironments of the Kachchh Basin, western India**

Franz T. Fürsich

Institut für Paläontologie der Universität Würzburg, Pleicherwall 1, 97070 Würzburg, Germany

e-mail: franz.fuersich@mail.uni-wuerzburg.de

The Kachchh Basin, a Mesozoic rift basin situated at the western margin of the Indian plate, was filled in the Jurassic with largely siliciclastic sediments. They represent environments ranging from coastal plain, fan delta, and brackish water embayments to shallow marine ramp and low energy basin, the latter exhibiting, at times, signs of sediment starvation. Sedimentation took place cyclically, controlled by eustatic sea level changes of different orders of magnitude as well as by regional tectonic events and by climate.

During the Bathonian–Oxfordian, the basin was populated by a diverse benthic macrofauna (approximately 450 taxa) that belonged to the Ethiopian faunal province. This fauna was dominated by bivalves, with brachiopods, gastropods, corals, serpulids, bryozoans, and sponges as additional elements. A cluster analysis of 220 quantitative samples with more than 23 000 individuals yielded 42 associations and several assemblages. The analysis of the spatial distribution pattern of these associations shows a clear relationship to substrate, energy level, salinity and climate. Many associations replaced each other along onshore–offshore transects. In the deeper parts of the basin the diversity of associations occurring in a particular facies type is higher than in shallower parts, but the size of individuals is, in most cases, distinctly smaller. The temporal distribution pattern of the associations is governed, on one hand, by shallowing-upward cycles, on the other hand by large-scale climatic changes. Thus, due to an assumed change from warm-arid to cooler and more humid conditions around the Bathonian–Callovian boundary, tropical elements of the fauna such as the bivalve *Eligmus*, high-diversity coral meadows, and meadows of lithistid and hexactinellid sponges disappear. The concurrent change from

oligotrophic to more eutrophic conditions resulted in the dominance of low-diversity associations characterized by deposit-feeding nuculid bivalves in the deeper parts of the basin.

### **Functional morphology of the hand of *Deinonychus antirrhopus* and its importance for the origin of flight**

Alan D. Gishlick, Department of Geology and Geophysics, Yale University, New Haven CT, USA  
e-mail: pterosr@minerva.cis.yale.edu

The transformation from grasping hand to wing while retaining functionality throughout the transition is one of the most persistent questions in the origin of avian flight. New data from hand morphology of basal maniraptors provides insight into how this may have occurred. The third digit of *Deinonychus antirrhopus* (Ostrom) has a curious morphology: bowed gracile metacarpal, buttressed joints between the first, second and third phalanges so that they move as a single unit and the finger is held slightly flexed, and a 50 degree twist in the long axis of the finger so that the ungual (claw) faces medially. This morphology, shared by *Archaeopteryx*, *Confuciusornis*, *Velociraptor*, and possibly *Protarchaeopteryx* and *Caudipteryx*, allows for the third digit to cross underneath the second digit. I suggest that this unique hand allowed the semi-opposable first and third digits to retain their grasping ability while the feathers (originating from the second digit) were elongated. This allowed feathered maniraptors to retain a functional grasping hand during the early development of a wing.

### **Structural-functional aspects in the evolution of the lid corals (Rugosa)**

Michael Gudo\*

Forschungsinstitut Senckenberg, Vergleichende & Funktionelle Anatomie, Senckenberganlage 25,  
60325 Frankfurt am Main, Germany  
e-Mail: gudo@stud.uni-frankfurt.de, mgudo@sng.uni-frankfurt.de

The Rugosa show some very conspicuous examples of solitary corals. These corals do not have a round shape but a unilaterally flattened shape (slipper-like shape, *Calceola*) or they have a rectangular shape (*Goniophyllum*). Furthermore, these corals have a lid by which they can close their polypars. The internal structure of the soft bodies of these corals and some of their structural-functional aspects are reconstructed on the basis of biological and morphological knowledge of the recent corals, in order to give a testable model for an evolutionary pathway from the rugose bauplan to the bauplan of *Calceola* and *Goniophyllum*. The soft body of a rugose coral consists of a gastrovascular cavity that is filled by water, an actinopharynx that closed in a valve-like manner, internal single mesenteries that act as tethers between the oral disc, pedal disc, and body wall, and tentacles that are formed on the oral disc at the sites of the mesenteries. During their individual development, new mesenteries are added only in four insertion zones. Septa and mesenteries behave like casts and moulds and as a consequence septa are added only in the four zones where new mesenteries are inserted. This arrangement of the soft body of the Rugosa causes structural-functional limitations for their evolution and for their abilities to form colonies or reefs. But in some cases structural-functional limitations open new evolutionary pathways. The examples of the lid corals represent such new pathways in evolutionary transformation of the rugose bauplan. *Calceola* as well as *Goniophyllum* evolve by quite simple modifications of the general bauplan of a rugose coral. Their peculiar shapes, the lids and especially the even hinges between the calyx and the lid(s) are caused only by mechanical necessities. Under special conditions (such as high sedimentation rates) these bauplans represent suitable survival strategies.

**Classification and distributional trends within the punctate orthide brachiopods**

David A.T. Harper

Geological Museum, University of Copenhagen, Øster Voldgade 5-7, 1350 Copenhagen K, Denmark

e-mail: dharper@savik.geomus.ku.dk

Cladistic organization of the dalmanellid brachiopods, involving over 150 genera and based on 42 coded characters, has provided a testable classification for the suborder; nevertheless the analysis indicates the homoplastic development of many features, dictated by functional considerations, locally within parts of the clade. Two superfamilies the Dalmanelloidea and the Enteletoidea are recognized on the basis of their contrasting cardinalia and include 14 and six families, respectively; both shared a common ancestor probably during the mid-late Cambrian. When matched with stratigraphical data both Relative Completeness and Stratigraphical Consistency indices for the dalmanellid clade are high and statistically significant. Investigation of biodiversity within the suborder reveals a major spike during the late Ordovician with subsidiary peaks during the early and mid Devonian associated with first the colonization of deeper-water habitats and second radiations in carbonate environments. Diversity stabilized during the late Palaeozoic when only three groups, the rhipidomellids (dalmanelloid), enteletids and schizophoriids (enteletoids), survived; all three taxa show some similarities in having biconvex profiles, deep notothyrial cavities and large muscle scars.

**The reliability of micropalaeontological data: an example from the Kimmeridge Clay of Dorset**

Andrew S. Henderson, Norman MacLeod, N. and S. J. Culver

Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

e-mail: A.Henderson@nhm.ac.uk

Biostratigraphical and palaeoenvironmental interpretations based on micropalaeontological assemblages generally assume that surface or sub-surface point samples are representative of the heterogeneous complex of species populations that comprise foraminiferal assemblages.

To investigate the reliability of such assumptions, a replicate-based sampling scheme was devised to study temporal and spatial variation in benthic foraminiferal assemblages from the type sections of the Kimmeridge Clay and from adjacent boreholes drilled as part of the NERC Special Topic Rapid Global Geological Events (RGGE). This sampling scheme allows direct measurement of the degree to which core samples are representative of the assemblages they sub-sample.

Multivariate analysis of census data from over 300 samples indicates significant vertical and horizontal variation over small scales (cm to m) in outcrop and significant variation between outcrop and core (5 km from the type section). Thus, faunal patterns obtained from surface or sub-surface point samples can reflect a localised subset of the range of assemblage patterns existing within a lithological unit. A fuller understanding of the types of distribution patterns that occur at a variety of spatial scales may be necessary before biostratigraphical and palaeoenvironmental interpretations based on micropalaeontological (and, indeed, macropalaeontological) distribution data are accepted with the level of confidence that we currently employ.

**Benthic foraminiferal response to the development of low oxygen conditions in the Pliensbachian–Toarcian (Lower Jurassic) of North-West Europe**

Mark D. Hylton

Department of Geological Sciences, University of Plymouth, Drake Circus, Plymouth, Devon PL4 8AA, UK

e-mail: M.Hylton@plymouth.ac.uk

Whilst the existence of a minor extinction event in the Early Jurassic has been confirmed by analyses of upper Pliensbachian and lower Toarcian macrofaunas, the microfaunal response has not received as much detailed attention.

High resolution sampling of Pliensbachian–Toarcian intervals in the United Kingdom, southern France and south-west Germany has revealed a fundamental turnover in the foraminiferal assemblages in the Toarcian *FalCIFerum* Zone during which many foraminiferal taxa became extinct.

Whilst large scale benthic foraminiferal trends have been previously identified, this study has revealed the existence of opportunist or disaster foraminiferal species. These species occur during times of environmental stress and exploit available habitat space for short periods of time. Uniserial forms such as *Nodosaria*, *FronDICularia* and *Lingulina* which dominate Pliensbachian assemblages become less important in Toarcian and subsequent assemblages whilst the coiled forms like *Lenticulina* dominate after the event. Generalists, e.g. *Lenticulina*, most probably had certain adaptations that allowed them to survive low oxygen conditions and contribute to the rapid recovery that started in the *falCIFerum* Subzone (*FalCIFerum* Zone) of the Early Toarcian.

The response of benthic foraminifera during the late Pliensbachian–early Toarcian interval can be linked to the changes in sea-level and the resulting development of low oxygen conditions.

**Developmental mode and macroevolutionary correlates in temnopleurid echinoids**

Charlotte H. Jeffery\* and Richard B. Emler

Oregon Institute of Marine Biology, University of Oregon, PO Box 5389, Charleston, OR 97420, USA

e-mail: cjeffery@darkwing.uoregon.edu

It is widely accepted that developmental strategy is closely linked with a number of biogeographical and macroevolutionary correlates, such as geographical range, geological longevity, speciation rate and survivorship at times of mass extinction. Many of these claims are anecdotal and none has been tested within a rigorous phylogenetic framework. Echinoids are unusual amongst marine invertebrates in that developmental mode can be simply and unambiguously deduced from examination of the adult test. The temnopleurid echinoids embrace taxa exhibiting all three primary modes of development: planktotrophic, lecithotrophic and brooded. A phylogeny of the temnopleurids is presented which allows an estimation of the number of times nonplanktotrophy has arisen in this group and enables the investigation of the links between larval type and macroevolutionary correlates.

**Quaternary reefs of eastern Sicily: growth history and control in a tectonically active region**

Stephen Kershaw

Department of Geography and Earth Sciences, Brunel University, Uxbridge, Middlesex, UB8 3PH, UK

e-mail: Stephen.Kershaw@Brunel.ac.uk

Uplifted Quaternary reefs on the eastern Sicily coast are frameworks of coralline algae and vermetid gastropods as veneers on steep bedrock surfaces. Reefs grew while sea level changed, so they are not biotically zoned. The reef at Aci Trezza near Catania grew in the early Holocene sea-level rise on eroded early Etnean basalt, and has a very complex growth history, seemingly involving interplay of tectonic and sea-level control, but finally underwent tectonic uplift over the last *c.* 8000 years, dated from boring bivalves. 40 km north, at Capo Sant Alessio, the upper surface of a reef coincides with a bedrock notch previously dated at *c.* 5000 y, representing the mid Holocene quasi-stillstand and the oldest age of this reef. The reef was simply uplifted in later Holocene times. 10 km south of Capo Sant Alessio, at Capo Sant Andrea near Taormina, an (algal) reef grew on the 45 degree dip of an eastward-dipping old fault plane in limestones associated with the Malta Escarpment-Messina fault system. The reef extends to *c.* +12 m, but is notched at *c.* +5 m (= *c.* 5000 y) and presumably grew during early Holocene times. It was drowned and buried in micrite prior to uplift. Sediments in contact with the fault do not show strain, so apparently it has not moved for a few thousand years. At Capo Milazzo peninsula in north-eastern Sicily, a coral from +2 m, previously dated at 6270±140 y BP, indicates either a small uplift, or a more complex history of uplift and subsidence. Observations from the biota in these four sites, combined with the fact that bedrock notches between Catania and Milazzo show poor correlation between sites, except over short distances. The reefs are therefore a useful tool to demonstrate differential uplift in eastern and north-eastern Sicily, to assist tectonic models of the region.

**Temporal separation of basin restriction and the latest Palaeocene warm water pulse in the North Sea: high resolution palynofacies data**

Adrian King

School of Ocean and Earth Science, University of Southampton, Southampton Oceanography

Centre, European Way, Southampton, SO14 3ZH, UK

e-mail: Adrian.King@soc.soton.ac.uk

The terminal Palaeocene of the North Sea Basin is characterized by a number of important events. In particular, there is evidence of the widely documented late Palaeocene warming and a phase of maximum basin restriction. Well 22/10a-4, situated in the Everest Field of the Central North Sea, yielded more than 100 m of continuous, well preserved core, representing a continuous section through the late Palaeocene Maureen, Lista and Sele formations of Knox and Holloway (1992). The stratigraphical interval of interest in Well 22/10a-4 spans the Lista/Sele boundary and the Sele Formation.

The palynofacies assemblages show a significant change at the Lista/Sele boundary from a sparse assemblage dominated by black (oxidized) wood in the green, bioturbated claystones of the Lista Formation to a more diverse assemblage dominated by brown (unoxidized) wood in the dark grey to black laminated mudstones of the Sele Formation. This significant palynofacies change reflects a change from well oxidized, open marine conditions in the Lista Formation to restricted, anoxic conditions in the Sele Formation. The tectonic event causing the significant restriction of the North Sea Basin is clearly temporally separated from the late Palaeocene warming, which in Well 22/10a-4 is indicated both by an influx of the warm water wetzelielloid dinocyst *Apectodinium* and para-tropical pollen, which first appear in the Sele Formation, some 15 m above the Lista/Sele boundary.

The preliminary data collected therefore indicate that the onset of maximum basin restriction and the late Palaeocene climatic warming are not coeval, being separated by some 15 m of sediment deposition at this locality.

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### **Jurassic vent**

Crispin T. S. Little (1), Taniel Danelian (2), Richard J. Herrington (3) and Rachel M. Haymon (4)  
(1) Departments of Palaeontology and Mineralogy, The Natural History Museum, Cromwell Road, London SW7 5BD, UK  
(2) Department of Geology and Geophysics, University of Edinburgh, Grant Institute, West Mains Road, Edinburgh EH9 3JW, UK  
(3) Department of Mineralogy, The Natural History Museum, Cromwell Road, London SW7 5BD, UK  
(4) Department of Geological Sciences, University of California, Santa Barbara, California 93106, USA  
e-mail: cril@nhm.ac.uk, tdanelia@glg.ed.ac.uk, rmh@nhm.ac.uk

The Figueroa massive sulphide deposit, located in Franciscan Complex rocks in the San Rafael Mountains of California, preserves the only known Jurassic hydrothermal vent fossils. The Figueroa fossil assemblage is specimen-rich but of low diversity and comprises, in order of decreasing abundance, vestimentiferan worm tubes, the rhynchonellid brachiopod *Anarhynchia* cf. *gabbi* and a species of ?nododelphinulid gastropod. The Figueroa community of animals lived at a deep-water, high-temperature vent site located on a mid ocean ridge or seamount at equatorial latitudes. The fossil vent site was then translated north-westward by the motion of the Farallon Plate and subsequently accreted to its present location. An iron-silica exhalite bed, the probable lateral equivalent of the Figueroa deposit, contains abundant filamentous microfossils with two distinct morphologies and probably represents a lower temperature diffuse flow environment. This is stratigraphically overlain by a 15 m thick sequence of bedded cherts containing early Jurassic radiolarians. The Figueroa fossil community was subject to the same environmental conditions as modern vent communities but it is unique amongst modern and other fossil vent communities in having rhynchonellid brachiopods.

### **Acid rain and Strangelove oceans over the Cretaceous Tertiary Boundary**

Barry Lomax (1), David Beerling (1) and Garland Upchurch (2)  
(1) Department of Animal and Plant Sciences, University of Sheffield, Alfred Denny Building, Western Bank, Sheffield S10 2TN, UK  
(2) Department of Biology, Southwest Texas State University, San Marcos TX 78666, USA  
e-mail: BOP97BHL@sheffield.ac.uk

Mass extinction of marine phytoplankton following the Cretaceous Tertiary (K-T) boundary event resulted in the collapse of the carbon isotope depth gradient in marine sections, the so called strangelove oceans. Coal and clay samples from the Raton Basin, New Mexico spanning the K-T boundary were examined for isotopic and elemental ratio variations. Results show a sudden positive  $\delta^{34}\text{S}$  excursion at the boundary and a large increase in the concentration of sulphur as shown through C/S and S/N elemental ratio analysis. A large negative  $\delta^{13}\text{C}$  excursion occurring after the K-T boundary is also detected. These events are interpreted as evidence for sulphuric acid rain and marine extinction driven degassing of  $\text{CO}_2$  as proposed under the strangelove ocean model.

**Fracture and osteomyelitis in PII of the second pedal digit of *Deinonychus antirrhopus* (Ostrom) an Early Cretaceous 'raptor' dinosaur**

Cynthia Marshall (1), Daniel Brinkman (1), Richard Lau (2) and Karl Bowman (3)

(1) Yale University, New Haven, CT, USA

(2) Cheshire Veterinay Clinic, Cheshire, CT, USA

(3) North Carolina State University, Raleigh, NC, USA

e-mail: [cynthia.marshall@yale.edu](mailto:cynthia.marshall@yale.edu)

We report here on a healing transverse, displaced, midshaft fracture of PII of the second pedal digit of Yale Peabody Museum 5205, the type specimen of *Deinonychus antirrhopus* (Ostrom). The affected phalanx bore the sickle-shaped talon for which the animal is named.

Radiographic examination of the fossil shows a caudal and ventral displacement of the distal fragment. The presence of osteomyelitis is supported by lytic areas at the fracture site with evidence of a sequestrum. Oblique views provide no evidence of longitudinal fracturing. Radiographs support the diagnosis of a fracture due to bending, which is compatible with damage during a slashing motion of the talon. However, pathologic fracture subsequent to primary osteomyelitis cannot be ruled out at this time.

Sufficient stability/immobility allowed partial healing to occur prior to the animal's death, as evidenced by lack of callous, remodelling and smoothing of dorsal and medial sides. That this animal survived for an unknown length of time with an injury to one of its purported major defence and food-gathering mechanisms may support Ostrom's analysis of gregarious/pack-hunting behavior for *Deinonychus*.

**The link between sea levels and climatic change in a non-glacial world: evidence from the Palaeozoic sequence of the Falkland Islands**

John E. A. Marshall

School of Ocean and Earth Science, University of Southampton, Southampton Oceanography Centre, Empress Dock, European Way, Southampton S014 3ZH, UK

e-mail: [jeam@mail.soc.soton.ac.uk](mailto:jeam@mail.soc.soton.ac.uk)

Palynomorphs have been found throughout a section in West Falkland. This section is, to date, the best and in fact only known high latitude palynostratigraphical reference section. These palynological assemblages contain a number of readily identifiable spores and chitinozoans which are known from both Laurasia and/or north Gondwana and which can be used to assign ages. But it is apparent that not only does assemblage composition differ in comparison with north Gondwana and Laurasia but that the inception of key marker spores can be much delayed. This can be seen from comparison of microfossils, chitinozoans and spores in the lower part of the Emsian Fox Bay Formation.

Within the West Falkland Group the key correlative horizons are the transgressive shales. As such the West Falkland Group can be correlated and sub-divided in the same way as the correlative Bokkeveld and Witteberg groups in South Africa. As recognized within South Africa, these shale horizons represent elements of a sea level curve and provide the method for more precise extra-Gondwanic correlations. Within each marine incursion the spore assemblages become more diverse and show the inception of species known from lower Devonian latitude. As such the linkage between sea level and climate change can be recognized. This high latitude observation is potentially very significant in our understanding of the mechanism for Devonian sea level change.



**Ectoparasites on a Cretaceous feather**

David M. Martill and Paul Davis

School of Earth, Environmental and Physical Sciences, University of Portsmouth, Burnaby Building, Burnaby Road, Portsmouth PO1 3QL, UK

e-mail: David.Martill@port.ac.uk

A vaned feather from the Nova Olinda Member of the Crato Formation of north-east Brazil has eggs of a probable ectoparasite distributed over the surface of the vane, barbs and barbules. The spherical eggs are operculate and in a few cases the operculum is missing, revealing a circular opening. The eggs are 70  $\mu$ m in diameter and appear to be smooth. There are at least 260 eggs spread over most of the feather surface, although there are some clusters of eggs. Preservation of both the feather and the eggs is as a reddish brown limonitic replacement typical of weathered sections of the Nova Olinda Member. The size of the eggs precludes them from being from mallophagans (feather chewing lice); rather the size is more comparable to that of avian parasitic mites.

The presence of ectoparasites on a feathered tetrapod from the Mesozoic indicates a long history of parasite-host co-evolution. The recent discovery in China of non-avian dinosaurs with feathers suggests that birds may have inherited some of their feather utilizing parasites from theropod dinosaurs. We speculate that the evolution of feathers in some theropod dinosaurs may have initially been a response to dermal parasitism rather than for insulation or flight.

**Microevolutionary transitions in a lower Ordovician pelagic trilobite lineage**

Tim McCormick

Division of Earth Sciences, Gregory Building, University of Glasgow, Glasgow G12 8QQ, UK

e-mail: mccormic@geology.gla.ac.uk

Microevolution patterns are typically characterized in terms of the end-member cases of punctuated equilibria and phyletic gradualism. If punctuational evolution is, as usually described, the result of allopatric processes, then gradualism can be predicted to occur in organisms not prone to such processes; i.e. organisms whose population structure and environment tend to preclude formation of peripheral isolates. Pelagic marine animals are prime candidates.

The trilobite *Carolinites* has been convincingly shown to have been epipelagic. A recent analysis of its visual geometry underlined this interpretation. *Carolinites* occurs with greater or lesser abundance at some 11 horizons spanning Ross-Hintze shelly fossil zones H (Ibex) to M (lower Whiterock) in the lower–middle Ordovician succession at Ibex, western Utah, a succession which itself meets the necessary geological requirements for an evolution case study.

Geometric morphometric analysis suggests that the visual impression of transitional change in the lineage is the result of subtly (sometimes less subtly) changing allometries affecting different parts of the exoskeleton. ‘Allometric pedomorphic’ and ‘allometric peramorphic’ processes affect different structures. The case study highlights a number of issues of importance in characterizing evolution patterns, and in particular the difficulty of quantitatively demonstrating gradualistic change.

**Biostratinomy of *Uintacrinus* Lagerstätten: Upper Cretaceous of Kansas and Colorado, USA**

David L. Meyer (1), Clare V. Milsom (2) and Andrew Webber (1)

(1) Department of Geology, University of Cincinnati, Ohio 45221, USA

(2) School of Biological and Earth Sciences, Liverpool John Moores University, Byrom Street, Liverpool L3 3AF, UK

e-mail: c.v.milsom@livjm.ac.uk

New, well-documented field occurrences in Kansas and Colorado, in laminated chalk (Niobrara Formation) and black shale (Mancos Shale) respectively, and re-examination of museum collections, have provided new information pertaining to the biostratinomy of *Uintacrinus* assemblages. In both facies, dense aggregations are preserved as thin lenses with articulated calyces and arms only on the lower surface, in contrast to disarticulation on the upper surface. Calyces may be imbricated within a lens and are mostly compressed laterally but specimens may also be preserved oral side up or down. Some specimens displaying the oral side retain soft part preservation of the tegmen, anal tube and ambulacra. Several aggregations display a spoke-like pattern in which arms are aligned towards the centre of the slab, suggesting inward collapse of crinoids with arms entangled centripetally. The dense aggregations also reveal a number of new preservational observations, including marginal indentations, hyporeliefs and reversal of typical upper surface disarticulation. These features indicate the likely occurrence of a cyanobacterial component of necrolytic origin which may have provided cohesion, explaining many of the taphonomic features. Microbial sealing during decay may help to explain other instances of similar crinoid preservation, including both benthic and pelagic forms, in which articulation is confined to lower surfaces.

**Supposed *Scomberomorus saevus* (Scombridae, Teleostei) hypural plates from the lower Tertiary, and scombrid relationships**

Kenneth A. Monsch

Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queens Road, Bristol BS8 1RJ, UK

e-mail: Kenny.Monsch@bristol.ac.uk

*Scomberomorus saevus* is a fish species from the family Scombridae, described from the Palaeocene and Eocene. Some of the hypural plates (bones from the tail region) used to describe this species and other specimens of hypural plates, that fit the descriptions of *S. saevus*, proved to be different scombrid genera and species. Hence, the validity of *Scomberomorus saevus* is questioned. The material includes a new fossil species of *Acanthocybium* and a species of a new bonito genus. This new genus provides evidence for a sister group relationship between bonitos and Spanish mackerels, with the Spanish mackerels as the plesiomorphous sister group.

**Direct correlation between the Llandovery-Wenlock (Silurian) chitinozoan and graptolite biostratigraphical schemes**

Gary L. Mullins, School of Earth, Environmental and Physical Sciences, University of Portsmouth, Burnaby Building, Burnaby Road, Portsmouth PO1 3QL, UK

e-mail: Gary.Mullins@port.ac.uk

The Banwy River section (mid Wales, UK), palaeogeographically situated close to the shelf edge, contains graptolites from the upper Llandovery-lower Wenlock series (*?turriculatus*) *crispus* to *riccartonensis* graptolite biozones (Loydell and Cave 1996). The Llandovery-Wenlock series bound-

ary (as currently defined) has been identified for the first time in the UK in the graptolitic facies of Banwy River and graptolites have enabled correlation with sections in Bohemia and Scandinavia.

Samples from known graptolite biozones have been processed for the recovery of Chitinozoa to enable the direct correlation between the graptolite biostratigraphical scheme and the chitinozoan biostratigraphical scheme. This study has enabled the first direct correlation between the base of the *Margachitina margaritana* Biozone and the graptolite biostratigraphical scheme and it also provides further evidence to suggest that the base of the *Angochitina longicollis* Biozone occurs in strata younger than previously thought.

The direct correlation between the *margaritana* chitinozoan Biozone and the graptolite scheme also indicates that the base of the Wenlock Series may correlate with an older graptolite biozone than currently defined (the base of the Wenlock Series is presently considered to be coincident with the base of the *centrifugus* graptolite Biozone).

Loydell, D. K. and Cave, R. 1996. The Llandovery-Wenlock boundary and related stratigraphy in eastern mid-Wales with special reference to the Banwy River section. *Newsletters on Stratigraphy*, **34**, 39–64.

#### **The Silurian of Gotland - a 'Fossil-Lagerstätte' of Palaeozoic calcareous micro- and nanofossils**

Axel Munnecke (1), Thomas Servais (2), and Daniel Vachard (2)

(1) Institut für Geowissenschaften - Geologie, Olshausenstraße 40-60, D-24118 Kiel, Germany

(2) Université des Sciences et Technologies de Lille, U.F.R. Sciences de la Terre - Bât. SN 5, F-59655 Villeneuve d'Ascq Cedex, France

e-mail: Munnecke@email.uni-kiel.de, Thomas.Servais@univ-lille1.fr,  
Daniel.Vachard@univ-lille1.fr

The Silurian of Gotland, Sweden, consists of about 450 m of carbonate sediments accumulated in a warm epicontinental sea near the Silurian equator. The strata never underwent tectonic stress or deep burial conditions. Therefore, the sediments show only minor late diagenetic alteration and an excellent preservation of microfacies characters and fossils, particularly those with originally calcitic skeletons. With the aim to understand the formation of micritic limestones and the development of limestone-marl alternations several hundreds of polished, slightly etched rock samples from the Silurian of Gotland were investigated with the SEM. One of the most surprising results of these investigations was the discovery of excellently preserved calcareous micro- and nanofossils, most of which remained unknown to date. Only few morphotypes can be assigned with varying degrees of confidence to organisms which are described in literature. These are possible ancestors of the foraminifera and diverse algal remains. Additionally, very abundant small spherical calcitic microfossils ('nannospheres' and 'calcispheres') and several other enigmatic groups of microorganisms ranging in size between 5 µm and 100 µm have been observed. The importance of these calcareous micro- and nanno-organisms in the production of Palaeozoic carbonate muds is so far unknown and needs further investigations.

**Clio's revenge: using historical data to explore tree-based historical reconstructions**

Paul David Polly

Department of Anatomy, St Bartholomew's and the Royal London School of Medicine and Dentistry, Queen Mary & Westfield College, London E1 4NS, UK, and Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

e-mail: d.polly@qmw.ac.uk

Historical explanations should never be confused with historical data themselves. Some new approaches in evolutionary biology invoke history in the form of phylogenetic trees when making among-species comparisons. Such historical reconstructions are used to explain correlations, character distributions, and other observations in extant taxa. But these reconstructions do not draw directly on historical data. Palaeontological data can potentially falsify such hypotheses.

A phylogenetic tree of fossil carnivorans (Viverravidae, Eutheria) from North America was used to explore this possibility. Branches of the tree were 'pruned' at the early Eocene and the resulting 'tips' were treated as extant taxa in calculating ancestor-node reconstructions. The reconstructions were compared with the actual palaeontological samples hypothesized to lie at those tree-nodes.

This experiment highlights several points: the original reconstruction methods are extremely sensitive to tree-topology, to the extinction of taxa, and to estimates of time-since-divergence; the addition of palaeontological data counterbalances these, but introduces phylogenetic issues about whether fossil samples fall at tree-tips or tree-nodes and statistical issues with comparing estimated means with sample means.

**Feeding mechanisms and the evolution of jawless fish**

Mark A. Purnell

Department of Geology, University of Leicester, University Road, Leicester LE1 7RH, UK

e-mail: map2@leicester.ac.uk

Probably the most widely held view of the early evolutionary history of the vertebrates explains diversity changes as a classic Darwinian struggle driven by competition for food resources. Jawless vertebrates radiated by outcompeting potential rivals for food or by moving into unoccupied niches; they in turn were outcompeted and replaced by gnathostomes with superior feeding mechanisms. Unfortunately, there are almost no data to support this scenario, and recent work raises serious doubts. These hypotheses of competition rely heavily on interpretations of the feeding mechanisms employed by extinct agnathans, and these are poorly known. Speculation regarding feeding in heterostracan fishes, for example, ranges from predation to mud grabbing, microphagous suspension feeding, deposit feeding, algal frond snipping, algal scraping, plankton feeding, detritivory, or sea-bottom mud ploughing. Similarly, anaspids have been interpreted as microphagous suspension feeders, suction feeders or macrophagous predators with a rasping tongue. This range of confusing and contradictory opinions has developed because of the scarcity of evidence for feeding mechanisms, and a lack of constraint in analyses of agnathan functional morphology. Rather than relying on analogies with extant jawless fish, direct analysis of functional morphology in extinct agnathans allows constrained and testable hypotheses of feeding mechanisms to be proposed.

**Microframe reefs built by calcified microbes, middle Cambrian, Jinan, North China**

Robert Riding (1), Huiming Bao (2, 3), and Xinan Mu (2)

(1) Department of Earth Sciences, Cardiff University, Cardiff CF1 3YE, UK

(2) Nanjing Institute of Geology and Palaeontology, Academia Sinica, 39 East Beijing Road, Nanjing, China

(3) present address: Department of Geological and Geophysical Sciences, Princeton University, New Jersey, USA

e-mail: [Riding@cardiff.ac.uk](mailto:Riding@cardiff.ac.uk)

Mid Cambrian reefs with microframe structure built by calcified microbes, probably cyanobacteria, are well-exposed in the Zhangxia Formation near Jinan in Shandong Province. Members of the *Epiphyton*, *Renalcis* and *Girvanella* groups are almost solely responsible for a series of extensive biostromes, individually up to 15 m thick, in which metazoans are scarce. These reefs are surrounded by coarse cross-bedded oolite-pisolite, reflecting rapid growth in a high-energy environment.

The two main reef lithotypes present are: (1) matrix-rich *Tarthinia-Tubomorphophyton* thrombolite-dendrolite microclusters, and (2) *Gordonophyton-Razumovskia* thrombolite microframes. The latter were created by rectilinear arrangement of prostrate and vertical microbial filaments, and the small (millimetric) size of the cavities contributed to framework strength.

Similar, but usually less well-preserved, mid-late Cambrian reefs appear to be widespread in Asia and North America. These North China examples establish microbial microframes as a distinctive reef-structure, and show that frame-building continued during the Cambrian despite archaeocyath demise.

**Volcanically mediated plankton blooms in the Silurian of the Southern Uplands**

Sue Rigby and Sarah Davies

Department of Geology and Geophysics, University of Edinburgh, West Mains Road, Edinburgh EH9 3DT, UK

e-mail: [suerigby@glg.ed.ac.uk](mailto:suerigby@glg.ed.ac.uk)

At Thirlestane Score, in the Southern Uplands of Scotland, the occurrence of graptolites corresponds closely with the occurrence of particular lithologies. All graptolite bearing horizons cluster around bentonite layers, and are found as a couplet of distinct populations. In the lower element of the couplet, which is found in a bioturbated, beige coloured and nodular layer, the graptolites are common, siculae are abundant, specimens are generally small and populations show a straight survivorship curve. In the upper element of the couplet, a dark coloured, laminated layer, the graptolites are relatively rare, siculae uncommon, specimens large and populations show a convex survivorship curve. The rest of the section appears to be barren.

The ingress of ash into the system seems to have stimulated primary productivity and hence graptolites. The beige couplet population pattern is consistent with an unstable environment, such as would be expected in a nutrient rich system (Rosenzweig, 1971). The upper element of the couplet has a pattern consistent with lower nutrient levels creating a more stable system. The most likely nutrient being added by ash falls is iron, suggesting that macronutrients were available in the system.

Rosenzweig, M. L. 1971. Paradox of enrichment: destabilisation of exploitation ecosystems in ecological time. *Science*, **171**, 385–387.

**Miocene palaeotemperatures of the Mediterranean region from zooxanthellate corals: application of the diversity-energy relationship**

Brian R Rosen

Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

e-mail: b.rosen@nhm.ac.uk

Fossil corals have long been used for palaeoenvironmental interpretation using simple uniformitarian qualitative extrapolation from the restriction of many extant taxa to warm shallow tropical marine waters. A preliminary attempt is made here to derive actual palaeotemperatures from the Miocene coral record of the Mediterranean region by invoking the 'energy hypothesis'. This is an inference from the empirical relationship (known in a variety of marine and terrestrial groups) of taxonomic richness to climate (ultimately solar energy input), e.g. richness of modern zooxanthellate coral genera increases in relation to mean prevailing temperatures.

A Miocene palaeotemperature curve based on 15 Mediterranean coral localities is generated from this relationship. Results show an overall cooling, with warmest conditions (c. 20°C) in the early Miocene. From the mid Miocene to late Miocene, climate cooled at an accelerating rate through about 4.5°C. This trend matches oxygen isotope evidence surprisingly well, although the coral-derived cooling lags behind the isotope curve by about 5 Ma. Reasons for this and other anomalies will be discussed, particularly with respect to dating and increasing biogeographical isolation of the Mediterranean over this time.

**Fire ecology of Cretaceous vegetation in the Isle of Wight, England and Nova Scotia, Canada**

Andrew C. Scott (1), G. Nicholls (1), J. Cripps (1), Margaret E. Collinson (1) and J. C. Calder (2)

(1) Geology Department, Royal Holloway University of London, Egham, Surrey, TW20 OEX, UK

(2) Department of Natural Resources, PO Box 981, Halifax, Nova Scotia, Canada.

e-mail: a.scott@gl.rhbnc.ac.uk

Fusain (fossil charcoal) is common in early and mid Cretaceous terrestrial sediments in England and Nova Scotia. In the Wealden sediments of the Isle of Wight, England, fusain is abundant in the Vectis Formation. Marginal marine channel sandstones contain abundant conifer wood charcoal, whilst higher in the sequence siltstones within gutter casts on coastal plains bordering fresh-saline lagoons contain charred fern fronds.

In central Nova Scotia in the Shubencadie and Musquodoboit basins, drilling beneath Quaternary cover has shown the presence of mid Cretaceous non-marine sediments filling palaeovalleys. These sediments include lignite horizons which are probably organic-rich sediments rather than true *in situ* peats. Charcoal occurs in many closely spaced layers. Uncharred plants include conifers which have leaves with xeromorphic characters such as sunken stomata and papillae. Charred plants include ferns and conifers which indicate the occurrence of crown, understorey and possibly surface fires. Evidence of post-fire soil erosion comes from the presence of large quartz grains in the lignite and diverse arthropod coprolites including those from termites.

Growth rings in conifer charcoal from Nova Scotia and England and from permineralized woods from England show evidence of a seasonal climate. Fire appears to have been a frequent feature in these two areas. Homogenized cell walls of the woods indicate charring temperatures greater than 275°C.

In the Isle of Wight evidence suggests the occurrence of conifer woodlands and fern dominated 'prairie'. In Canada the ferns and conifers appear more mixed but fern dominated horizons may indicate that fire frequency prevented the re-establishment of the climax vegetation. The occurrence of charcoal in such contrasting geological settings in the early-mid Cretaceous emphasizes the importance and significance of regular wildfires in pre-angiosperm dominated vegetation.

### **Explaining the Quaternary paradox**

Peter R. Sheldon

Department of Earth Sciences, The Open University, Walton Hall, Milton Keynes MK7 6AA, UK

e-mail: P.R.Sheldon@open.ac.uk

"The current facts and understandings of population genetics would be thoroughly compatible with major changes in the adaptations of most lineages of animals and plants during the last million years. Instead, a large proportion of Recent species are essentially identical to their Pliocene ancestors." (George C. Williams, 1992, *Natural Selection*, p. 131). According to the Plus ça Change Model, morphological stasis over geological timescales tends to arise not from the stability of physical environments, but from their *instability*. Because of the Quaternary climate upheavals, many of today's species may be relatively inert to environmental twists and turns. They are generalists in a long-term, non-ecological sense, with properties that have enabled them to survive with little change throughout wide fluctuations in various aspects of the physical environment for about 2 million years. Were it not for human influences, relatively little microevolution might be occurring world-wide: indeed, most reported cases of rapid microevolution in macroorganisms today are in new environments associated with human activity. Although the climate of the last 10000 years has been relatively stable, this interval has not been long enough to relax the influences promoting net stasis.

Of course, many fossil lineages also show approximate stasis at times other than the Quaternary. According to the model, this is because most of the fossil record comes from dynamic shallow marine environments, whereas the relatively stable environments in which gradualism tends to occur (such as on land in the tropics and in the deep sea) are rarely represented.

### **Evolution in a fluctuating environment**

Andy Swan

Centre for Earth and Environmental Science Research, School of Geological Sciences, Kingston University, Kingston-upon-Thames KT1 2EE, UK

e-mail: gl\_s402@crystal.kingston.ac.uk

As a population of organisms evolves towards a hypothetical optimum morphology, the range of variation in the population will increasingly straddle the optimum. Consequently, the rate of evolution declines gradually, with a convex curve, until the mean morphology equals the optimum. If the environment is fluctuating, the optimal morphology fluctuates accordingly. This has the effect of sampling a range of evolutionary rates and the convexity of the curve results in this sampling producing a slower mean rate of evolution. This effect can be seen in genetic algorithm simulations. The implication is that evolution will be slower in climatic zones, environments or times when conditions fluctuate; comparisons can be made with Sheldon's (1996) 'plus ça change' hypothesis, which predicts stasis under these conditions.

**Permian non-marine ichnofaunas from the Falkland Islands; the South Africa connection**

Nigel H. Trewin

Department of Geology and Petroleum Geology, Meston Building, King's College, University of Aberdeen, Aberdeen AB24 3UE, UK

Thick Permian deltaic to turbiditic sandstones and mudrocks were deposited in the eastern end of the Karoo Basin of South Africa, and following Mesozoic break-up of Gondwana are now located in the Falkland Islands. The deeper water, off-delta facies which include glacial rhythmite and turbiditic sandstone and shale units locally contain a spectacularly well-preserved ichnofauna.

Characteristic forms are *Umfolozia* arthropod trackways comparable with South African forms, and *Undichna* produced by swimming fish. The *Undichna* traces include a new form as well as abundant *U. bina* which is also characteristic of rocks of the Eccla Series in South Africa.

Other traces present include *Cochlichnus*, *Diplocraterion*, *Haplotichnus*, *Helminthoidichnus*, *Isopodichnus*, *Kouphichnium*, *Planolites*, *Scoyenia*, *Skolithos*, *Stelloglyphus* and several new or unidentified forms.

The assemblages collected strongly resemble those of late Palaeozoic freshwater basins in South America, which are generally assigned to deep water lacustrine conditions. However, it is thought that oxygenation levels and substrate type were the major controlling factors rather than water depth.

**The preservation of bone**

Clive Trueman

Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queens Road.

Bristol BS8 1RJ, UK

e-mail: c.n.trueman@bristol.ac.uk

Fossil bones are fairly common in many sedimentary systems, and have been extensively collected for 150 years or more. However, biogenic apatite is more unstable in pore waters than biogenic (shell) calcite. To be preserved, biogenic apatite must recrystallize to a less reactive mineral.

Despite the huge number of fossil bones found, from a wide variety of locations, very few fossil bones are pseudomorphed by minerals other than apatite. In all cases bones fossilize by recrystallization of biogenic apatite to francolite (carbonate fluorapatite). This recrystallization is pervasive and affects all portions of the bone, but commonly very fine histological detail is preserved.

These observations can be explained by a simple model of bone recrystallization, which requires specific geochemical and hydrological conditions for preservation of bone. These conditions vary both between burial sites and within bones, and affect the relative rates of bone recrystallization and degradation.

Having established a simple model for bone preservation, we are better equipped to predict taphonomic biases, and to select bones for geochemical analysis.



**‘And the small shall inherit the Earth...’**

Richard Twitchett\*

Department of Earth Sciences, University of Leeds, Leeds LS2 9JT, UK

e-mail: R.Twitchett@earth.leeds.ac.uk

The Permian–Triassic strata of East Greenland have yielded an abundant, diverse and exceptionally well-preserved fossil fish fauna. From an evolutionary point of view fish are extremely interesting as they are often said to be unaffected by mass extinction events and may even radiate through such times of global crisis. However, study of the Greenland fauna has shown that these are myths and that fish suffer in a similar way to the rest of the marine fauna.

One very obvious characteristic of the post-extinction Lower Triassic fauna is its very small size. Late Permian species have a mean body length of some 0.5 m, with a number of genera exceeding several metres in size. In contrast, basal Lower Triassic species rarely exceed 0.25 m long (most are around 0.1 m). This ‘Lilliput Effect’ is observed in all other marine organisms at this time: e.g. shelly invertebrates, foraminifera, burrowing infauna etc. In addition, palaeoecological data show that all these fish were benthic or nektobenthic predators. The other major group of nektobenthic vertebrate predators in the Permian–Triassic (conodonts) also show a similar size reduction in the post-extinction fauna. Small size in post-extinction survivors has also been documented in other mass extinctions (for both fish and conodonts).

The reason for this ‘Lilliput Effect’ is unclear. While some authors suggest that animals with large body size may be more prone to extinction events, the data are equivocal. A more likely explanation is that small size develops in response to a prolonged decrease in food supply after the extinction event. Isotopic evidence (low  $\delta^{13}\text{C}$ ) suggests that plankton biomass was much reduced for most of the Griesbachian. A similar isotopic signature also appears after all other mass extinction events.

**The palynology of the upper Wenlock Series (Silurian) of the Much Wenlock and Ludlow areas, Shropshire, England**

Jane Washington-Evans

Department of Environmental Sciences, Room MA 122a, University of Wolverhampton, Wulfruna Street, Wolverhampton WV1 1SB, UK

e-mail: in5741@wlv.ac.uk

The upper Wenlock Series from the Sheinwoodian-Homerian to Homerian-Gorstian boundary includes the upper part of the Coalbrookdale Formation and the Much Wenlock Limestone Formation in the type area. The palynological assemblages are generally well preserved and of low geothermal alteration, with acritarchs, prasinophycean algae, chitinozoans and terrestrial sporomorphs regularly recorded. In most samples, acritarchs are the most abundant palynomorphs present, with *Leiosphaeridia*, *Michrystidium*, *Multiplicisphaeridium*, *Diexallophasis*, *Helosphaeridium*, *Cymatiosphaera*, *Gorgonisphaeridium* and *Veryhachium* the common genera recorded.

**Poikiloaerobic, exaerobic and dysaerobic biofacies – which is correct?**

Paul Wignall

Department of Earth Sciences, University of Leeds, Leeds LS2 9JT, UK

e-mail: P.Wignall@earth.leeds.ac.uk

Many, if not most, organic-rich, laminated shales contain abundant, low diversity assemblages of benthic species often concentrated on discrete bedding planes. Intense debate in the past decade has seen the proliferation of names for this biofacies. For the most part, this discussion reflects a dichotomy in interpretation that was first realised in the debate between Seilacher and Kauffman over the origin of the benthic fossils of the Posidonia Shale of Germany. Exaerobic, quasianaerobic and (the original definition of) dysaerobic biofacies were interpreted to record persistent, but low benthic oxygen levels, whereas poikiloaerobic and episodically dysaerobic biofacies record alternating anoxic and dysoxic benthic conditions. Measurement of pyrite framboid sizes in these biofacies may help to distinguish between these conflicting interpretations.

Modern pyrite framboids are observed to form rapidly in a narrow zone at the top of the sulphate reduction zone (SRZ) where iron oxidation occurs. In euxinic environments, where the SRZ extends into the lower water column, pyrite framboids can only reach small sizes (5  $\mu$ m) before sinking to the seafloor. In contrast, diagenetic framboids from dysoxic environments can grow to considerably larger sizes. Analysis of framboid sizes from the benthos-rich, organic-rich shales of the Kimmeridge Clay (Upper Jurassic, Dorset) reveals that they are dominated by syngenetic framboids with only a tiny proportion of larger, diagenetic framboids. This implies that shale deposition records long-term euxinic conditions interrupted by a few brief oxygenation events of perhaps a few months duration. This interpretation of the Kimmeridge Clay shales is closest to Seilacher's original interpretation of the Posidonia Shale.

## POSTERS

### **New Early Devonian arthropods from the Windyfield Chert, Rhynie, Aberdeenshire, Scotland**

Lyall I. Anderson (1), Nigel H. Trewin (1) and Charles H. Wellman (2)

(1) Department of Geology and Petroleum Geology, Meston Building, King's College, University of Aberdeen, Aberdeen AB24 3UE, UK

(2) The Centre for Palynological Studies, Department of Earth Sciences, University of Sheffield, Dainton Building, Brookhill, Sheffield S3 7HF, UK

e-mail: gmi292@abdn.ac.uk

An intensive drilling and trenching program centred around the Early Devonian Rhynie chert hot spring deposit during the summer of 1997 has provided many new insights into the stratigraphy, sedimentology and palaeontology of this unique style of Konservat-Lagerstätte where early terrestrial land plants and animals are preserved within siliceous sinters. Part of this work involved the location and study of the Windyfield cherts, a similarly hosted, yet apparently discrete hot spring centre some distance from the Rhynie cherts and perhaps at a different stratigraphical level in the local succession. This is reflected in the floral and faunal composition of these beds, which have revealed a new early land plant taxon and a number of new arthropods including whole body fossils and cuticle fragments of millipedes, eurypterids, scorpions, crustaceans and as yet unidentified groups. Cuticular fragments are widespread throughout all chert textures, as well as the enclosing clastic sediments, whilst complete arthropods tend to be concentrated within a discrete layer approximately 20 mm thick which appears to be rich in micro-coprolites. The discovery of these additional faunal elements at Rhynie indicates a broad compositional similarity between this and other preserved early terrestrial ecosystems such as Alken an der Mosel, Germany and Gilboa, USA.

### **Vertebrate taphonomy of the Cromhall Quarry palaeokarst**

Byron Blessed

Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol BS8 1RJ, UK

e-mail: BB7503@bristol.ac.uk

### **A pseudoplanktonic inarticulate brachiopod attached to graptolites and algae**

Joseph P. Botting and A.T. Thomas

School of Earth Sciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK

e-mail: jpb709@ERS.bham.ac.uk

Small inarticulate brachiopods from graptolitic facies have typically been interpreted as pseudoplanktonic on an unknown, probably algal host. Clusters of valves, sometimes associated with organic stains on bedding planes have supported this conclusion, although an alternative explanation relates to the benthic colonization of decaying algae on the sea floor.

The Upper Murchisoni Shales of the Llanvirn (Darriwillian) of the Builth Inlier of Central Wales contain abundant specimens of the small inarticulate *Schmidtites? micula*. Recent discoveries above a bentonite show clusters of *S. micula* valves associated with the graptolite *Pseudoclimacograptus scharenbergi*. Attachment is either directly to the rhabdosome, or secondarily, via filamentous algae. Clusters of valves with no obvious nucleus, presumably representing a purely algal host, are abundant. Associations do not occur with *Didymograptus Murchisoni*, *Callograptus* sp., an orthoconic nautiloid, or the larger inarticulates, *Palaeoglossa attenuata* and *Monobolina crassa*.

The implications of these specimens include a definite pseudoplanktonic lifestyle for *S. micula*, the recognition of graptolites as a host for Early Palaeozoic pseudoplankton, possible fine-scale depth zonation among the epeiric graptolites, and the importance of ash-fall in the preservation of planktonic associations.

#### **Evolution of the *Turborotalia cerroazulensis* lineage (Eocene planktonic foraminifera)**

Huw Boulton

Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol BS8 1RJ, UK

e-mail: hb7386@bristol.ac.uk

#### **Palaeoecological reconstruction of Lower Cretaceous (Barremian–Aptian) shallow-water coral communities of the Neo-Tethyan Realm**

Nick Clack\* (1), Enzo Insalaco (1) and Brian Rosen (2)

(1) School of Earth Sciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK

(2) Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

Equable climatic conditions coupled with high sea level stands in the Early Cretaceous gave rise to periods of significant coral development on expansive carbonate platforms in the Neo-Tethys. The coral units are frequently laterally extensive and exhibit diverse palaeoecologies, geometries and sedimentary systems. Whilst there have been local studies of Barremian–Aptian coral communities, there has been no attempt to produce an overview. Documentation of a significant number of coral-bearing sequences in Europe and the Middle East will allow the formulation of a regional palaeoecological synthesis.

Field observations in Provence and the French Pyrenées intimate the existence of four groups of coral-bearing units based on geometry and sedimentology: (1) biostromes dominated by shallow-water carbonates; (2) small reefal mounds dominated by shallow-water carbonates; (3) biostromes proximal to, or intimately related with, muddy sediments; and (4) broad reefal mounds closely associated with muddy sediments. The coral and associated faunas studied are subject to laboratory examination to verify taxonomic affinities. Nevertheless, preliminary systematic assignments have revealed that hydnochoroid Scleractinia such as *Hydnophoromeandraraea* sp. and *Eohydnophora* sp. are important components of the communities within each of the above groups.

#### **A morphometric analysis of the hind limbs of flying vertebrates**

Daniel Elvidge.

Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol BS8 1RJ, UK

e-mail: de7397@bris.ac.uk

#### **The diverse angiosperm leaf flora of the Late Cretaceous Antarctic Peninsula**

Peta Hayes

School Of Earth Sciences, University Of Leeds, Leeds, LS2 9JT, UK

e-mail: peta@earth.leeds.ac.uk

In the Late Cretaceous Antarctica was connected to South America, Australia and New Zealand, which allowed the migration of animals and plants across Gondwana. The Antarctic Peninsula, which was an active volcanic arc at about 65°S, was a crucial link during the radiation and diversification of the

angiosperms. Fossil plants from the Hidden Lake Formation (Santonian) and the Santa Marta Formation (Santonian–Campanian) on James Ross Island, east of the northern peninsula, provide new evidence about forests with a diverse angiosperm component flourishing in the region. Although there is no cuticle present, the leaf impressions are excellent and show intricate detail of the leaf architecture.

Many of these ancestral leaf fossils cannot be clearly assigned to modern families. Numerous and subtle variations in angiosperm leaves of the mid and early Late Cretaceous are such that they appear to form a morphological continuum. For this reason multivariate statistical methods were used to cluster the leaves using characters such as the style of the apex and base, angles, marginal features, and primary, secondary and tertiary venation patterns. There are 18 clusters of leaves within the Hidden Lake Formation, representing 18 form genera of Antarctic Cretaceous angiosperms and exposing a diverse polar flora.

### **A conodont, thelodont and acanthodian fauna from the lower Prídolí (Silurian) of the Much Wenlock area, Welsh Borderland**

C. Giles Miller (1) and Tiiu Märss (2)

(1) Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

(2) Institute of Geology, Tallinn Technical University, Estonia Ave. 7, Tallinn EE10143, Estonia  
e-mail: G.Miller@nhm.ac.uk

Conodonts, thelodonts and acanthodians have previously been collected from the Prídolí of the Welsh Borderland from bone beds such as The Ludlow Bone Bed. In general, specimens collected from these types of deposit are very abraded and make taxonomic studies difficult. This poster shows well preserved thelodont microelements from two samples from the Downton Castle Sandstone Formation (Prídolí, Silurian) of the Much Wenlock area of the Welsh Borderland. Head scales, a wide variety of transitional scales, and pore scales of the lateral line sensory canals of the thelodont *Paralogania ludlowiensis* (Gross) are shown for the first time. A new acanthodian *Nostolepis linleyensis* sp. nov. and elements from the apparatus of the conodont *Ozarkodina? hemensis* sp. nov. are illustrated from the same samples. The thelodonts in both samples are typical of upper Ludlow–Prídolí faunas from across the Welsh Borderland, and are also present in smaller numbers in the Ludlow Series of Gotland Island, Sweden, Saaremaa Island, Estonia, and in Latvia and Lithuania. The conodont *O.? hemensis* sp. nov. is restricted to this area of the Welsh Borderland. The co-occurrence of well preserved elements of conodonts and thelodonts suggests that they were deposited fairly rapidly with little or no reworking and that a restricted marine environment prevailed in the early Prídolí in the Much Wenlock area of the Welsh Borderland.

### **Heterochrony in cavusgnathid conodonts and possible paedomorphism of the ‘Granton Animals’**

Mark A. Purnell

Department of Geology, University of Leicester, University Road, Leicester LE1 7RH, UK  
e-mail: map2@leicester.ac.uk

The fossils preserving traces of conodont soft tissues have revolutionized many aspects of the study of conodonts: after more than 100 years of uncertainty and speculation we finally have some understanding of the nature of conodonts as animals. Reconstructions of conodont anatomy are an important component of this new conceptual framework. Not only do these reconstructions satisfy our basic curiosity about a group of enigmatic, extinct organisms, they are a powerful influence on developing

concepts of conodonts as living animals, and reconstructions themselves become the subject of biological interpretation and speculation.

Almost all recent reconstructions of conodonts are based primarily on the best known and best preserved material: the Carboniferous cavusgnathids (*Clydagnathus windsorensis*) from Granton, Scotland. But how well do these few specimens represent the Conodonts as a whole? Analysis of apparatus growth in cavusgnathid conodonts based on the Granton specimens and natural assemblages from Montana, provides strong support for the hypothesis that *Clydagnathus windsorensis* is progenetic (i.e. paedomorphic). This does not call into question any of the key anatomical attributes of conodonts, or their assignment to the vertebrates. Neither does it indicate that the Granton conodonts are larval forms. It does suggest, however, that some details and proportions of reconstructed animals may reflect juvenile morphology rather than that of a typical adult conodont (whatever that may be).

### **Graptolite adolescence – the awkward age**

Lesley Rantell

Department of Geology and Geophysics, University of Edinburgh, West Mains Road, Edinburgh EH9 3DT, UK

e-mail: lrantell@glg.ed.ac.uk

When Graptolites moved from the benthos into the plankton early in the Ordovician, the free-floating planktonic forms rapidly evolved highly organized geometric shapes. Many of these changes were adaptations to life in the open water, and were largely driven by hydrodynamic considerations.

The key to studies of fluid dynamics is the Reynolds number, which determines how a fluid flow behaves. 'Equality of Re does not mean that forces are unchanged, but patterns of flow will be the same even if one fluid is a gas and the other a liquid' (Vogel 1981). This allows valid experimentation using different fluids; in this case air instead of water.

My work to date has focused on *Amplexograptus maxwelli*, using models of early growth stages. I am investigating the effect of proximal spines through the asymmetrical period when the graptolite develops from an individual to a colony. The sicular spines had a profound effect on flow over the model colonies which appears too dramatic to be coincidental, and therefore they are likely to have had a hydrodynamic function. Results indicate that the spines are intended to disrupt vortex formation during the building of th11 and th12 only.

Vogel, S. 1981. *Life in moving fluids*. Willard Grant Press, 352 pp.

### **Natural assemblages of *Phragmodus* and the apparatus architecture of prioniodontid conodonts**

John E. Repetski (1), Mark A. Purnell (2) and Stephanie F. Barrett (2)

(1) U.S. Geological Survey, MS 926A National Center, Reston, VA 20192 USA

(2) Department of Geology, University of Leicester, University Road, Leicester LE1 7RH, UK

e-mail: map2@leicester.ac.uk, SFB4@leicester.ac.uk

The composition of the apparatus of the Ordovician conodont *Phragmodus* is well known, but the number of elements and their spatial arrangement are more problematic. This can only be determined directly from natural assemblages, without which hypotheses of apparatus architecture must be derived from inferred element homologies with Late Palaeozoic taxa assigned to the order Ozarkodinida.

The reliability of this approach is open to question as it is unclear whether architectural and skeletal templates based on ozarkodinids are applicable to prioniodontids such as *Phragmodus*. Similarly, although the architecture of the giant late Ordovician prioniodontid *Promissum pulchrum* is well understood, the degree to which its apparatus reflects the architecture of other prioniodontids remains untested.

Natural assemblages of *Phragmodus inflexus* reveal the architecture of the apparatus. The rostral array comprised nine subparallel, bipennate S elements, above the cusps of which lay a pair of dolabrate M elements. Caudal to the S elements were opposed pairs of Pb and Pa elements, arranged with their long axes almost perpendicular to the long axes of the S elements. This has important implications for the reconstruction of other prioniodontid taxa and the recognition of homologies. The architectural similarities between *Phragmodus* and taxa assigned to other orders support the hypothesis that the conodont apparatus was more conservative than has been thought.

### **The phylogeny of the Ichthyosauria, characters and congruence**

Tamsin Rothery

Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol BS8 1RJ, UK

e-mail: tr7401@bristol.ac.uk

### **Exceptionally preserved dendroid graptolites from Silurian *Konservat-Lagerstätten***

Kate Saunders\*

School of Earth Environmental and Physical Sciences, University of Portsmouth, Burnaby Building, Burnaby Road, Portsmouth PO1 3QL, UK

e-mail: Kate.Saunders@port.ac.uk

Dendroid graptolites have been collected from two *Konservat-Lagerstätten* localities in east central USA: from the Racine Dolomite Formation (Wenlock) at Thornton Quarry, Illinois and the Brandon Bridge Formation (Upper Llandovery) at Waukesha Lime and Stone Quarry, Wisconsin. At Thornton, two dendroid-rich beds have been identified in the non-reef strata below the overlying reef flank beds. Dendroid graptolites at Waukesha are found abundantly in ten beds but are completely absent in others.

The aim of my research is to investigate all aspects of Silurian dendroid graptolites from *Konservat-Lagerstätten*. This will include: taphonomy, to determine the methods of preservation and variations in preservation; and taxonomy, particularly the potential use of ultrastructure in classification. I will also be looking at morphological variation within species and at the affinities of some species of the genus *Inocaulis* which may be marine algae. Further areas of research include palaeoecology, the use of ultraviolet light to reveal soft tissue abnormalities as environmental indicators, and the potential use of dendroid graptolites in biostratigraphy.

### **Crinoid faunas of the Much Wenlock Limestone Formation of the UK**

Rosanne Widdison\*

School of Earth Sciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK

e-mail: R.E.Widdison@bham.ac.uk

The lack of interest in Wenlock Crinoidea in recent years has left the taxonomy of the group in great need of work. A reliable taxonomic framework relies heavily on a thorough understanding of variations among species, something not considered in detail when the majority of taxonomy was done in

the last century. *Marsupiocrinus coelatus* is an example of the variability in arm number commonly observed among the Camerata yet ignored in past studies. The species typically has four arms per ray, 20 arms in total, yet many individuals have two, three, or five arms in any number of rays. Arm gain is very rare among the collections but arm loss, particularly of a single arm per ray, is very common. Studies of the orientation of deformed rays and the distributions among different specimen sizes offer little in the way of an explanation for the variations. Environmental pressures can be ruled out as 'normal' specimens share common attachment sites, and similar sized specimens have different arm numbers. Modern crinoids are known to grow back more arms than they had prior to an attack by a predator. This would provide an explanation for arm gain; however, there are no damaged plates visible in these rays, nor is there any evidence of predation in the case of arm loss.





## Palaeo-Reply C

I was slightly nonplussed to discover Chuck Mitchell's Comment in *Newsletter* **38**. Since most of it was concerned with what he described as "Richard Fortey's ... Quixotic 'Save the British Ordovician' campaign", I am obliged to set the record straight for those members of the Association who may not have followed the developments in Ordovician Series subdivision over the last few years.

The first thing to say is that it is not "Richard Fortey's campaign" at all. Virtually all the published work has been by a team of the most active Ordovician workers in Britain – including Alan Owen, David Harper, Keith Ingham, Adrian Rushton, and many others. The summary of British Series as we now understand them was published in the *Geological Magazine* **132**, 15-30 (1995). My name appears first because I was charged by the Stratigraphy Committee (now Commission) of the Geological Society to head up a team to sort out problems of British Ordovician correlation. I am sure that my co-authors will not find the image of being a kind of collective Sancho Panza very flattering – they have minds of their own, and our discussions were all democratic and even occasionally heated. Nor is this work a "Save the British Ordovician" campaign at all – which makes it sound narrowly chauvinistic and politically motivated. Rather we sought to refine a common language for correlation purposes which still is in use around the world.

All our deliberations were, as we have described it in the paper, "in the interests of international correlation". The British Ordovician Series had served as a global standard for correlation since before the turn of the century – but their definitions of bases were made by the standards of that time (e.g. at unconformities), and were clearly unsatisfactory for modern use. Our intention was both to improve their definition and to serve international correlation. It seems extraordinary to me that Mitchell seems to have missed this intention (the last thing we wanted was "to carry on in our own private language"), and I can only assume he has not read the papers themselves, or reacted excessively to a remark by Graham Budd – who is not part of the Ordovician group, but obviously entitled to his own opinion. I doubt whether any single example of anti-North-American sentiment can be found in the 1995 paper.

The reader might find it useful to see how we have essentially preserved traditional usage, while keeping an eye on international correlatability. Chronostratigraphic units are defined by their bases – and only one of these has changed significantly.

- The TREMADOC is the basal series of the Ordovician and remains so. Its base at the appearance of flabelliform graptolites approximates closely to the hoped-for international definition of the base of the Ordovician.
- The ARENIG base was redefined at or close to the base of the T. *approximatus* Zone, the same horizon that Mitchell recommends in his 'comment'.
- The LLANVIRN base remains where it was – at the base of the D. *artus* Zone (formerly 'bifidus' Zone). This horizon is widely recognisable in Ordovician Gondwana (i.e. over more than half the world's Ordovician deposits).
- The major change concerns the relationship of the LLANDEILO and CARADOC. It has been known since 1972 that in classical usage much of the Llandeilo overlapped the Caradoc. Something had to be done. What we did was to define the base of the CARADOC at the *gracilis* Zone (many workers abroad thought that that was where it was anyway), thus reducing

the scope of the Llandeilo to a stage within an enlarged Llanvirn Series. Barry Webby (1998) – the former chairman of the IUGS Ordovician Subcommittee – considered the gracilis Zone base a favoured candidate for international recognition as a GSSP.

The ASHGILL Series was defined in a section in northern England. We regard the correlation problems of this level as not fully resolved, but recently-investigated sections in South Wales should enable its international correlation.

So far as we can tell, all these units are correlatable widely, and in most cases globally. The British Series can surely serve as “Gondwana” standard at the very least. Most domestic remarks on the redefinitions have commented on their common sense – there has been only one published comment on the most difficult decision relating to the Llandeilo. Rather pompous lectures about ‘esperanto’ in stratigraphy notwithstanding, a British standard has been employed effectively in investigating the major global biological questions of the Ordovician. Our concern was that we should not lose a common language which has proved its utility. Is this a windmill to be tilted at – or a laudable aim to be pursued pragmatically and with an eye on the wider scientific world? We tried for the latter.

Most mystifying of all in Mitchell’s Comment is the feeling that we are in some sense anti-North-America. Most of the rhetoric rather seems to be the other way (are we supposed to be flattered by receiving ‘permission’ to use our Series for local purposes alone?). I assume this must refer to one respect in which I am, genuinely, and on scientific grounds, opposed to an Ordovician Subcommittee decision. This is the decision to base global Middle Ordovician at an horizon at the base of the North American “Whiterockian” (Webby 1998). This is a separate question from that of the Series definitions, and my colleagues may well have a different view than my own. My point is that this horizon is not correlatable into Britain, or indeed most of Ordovician Gondwana. Even so, there’s nothing ‘anti-American’ about it – it’s just a daft decision. I have spent a lot of time in the last five years actually working on the Laurentian Whiterockian in Nevada and Utah, and there are interesting scientific questions there, but politics doesn’t come into them. The austrodentatus horizon – on which Chuck Mitchell and Chen Xu have done such good work – would be a far more acceptable base to the Middle Ordovician in my view. It can be recognised globally, and would do less violence to previous usages.

*Richard A. Fortey FRS*

*Department of Palaeontology, The Natural History Museum, Cromwell Rd, London SW7 5BD, U.K.*

*email: raf@nhm.ac.uk*

*tel: 0171 938 9224*

*fax: 0171 938 9277*

#### Reference

Webby, B.D.E., 1998. Steps towards a global standard for Ordovician stratigraphy. *Newsletters in Stratigraphy*, **36**, 1-33.

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## MEETING REPORTS



### Progressive Palaeontology

University of Plymouth

27th May 1998

Let me start off by thanking Gary Aillud and Mark Hylton for organizing a well run and stimulating conference. I can honestly say that those of you who didn't attend missed some very good talks and a rather excellent lunch. I have to commend all the speakers, who all did a very fine job presenting research that spanned between the Cambrian explosion and Viking toilets; they really showed that there are some exciting research projects underway around the country.

Beatrice Dower came all the way from the University of Pennsylvania to talk about her undergraduate project on exceptionally well preserved cycadophyte leaves from the Jurassic of Skye. She hopes the well preserved nature of the material (as calcite permineralizations in nodules) will provide significant data on the anatomy and structural adaptations of two Orders of cycads, the Cycadales and Bennettitales.

Gareth Dyke (Bristol) introduced us to the problems surrounding the radiation of modern birds (the neornithines). Gareth is looking at the Lower Eocene fauna of the London Clay, which provides one of the earliest, and most diverse, records of modern birds in the Cenozoic. He intends to revise the higher level taxonomy of the London Clay fauna to observe the taxonomical and morphological radiation of modern birds after a major extinction event.

Those of you who were thinking 'whatever can Viking toilets have to do with palaeontology' should have attended the talk by Lucy McCobb (Bristol) on the contents of a 10th Century cess pit in Coppergate, York. Lucy presented the results of a preliminary study of crab apple pips and the early diagenetic changes that they have undergone. Lucy hopes that this research will shed light on our recent history and have implications for our understanding of the ancient terrestrial fossil record.

The possible functions of pterosaur head crests were discussed by Lorna Steel (Portsmouth). Many pterodactyloid pterosaurs possess morphologically variable bony crests, although, as Lorna told us, recent discoveries have shown that some had soft tissue crests supported by bony structures. Lorna is looking into the possible functions of these crests, which appear diverse and were likely to be different between taxa, with perhaps a single taxon having a crest that served several functions.

Karen Cochrane (Birmingham) gave a talk on the apparatus architecture and histology of the Late Cambrian conodonts of the Gallatin Formation (Wyoming). Her research has highlighted that the apparatuses of three genera (*Proconodontus*, *Eoconodontus* and *Cambroistodus*) are more complex than was previously thought, and Karen has also found structures interpreted as vertebrate hard tissue and globular calcified cartilage in related euconodont taxa.

Evolutionary response in the Quaternary was the basis for the talk by Jon Roberts (Kingston). Looking at published data and a new morphometric analysis of ostracodes from high resolution sequences in the Pleistocene and Holocene, Jon is examining the impact that climate has on the rate of evolution.

Stig Walsh (Portsmouth) is working towards a greater understanding of bone-bed formation by examining a new Pliocene bone-bed from Chile. He is looking at the palaeoecology, taphonomy and sedimentology of the bone-bed and also examining the Recent biotope in the surrounding area, which has many similarities with the constituents of the bone-bed, to assess the changes in transition from bio-coenosis to oryctocoenosis.

Aaron O'Dea (Bristol) discussed the changes in size of zooids in colonies of bryozoans as an indicator of seasonality in ancient seas. He has applied the technique of calculating Mean Annual Range in Temperature (MART) to collections of encrusting bryozoans from the upper Pliocene Coralline Crag and from Middle Miocene material from NW France.

Is there life on Mars? Jan Toporski (Portsmouth) hopes to go some way into providing us with an answer in light of the recent "Martian bacteria" debate. Jan is using Atomic Force Microscopy, SEM and TEM techniques to examine the way in which bacteria become mineralized and fossilized. Jan is also looking at terrestrial microfossils, Martian meteorites, and ordinary chondrites, as well as recent Antarctic cryptoendolithic communities.

Trilobites are considered by Trevor Cotton (Bristol) to be the best way of examining the Cambrian explosion. To do this, Trevor is reassessing the systematics of trilobites with cladistic analysis to assess the taxonomic diversity, since many Cambrian taxa are considered to be para- or polyphyletic.

The differences between tropical and temperate carbonates was discussed by Joanne Lucas (Imperial & NHM). Joanne is looking at macrofauna, microfacies, trace elements and oxygen isotopes from the High Tor Limestone of S. Wales to try and assess why temperate water carbonates exist in an area that was positioned in the tropics at time of deposition.

Kate Saunders (Portsmouth) talked about her research on dendroid graptolites from Silurian Konservat-Lagerstätten deposits in Illinois and Wisconsin. Kate is looking at the taphonomy, taxonomy, palaeoecology and potential biostratigraphical use of Silurian dendroids, as well as keeping an eye out for that elusive graptolite animal soft part.

Another Portsmouth speaker, Darren Naish, gave a talk on a femur of a theropod dinosaur from the Wealden of the Isle of Wight. This specimen, which probably comes from a juvenile, has several morphological features similar to those seen only in Triassic and Early Jurassic theropods, suggesting that it is a previously undescribed Lazarus taxon.

The trigonid bivalve genus *Myophorella* is the subject of Andrew Francis' (Birmingham) research. Looking at collections from the NHM and BGS, Andrew has undertaken a detailed morphological study of the genus, which suggests that previous workers have oversplit the genus; Andrew believes that there are only a handful of British Jurassic species.

Wenlock crinoidea are being examined by Rosanne Widdison (Birmingham). Rosanne is looking at Victorian collections of crinoids, which have been little researched, with the intention of updating the taxonomy and also on improving previous descriptions and classifications by incorporating stem morphology.

Fred Titchener (Royal Holloway) brought the session to a close with a talk on galls from the Pliocene of Willerhausen. For those of you who don't know, galls are growths induced in a plant by an animal or plant parasite. Fred showed some wonderful pictures of 3D specimens from Willerhausen and discussed the problematic taxonomy of this group of trace fossils.

Paul Smith brought the meeting to a close by giving thanks from the PalAss council to Gary Aillud and Mark Hylton, the speakers and attendants (of which there were 35). This was followed by a session of relaxing, unwinding and further discussion of people's research in one of Plymouth's fine hostels.

Once again thanks to Gary and Mark for organizing, and to Plymouth for hosting, a very fine Progressive Palaeontology.

*Dr Gary Mullins*

*SEEPS, University of Portsmouth, Burnaby Building, Burnaby Road, Portsmouth PO1 3QL*

## FUTURE MEETINGS OF OTHER BODIES

### **BSRG workshop – Palaeoecological-sedimentological interactions**

Natural History Museum (Len Moore Room), Kensington

*19th December, 1998, 10am – 5.30pm*

The workshop will address the interactions between sedimentology and palaeoecology, by addressing three main questions: (1) What can sedimentology reveal about habitats in the past; (2) How can palaeoecology contribute to the refinement of sedimentary facies interpretations; and (3) Do sediments control organisms or organisms control species?

For more information contact Brian Rosen, Dept. of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD; e-mail [b.rosen@nhm.ac.uk](mailto:b.rosen@nhm.ac.uk).

### **Life and Environments in Purbeck Times**

Dorset County Museum, Dorchester, Dorset, UK

*19 – 22 March 1999*

A multidisciplinary symposium sponsored by the Palaeontological Association: three days of papers and discussions and a one-day field excursion to classic Purbeck localities. For details and first circular, contact Dr Andrew Milner, Department of Biology, Birkbeck College, Malet Street, London WC1E 7HX (fax 0171 631 6246, e-mail [a.milner@biology.bbk.ac.uk](mailto:a.milner@biology.bbk.ac.uk)) or Paul Ensom, Department of Palaeontology, Natural History Museum, Cromwell Road, London SW7 5BD (fax 0171 938 9277, e-mail [p.ensom@nhm.ac.uk](mailto:p.ensom@nhm.ac.uk)).

### **Major Events in Early Vertebrate Evolution – Phylogeny, Palaeontology and Development**

Natural History Museum, London, England

*8 – 9 April 1999*

Our understanding of the origin and early evolution of vertebrates is advancing rapidly, not only due to new fossil discoveries and phylogenetic analyses, but also to discoveries in developmental genetics. This conference, sponsored by the Systematics Association and the Natural History Museum, will bring together leading workers from palaeontology, developmental biology and comparative anatomy to address the major questions in this field.

The story of vertebrate origins is the story of how the various vertebrate body plans, and the developmental cascades which generate them, were assembled by evolution. General problems include recognising homologous structures and gene expression patterns between groups, and understanding the steps by which major morphological transformations were accomplished.

Specific topics to be addressed by the meeting include the origin, patterning and early evolution of jaws, appendages and mineralised tissues, as well as the early diversification of vertebrates.

The meeting will be held at London's Natural History Museum, one of the foremost centres in the world for systematic and evolutionary research. All speakers are invited, but there will be an Open Poster Session allowing non-speaking delegates to present their work.

*Provisional Speaker List*

P.E. Ahlberg (Convenor), W.E. Bemis, J.A. Clack, M.I. Coates, P. Donoghue, P.L. Forey, H.E. Gee, J. Hanken, J.R. Hinchliffe, R. Hitchin, N. Holder, L.Z. Holland, P.W.H. Holland, P. Janvier, R.P.S. Jefferies, J. Joss, J. Mallatt, J.G. Maisey, B.D. Metscher, R.G. Northcutt, M.A. Purnell, I.J. Sanson, H.-P. Schultze, M.M. Smith, M.P. Smith.

If you are interested in the meeting and would like the second circular, please contact:

Dr Per Ahlberg,  
Department of Palaeontology,  
The Natural History Museum,  
Cromwell Road  
London SW7 5BD, UK  
e-mail: p.ahlberg@nhm.ac.uk  
fax: +44 (0)171 938 9277

If you would like to present a poster, please mention this, with a note of its provisional title.

 **Mary Anning and her Times: The Discovery of British Palaeontology, 1820-1850**


Lyme Regis Museum, UK

2 – 4 June 1999

Palaeontologists, historians of science, geologists, and social historians will number among the contributors to this symposium, which is intended to recognise the achievements of Mary Anning and the scientific importance and cultural context of her discoveries. The meeting will be held over three days in Lyme, which has many rich scientific, historical, and literary associations. Activities will include evening lectures by Hugh Torrens and Stephen Jay Gould; keynote addresses by noted author John Fowles and Sir Crispin Tickell, a descendant of Mary Anning; and a geological excursion in the environs of Lyme Regis.

There are a few open spots on the programme for contributors interested in exploring aspects of Mary Anning's life, times, and contributions.

For information on contributing to the programme please contact Kevin Padian, Museum of Paleontology, University of California, Berkeley CA 94720-4780, USA (email [kpadian@socrates.berkeley.edu](mailto:kpadian@socrates.berkeley.edu)). For all other inquiries about the meeting, including registration and housing, write to the Lyme Regis Museum, Lyme Regis, Dorset DT7 3QA, UK (fax +44 (0)1297 443370). The size of the meeting will be limited by the capacity of local facilities, so it is advisable to inquire early.


 **European Paleontological Association Workshop**

Lisboa, Portugal

15 – 18 July 1999

The links between fossil assemblages and sedimentary cycles and sequences.

To receive first circular contact CEPUNL - Rogerio Bordalo da Rocha, Quinta da Torre, P-2825 Monte de Caparica, Portugal (tel 351.1.2948573, e-mail [cepunl@mail.fct.unl.pt](mailto:cepunl@mail.fct.unl.pt)). Online information is at <http://www.si.fct.unl.pt/~w3cepunl>

 **5th International Ichnofabric Workshop (IIW-5)**

Scarborough and Manchester, UK

*15 – 20 July 1999*

As with the four previous, highly successful workshops, the purpose of this meeting is to bring together trace fossil workers to consider the applications of ichnofabric (trace fossil-sediment) analysis in facies recognition, event correlation, palaeoenvironmental and palaeoecological reconstruction. The workshop will be field-based on the rocks of the Yorkshire coast, and linked to a preceding conference “Ichnofabrics in Petroleum Geology 1999” at Aberdeen, 12 - 14 July 1999. This provides a unique opportunity to exchange and develop understanding and applications of ichnofabric analysis between academia and industry. The meeting terminates in Manchester, considering the educational and museum aspects of trace fossil studies.

To request further details please contact: J.E. Pollard, Dept. of Earth Sciences, University, Manchester, M13 9PL, UK (tel +44 (0)161 275 3817, fax +44 (0)161 275 3947, e-mail [john.pollard@man.ac.uk](mailto:john.pollard@man.ac.uk)) (IIW-5) or M.J.F. Lawrence, Z & S Geoscience, Campus 2, Balgownie Drive, Bridge of Don, Aberdeen, AB22 8GU, UK (tel +44 (0)1224 8222555, fax +44 (0)1224 823777, e-mail [mark.lawrence@zands.com](mailto:mark.lawrence@zands.com)) (Ichnofabrics in Petroleum Geology).

 **Cephalopods – Present and Past**

Vienna

*6 – 9 September, 1999*

To register or for information contact: Herbert Summesberger, Museum of Natural History, Vienna. Tel (0043) 1 52177/251, fax (0043) 1/52 177/459, e-mail [herbert.summesberger@nhm-wien.ac.at](mailto:herbert.summesberger@nhm-wien.ac.at).

 **47th Symposium of Vertebrate Palaeontology and Comparative Anatomy**

Edinburgh, Scotland


*8 – 11 September 1999*

The Symposium will be preceded by the 8th Symposium of Palaeontological Preparators and Conservators, on 7th September 1999.

Both meetings will be hosted by the National Museums of Scotland in central Edinburgh, and organised by the staff of the Department of Geology and Zoology. There will be a reception in the new Museum of Scotland. The independent Dynamic Earth interpretive centre will be open by then; it is the provisional venue for the Conference Dinner. There will be the usual day field trip on the 11th.

These dates have been arranged to allow delegates to go on to the ‘Secondary Adaptation to Life in Water II’ meeting in Copenhagen the following week. Daily direct flights are available from Edinburgh to Copenhagen so that both meetings can be attended in entirety.

Enquiries to Mike Taylor, Department of Geology and Zoology, National Museums of Scotland, Chambers Street, Edinburgh EH1 1JF (fax 0131 220 4819, e-mail [mat@nms.ac.uk](mailto:mat@nms.ac.uk)).

 **The biology and evolution of bivalves**

University of Cambridge, UK

14 – 17 September 1999

Organised on behalf of The Malacological Society of London by E.M. Harper, J.D. Taylor and J.A. Crame.


An international meeting to focus solely on the Bivalvia. The organisers welcome papers and posters on all aspects of the biology and palaeontology of bivalves, in particular studies of the ecology, phylogeny and palaeobiology of the class. The Society hopes that the proceedings of the meeting will be published as series of refereed papers.

The meeting is to be held over three days in the historic and picturesque city of Cambridge (UK) within the ancient university. This is a call for offers of papers and posters, for which the deadline is 31st May 1999. It will be possible to organise workshops and themed sessions to accommodate those with similar interests.

Registration Fee: £100 (sterling), £90 for members of The Malacological Society, £50 for students.

For offers of contributions and to request further details please contact: E.M. Harper, Dept. of Earth Sciences, Downing St, Cambridge, CB2 3EQ, UK (tel +44 (0)1223 332846, fax +44 (0)1223 333450, e-mail emh21@cus.cam.ac.uk), or J.D. Taylor, Dept. of Zoology, The Natural History Museum, Cromwell Rd, London, UK (e-mail J.Taylor@nhm.ac.uk), or J.A. Crame, The British Antarctic Survey, High Cross, Madingley Rd, Cambridge, UK (e-mail JACR@pcmail.nerc-bas.ac.uk).

The first circular is online at <http://www.sunderland.ac.uk/~es0mda/ms11.shtml>

 **VII International Symposium on Mesozoic Terrestrial Ecosystems**

Buenos Aires, Argentina

26 September – 2 October 1999

A wide-ranging scientific programme and several field trips are planned; further information from the Secretary to the Symposium at Museo Argentino de Ciencias Naturales “B. Rivadavia”, Avda. Angle Gallardo 470, 1405 Buenos Aires, Argentina (tel/fax 54-1 983 4151).

 **7th International Symposium on Fossil Algae**

Nanjing, China

13 – 17 October 1999 + excursions

Themes cover a wide range of studies on benthic algae, cyanobacteria and stromatolites through time, including taxonomy, biostratigraphy, evolution, palaeoecology, sedimentology, ultrastructure, and biomineralization.

Pre- and post-symposium excursions will visit Jixian (Proterozoic), Jinan (Cambrian), and Guilin (Devonian).

For details contact: Xi-nan Mu, Nanjing Institute of Geology and Palaeontology, Academia Sinica, 39 East Beijing Road, Nanjing 210008, China (fax +86 25 335 7026, e-mail algae@pub.nj.jsinfo.net).



 **5th International Meeting of the Society of Avian Palaeontology and Evolution**

Beijing

*June 2000*

For information contact: Huiling Wu or Yonghong Zhang, 2000 SAPE meeting, P.O. Box 643, Beijing 100044, China, fax 86-10-68337001.

 **Third International Conference on Trilobites and their relatives**

Oxford, UK

*2 – 6 April 2001*

There will be a pre-conference field trip to Scotland and Northern England, and a post-conference trip in Wales and the Welsh Borders. Organiser-in-chief: Derek Siveter (Oxford).

## BOOK REVIEWS

### ***Palaeontographica Canadiana No. 13***

Latest Ordovician-Silurian articulate brachiopods and biostratigraphy of the Avalanche Lake area, southwestern District of Mackenzie, Canada. Jisuo Jin and Brian D.E. Chatterton, 1997. Canadian Society of Petroleum Geologists and Geological Association of Canada, Calgary, Alberta, Canada. 167 pp. ISSN 0821-7556, ISBN 0-920230-59-8.

This is a good solid systematic study of silicified brachiopod faunas of late Ashgill to Wenlock, and maybe Ludlow, age from the upper Whitaker Formation and Delorme Group of the Avalanche Lake area of the Mackenzie Mountains in the North West Territories. Of 62 genera and 86 species described, one genus and 17 species are new, including the oldest terebratulid so far known. The diverse faunas of orthids, strophomenids, pentamerids, rhynchonellids, atrypids, athyridids and spiriferids are described in pages 12 to 65, with 50 excellent plates illustrating the material. Some statistical data for larger samples is included in appendix form, whilst appendix 1 is a taxa/locality listing. The collections are from five sections through the stratigraphy with samples at frequent intervals.

This detailed work allowed the authors to identify four brachiopod assemblage zones within the largely shelf carbonate sequences. The first part of the publication contains detailed but succinct data on the brachiopod distributions, assemblage zones, and palaeoenvironments, linking in the brachiopod data to previous biostratigraphical work on the same sections. It is this section that makes the work potentially useful to anyone with a palaeontological, stratigraphical or regional interest, making it of wider relevance for a bigger audience than simply for brachiopod workers. As with others in this series, it is a well produced, well illustrated, high quality, attractive publication of potential relevance to anyone with an interest in biostratigraphy of Canada and the wider correlations.

*Matthew Parkes*

*Geological Survey of Ireland, Beggars Bush, Haddington Road, Dublin 4, Ireland*

### ***The Early Evolutionary History of Planktonic Foraminifera***

Edited by M.K. Boudagher-Fadel, F.T. Banner, and J.E. Whittaker. 269 pp. Chapman and Hall, London. ISBN 0-412-75820-2. Hardback £69.

Planktonic foraminifera are used routinely for the biostratigraphy of sediments of Aptian age and younger, but the origin of the group was much earlier and has hitherto been obscured by a degree of taxonomic muddle. There are several good reasons to re-evaluate the origins of the planktonic foraminifera. First, the early history provides the key for the subsequent high-level taxonomy, in much the same way as Burgess Shale faunas are key to modern metazoan relationships. Second, it may be possible to extend the biostratigraphic usefulness of the group back toward their origins. Third, there is simple curiosity; it seems to be disproportionately fascinating to study the early history of other important fossil groups (e.g. ammonoids or graptoloids), and so it is with planktonic foraminifera.

This book is an admirable re-evaluation of all the species up to the Albian and their stratigraphical ranges. It is principally a taxonomic atlas rather than a work of palaeobiology, although it ends with a speculative chapter on the physiology and ecology of the early forms. The main value of the book

is that the taxa are described, discussed and well illustrated, with as many SEM pictures as possible, together with reproductions of the original illustrations in many cases. There are also some new SEM pictures of holotypes that were originally poorly illustrated, which enable the authors to clear up some key synonymy issues. A number of new genera and species are described.

I have one or two minor complaints. The plates (which were prepared electronically) are intrinsically of good quality but the reproduction is disappointing, with the backgrounds often being mid-grey rather than black. Also, I would like to have seen scale bars next to individual figures since they are usually all of different magnifications. The terms “murica” and “pseudomurica” are used inconsistently (e.g. so-called “muricae” on favusellids on pages 53 and 230). Finally, I do not think it is necessary to reserve the widely used term “pores” for the holes in Neogene *Orbulina* and *Globigerinatella* which, in any case, are not homologous to one another.

To understand the origin of the planktonic foraminifera we need to answer two related questions: 1) when did the clade encompassing the modern planktonic foraminifera originate (if indeed they are monophyletic)?; and 2) when did the planktonic habit arise? The answers to these questions are not necessarily the same, but this work presents an essentially simple view. Previous speculations about Triassic origins are dismissed. According to these authors, the first truly planktonic genus is believed to be *Conoglobigerina* (Superfamily Favusellaceae), which appeared in the Bajocian, and all subsequent species are believed to be descended from it.

This thesis seems reasonable, but is far from well established. One problem is that rather simple morphological criteria are used for deciding whether or not a species was planktonic, which would in fact exclude some subsequent species that are undoubtedly planktonic. Also, although a good ultrastructural case is made for *Conoglobigerina* being ancestral to the aragonitic favusellids and perhaps later microperforate forms, the idea that it was also ancestral to calcitic macroperforate species via the Praehedbergellidae and Shackoinidae is less convincing.

The main problem is a lack of sufficiently well preserved material from the Early Cretaceous. Although one or two of the illustrated specimens are stunning (e.g. the Bathonian *Globuligerina* on Plate 2.8), many specimens are too poorly preserved to identify the wall texture, making the chain of supposed ancestors and descendants questionable. The authors have made every effort to locate the best possible material and have used innovative preparatory techniques to make the most of it, but the search for more and better material must go on.

While this work was in press, genetic sequences of various modern planktonic foraminifera have appeared. These seem to indicate that the modern microperforate and macroperforate superfamilies may have evolved independently from the benthos. Perhaps the palaeontological record will benefit from re-evaluation in this light. If true, it would also cast doubt on the scenario of evolving depth-habitats developed in the final chapter, which relies on the questionable view that large pores evolved in response to low oxygen conditions.

Major taxonomic works like this are never “right” in every respect. However, they are landmarks in our evolving understanding of fossil groups and tend to stimulate research by focusing the issues. They are also extremely useful to non specialists who may want to “dabble” – or even do science – but would otherwise be confronted by an army of obscure and conflicting publications. The shelf-life of this work will be measured in decades and no good geological library should be without it.

*Paul Pearson*

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

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