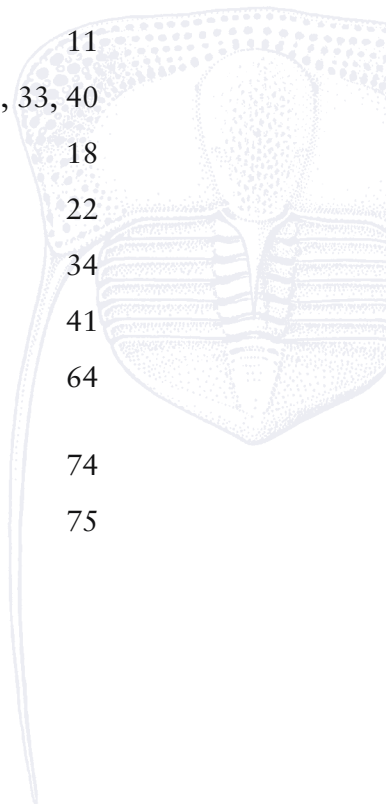


The Palaeontology Newsletter

51

Contents

Association Business	3
News	4
Meeting Reports	11
Association Meetings	16, 21, 33, 40
Sylvester-Bradley Award Report	18
Correspondence	22
Future meetings of other bodies	34
Book Reviews	41
Post-graduate opportunities	64
<i>Palaeontology</i> vol 45 parts 6	74
ANNUAL MEETING abstracts	75



Reminder: The deadline for copy for Issue no 52 is 12th February 2003

On the Web: <http://www.palass.org/>



CAMBRIDGE

Cladistics

A Practical Primer on CD-ROM

Peter Skellton

The Open University, Milton Keynes
and Andrew Smith

Natural History Museum, London
with accompanying booklet by Neale Monks

Key Features

- The first interactive CD-ROM to teach cladistic methodology.
- Assumes no prior knowledge and is designed for self-study.
- The accompanying booklet allows further study when away from a computer.
- Compatible with both PC and Macintosh



Contents:

Introduction; Part I. First Principles: 1.1 Reconstructing evolutionary history from observed differences; 1.2 Parsimony and tree construction; Part II. Characters and Homology: 2.1 Homology and homoplasy; 2.2 Homology in molecular data; 2.3 Character definition; 2.4 Weighting; Part III. Cladograms and Trees: 3.1 Rooting procedures and character polarity; 3.2 Cladograms, phylograms, and phylogenetic trees; 3.3 Monophyly, paraphyly, and polyphyly; 3.4 Consensus trees; Part IV. Fit and Robustness: 4.1 Measuring goodness of fit; 4.2 Tests of robustness; Part V. Practical Exercise: 5.1 Phylogenetic analysis of eight species of sea-urchins; 5.2 Cladistic analysis of morphological characters; 5.3 Cladistic analysis of molecular characters; 5.4 Comparison of results and conclusions.

2002 | CD-ROM with booklet | 92pp

£29.95 +VAT | CD-ROM | 0 521 52341 9

Co-published by Cambridge University Press and the Open University; in Association with the Natural History Museum.

Lecturers: You may order inspection copies of these books by email to inspectioncopy@cambridge.org or visiting our website at <http://www.cambridge.org/textbooks>

www.cambridge.org

 **CAMBRIDGE**
UNIVERSITY PRESS

Association Business

Sylvester-Bradley Awards

Awards are made to assist palaeontological research (travel, visits to museums, fieldwork etc.), with each award having a maximum value of £1,000. Preference is given to applications for a single purpose (rather than top-ups of other grant applications) and no definite age limit is applied, although some preference may be given to younger applicants or those at the start of their careers. The award is open to both amateur and professional palaeontologists, but preference will be given to members of the Association. The deadline for applications is the **30th November 2002**, with awards announced at the AGM.

Applications consist of a CV, one A4 page account of research aims and objectives, and a breakdown of the proposed expenditure. Each application should be accompanied by the names of a personal and scientific referee. Successful candidates must produce a report for *Palaeontology Newsletter* and are asked to consider the Association's meetings and publications as media for conveying the research results.

2002 Association Awards and Annual Address to be made at the Annual Meeting.

2002 Hodson Fund Award winner

Dr Matthew A. Wills

Matthew Wills (University of Bath) has thusfar had a short and illustrious career. He was a graduate zoologist who turned to palaeontology. His PhD was to test Gould's main thesis in *Wonderful Life*, that life in the Cambrian was much more varied (more disparate) than life since. This resulted in a series of papers, including one in *Science*, which clearly showed that the range in morphology seen in living arthropods outweighs that seen among their Cambrian ancestors. Post docs at the Smithsonian and Oxford University Natural History Museum followed working on morphometrics and disparity through time. As part of this work he developed a new computer program for assessing the fit of cladograms to stratigraphy, which is now widely used. Matthew is one of the few palaeontologists to gain a lectureship in a 5* biology department and his publishing career has continued with vigour with highly cited papers in many international journals.

2002 Mary Anning Award winner

Michael J. Newman

Michael is an amateur collector specialising in fossil fish from northern Scotland. He is a research associate at Aberdeen University and has undertaken research collecting with Nigel Trewin, amassing an internationally important collection. A number of his specimens have already been donated to national museums. Michael has already published two papers in *Palaeontology*, describing unique jawless fishes from the Achanarras fish bed.



Change in copyright arrangements for Pal Ass publications

The more eagle-eyed amongst you will have noticed a subtle though significant change in the wording of the copyright policy on Palaeontological Association publications, as stated on the inside cover of *Palaeontology*. This allows reproduction, in print or through electronic media, of images and text from any Palaeontological Association publication for any not-for-profit research or educational enterprise without seeking permission, provided that the exact source, and the Association (with whom copyright remains), is acknowledged directly. Reproduction of images and/or text in for-profit enterprises (including commercial publishing) should proceed through a formal request to the Executive Officer <palass@palass.org> and a fee will be payable.

The driving force behind the establishment of this copyright waiver was the Copyright Licensing Authority's introduction of a new charging policy for the reproduction of published images in teaching packs; this had been deemed to introduce new financial problems for education while providing little benefit to the copyright holder, the Association. The CLA's charging policy has subsequently introduced a revised charging policy but it is hoped that the new copyright permission policy will encourage educators to utilise elements of Palaeontological Association publications in their teaching, as well as reducing the administration associated with preparation of new research publications in which image reproduction is necessary.

The Jurassic Coast

Following inscription by UNESCO on the list of World Heritage Sites in December 2001 the Dorset/East Devon Coast was officially launched on the 3rd October by H.R.H. Prince Charles. For those lucky enough to be in Lulworth Castle for the event it was a great day and we were all impressed by the genuine interest shown by the Prince. He thanked those responsible for gaining World Heritage status for the coast and 'instructed' us to take good care of it for the nation.

The site was inscribed by UNESCO on the basis of its geology and geomorphology and it is important that all those with a scientific interest in the Dorset/East Devon Coast join the "Scientific Network" that is now being created. Anyone from the palaeontological community that is interested in joining the network should email me with a copy to Richard Edmonds of Dorset County Council <r.edmonds@dorset-cc.gov.uk>. Once formed the network will be able to circulate all those interested with information about the coast, details of meetings and conferences, etc. There will clearly be those who will want to become heavily involved in the work of the Network while there are others who may just want to be kept 'in touch'. My contact is <mhart@plymouth.ac.uk> and it would be useful if you could indicate your area of interest (in case I do not already know what it is!).

Professor Malcolm Hart
University of Plymouth, UK

Unveiling the Sedgwick

Sir David Attenborough had the enjoyable task of officially opening the new displays at the Sedgwick Museum on Friday 27th September. A large number of guests attended the event in the splendid surroundings of one of the UK's finest University Museums.

The redevelopment of any museum gallery entails a great deal of thought, planning and careful implementation. The staff responsible for the new galleries at the Sedgwick seem to have undertaken their task with care and attention to detail. The resultant displays reflect the diversity, depth and importance of the Sedgwick collections, whilst retaining a narrative that is accessible at many levels. This is no easy task and the staff should be more than satisfied with the end result. A museum display that is accessible to researchers, undergraduates, schools and family visitors is a worthy aim for any institution; the Sedgwick displays appear to have achieved this important benchmark.

Dr David Norman, Director of the Sedgwick Museum, said: '*The Sedgwick is one of the country's most important scientific resources, and we are delighted to be able to display our collections and the work that we do in such a beautiful new gallery*'. Dr Norman played a key role in raising the funds for the redevelopment and putting into action the processes that led to the new gallery.

The renovation of the galleries began in 2000 and was funded through Resource by the Designation Challenge Fund, supporting increased access to museum collections. The Yorkshire-based design company, Blue, was responsible for interpreting the detailed brief and design concepts. These were generated by the Sedgwick Museums Project Redevelopment Manager, Liz Hide, with the help of many other Sedgwick staff. The Museums Project Redevelopment Assistant, Leslie Noe, indicated at the opening that a key component of the gallery redevelopment was the retention of large numbers of specimens on display. At a time when many institutions are preaching 'less is more', it is refreshing to find a Museum that has realised that more real material and less interactives does not detract from the overall experience.



The two Davids, Norman (left) and Attenborough.

Sir David Attenborough, in his opening speech, raised issue on the absence of real material in some museum displays, suggesting that *'the objects themselves were often extraordinarily difficult to discover'*. He went on to say that *'in a way, this is an easy way out'* and in his view *'a philistine way out'*. However, his praise for the new displays at the Sedgwick clearly indicated that the Museum had achieved a unique balance between content and interpretation. He concluded that *'the displays have retained a historical format, with a serious image, but at the same time making it accessible and exciting through its subtle lighting and superb labelling'*.

So far, all that have seen the new displays at the Sedgwick have given positive praise, even if some were a little perturbed by the superb kite-like sculptures of a trilobite, *Dunkleosteus*, *Hallucigenia*, and Volcano that sat upon some of the cases! I look forward to taking a group of undergraduates to this wonderful new display, but am thankful that I can also bring my young children, knowing that they too will delight in the story held in these stunning collections.

Dr. Phil Manning

Keeper of Geology, Yorkshire Museum, York
Lecturer in Vertebrate Palaeontology, University of Liverpool
Publicity Officer, The Palaeontological Association
 <palaeomedia@tiscali.co.uk>

New: Dictionary of Paleontology: English–Spanish // Spanish–English

Science Dictionary publisher Editorial Castilla La Vieja has just released the Dictionary of Paleontology (English–Spanish // Spanish–English; ISBN: 0-9643569-8-8). This is an exhaustive reference work of 1,122 pages and over 30,000 entries, providing in-depth treatment of terminology in vertebrate/invertebrate palaeontology, palaeobiology, palaeobotany, palaeoecology, biostratigraphy, oil and coal formation and other related fields. Sample translation sentences abound throughout the book. More information as well as sample pages can be obtained by visiting the website <<http://castilla1492.freeyellow.com/>> or by inquiring via e-mail to <castilla@technologist.com> or <normandy1@sprynet.com>

More news on Palaeontology Collections from Aberystwyth

In the Association Newsletter No. 49 (p.19), Mark Williams, Mike Howe and Pauline Taylor reported that part of the fossil collection from the former Department of Geology at the University of Wales, Aberystwyth has been transferred to the British Geological Survey at Keyworth. This note is to inform the membership that a significant part of the same collection was transferred previously to the National Museum of Wales.

Apart from wide ranging collections of general importance, the material now in Cardiff contains most (and possibly all) of the type, figured and cited fossils incorporated previously within the holdings at Aberystwyth. Among the well known geologists/palaeontologists whose publications describe this material are Denis Bates, John Challinor, O.T. Jones, Edward Neaverson, Alan Wood, Archie Lamont, W.F. Whittard and H.P. Lewis. Of some interest is the fact that some of

the H.P. Lewis Carboniferous coral specimens were 'removed' from Aberystwyth by the notorious Indian palaeontologist V.J. Gupta, who then re-described them as coming from Kashmir (Wyatt 1990).

Antony Wyatt, former curator of the collections at Aberystwyth, has previously drawn attention (1974, 1975) to type material then housed there. A full catalogue of all the type, figured and cited specimens now housed in Cardiff will be published in a future edition of the *Geological Curator* (the journal of the Geological Curators' Group), together with a summary of the content of the full collection.

References

Wyatt, A.[R.] 1974. Geological collections at U.C.W. Aberystwyth. *Newsletter of the Geological Curators' Group*, 2: 65.

Wyatt, A.[R.] 1975. Geological collections at U.C.W. Aberystwyth. *Newsletter of the Geological Curators' Group*, 3: 154.

Wyatt, A.R. 1990. V.J. Gupta and the Aberystwyth fossil collections. *Journal Geological Society of India*, 35: 587-592.

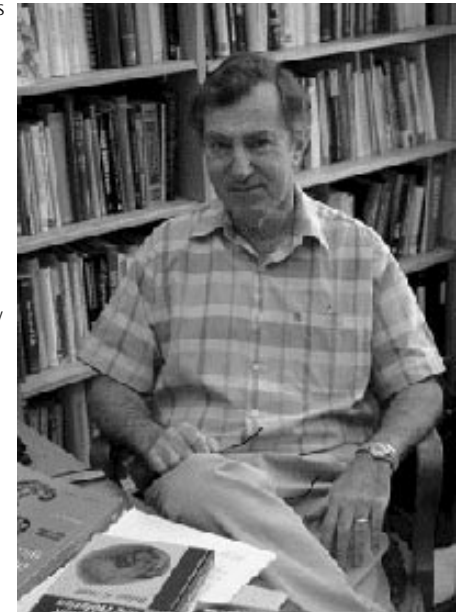
Michael G. Bassett

Department of Geology, National Museum of Wales, Cardiff CF10 3NP
 <Mike.Bassett@nmgw.ac.uk>

2002 Gerhard Herzberg Canada Gold Medal for Science and Engineering

Brian K. Hall, one of the regular columnists in *Palaeontology Newsletter*, has been short listed for the 2002 Herzberg Medal. The NSERC Herzberg Medal, the Council's highest honour, recognizes research contributions characterized by both excellence and influence. It is awarded annually to an individual who has demonstrated sustained excellence and influence in research, for a body of work conducted in Canada that has substantially advanced the natural sciences or engineering fields.

Brian, who is George S. Campbell Professor of Biology at Dalhousie University (Nova Scotia, Canada) is a founder of the emerging field of evolutionary developmental biology, or 'Evo-Devo' as its devotees prefer to refer to it. He has been keen both to trail blaze and to ensure that



everyone is welcome at the party, emphasizing the roles to be played by palaeontologists and population geneticists, as well as developmental biologists and developmental geneticists in this new, *New Synthesis* of evolutionary biology.

A prolific writer, Brian Hall has been classed with the late Stephen J. Gould for his ability to explain complex evolutionary concepts insightfully. Writer or editor of more than 16 books (with five more in press or preparation), his widely used 1988 text *The Neural Crest* is already considered a modern classic. Brian's *Evolutionary Developmental Biology* (1992) was one of the first books to provide a conceptual framework for this emerging discipline, and as such fuelled its growth. The second edition (1998) has been translated into Japanese. An avid and productive experimentalist, he has written more than 200 scientific articles for peer-reviewed journals. He has also mentored more than 60 undergraduate and graduate students and postdoctoral fellows.

Brian is the recipient of numerous Canadian and international honours, including the Fry Medal from the Canadian Society of Zoologists (1994) for outstanding contribution to knowledge and understanding in one area of zoology. In 1996, he received the International Craniofacial Biology Distinguished Scientist Award. Last year, the St. Petersburg (Russia) Society of Naturalists awarded him the Kowalevsky Medal, presented to the eight most distinguished scientists of the 20th century in comparative zoology and evolutionary embryology. Earlier this year he was elected a Foreign Honorary Member of the American Academy of Arts and Sciences.

The 2002 winner of the Herzberg Medal will be announced on 25th November and will receive the medal at a gala event in Ottawa that day. Canadian Nobel Laureate John Polanyi will give the address. The winner's NSERC Discovery Grant will be increased to \$1 million over five years. If the annual grant is already greater than \$150,000 a year, it will be topped up by a further \$50,000 a year. The two other finalists will receive \$50,000 each. This is in stark contrast to his recent Kowalevsky Medal, the ground rules for which were established in 1910, and allowed for an accompanying award of 250 gold rubles; this was probably a year's salary in 1910, but is now worth about \$13 Canadian!

The two other finalists for the 2002 Herzberg Medal are Barrie Frost and Tito Scaiano. Barrie Frost (Queen's University, Kingston) is an internationally renowned visual neuroscientist, who has pioneered research into how our brains see and hear, and how animals like monarch butterflies and seabirds navigate amazing distances. Tito Scaiano (University of Ottawa, Ottawa) is the "global dean" of photochemistry. Dr Scaiano is helping find out what happens when light hits a molecule, and how the fleeting "billionth of a second" processes that result can be understood and harnessed.

See also:

NSERC press release <http://www.nserc.ca/news/2002/win_hall_e.htm>

Brian Hall's website <<http://www.dal.ca/%7Ebiology2/us/f/hall/hall.html>>

2001 Joseph A. Cushman Award

The recipient of the 2001 Joseph A. Cushman Award is Professor John W. Murray (Southampton, UK) in recognition of his unique contribution to the study of foraminifera, particularly in the fields of ecology and palaeoecology. John began his foraminiferal career work on Cretaceous planktonic forams from the very first borehole drilled in connection with the Channel Tunnel, while an undergraduate at Imperial College, London. He continued at Imperial with a Ph.D. in Micropalaeontology (1961), studying the ecology of a small estuary in southern England, constraining the distribution of living forams to variation in temperature, salinity, dissolved oxygen and pH. Indeed, ecology and palaeoecology have been the mainstays of his career, taking him from a postdoc at the Plymouth Marine Laboratory (1961-2), through a lectureship at the University of Bristol (until 1975), Professor of Geology and Head of Department at the University of Exeter (1975-89) and, eventually, as a result of the dreaded Earth Sciences Review (1989) to the Southampton Oceanographic Centre (following merger of the Department of Geology and Institute of Oceanographic Sciences).

John has been responsible for the education of many, both at undergraduate level, as well as at research level through his roles as Ph.D. supervisor, through the M.Sc. Micropalaeontology that was run from Southampton, and through his books on ecology, palaeoecology and stratigraphic utility of forams. These include the *Atlas of British recent foraminiferids* (1971), two editions of the *Stratigraphic atlas of fossil foraminifera* (1981 and 1989, both through the British Micropalaeontological Society), the *Atlas of invertebrate palaeontology* (1985, through the Palaeontological Association), and *Ecology and palaeoecology of benthic foraminifera* (1991), as well as over 150 articles.



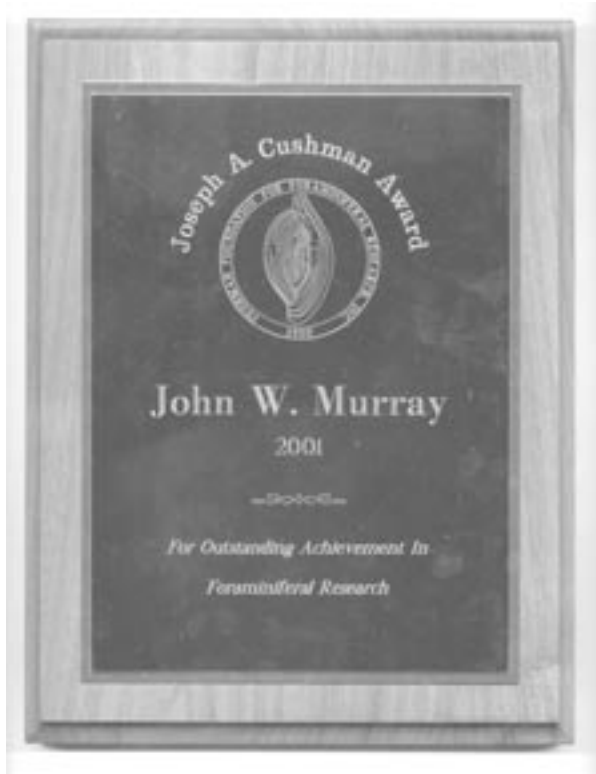
Amongst these achievements, John has also found the time to serve our community through a variety of roles in learned societies including President of the Palaeontological Association, Chair of the British Micropalaeontological Society, Honorary Secretary of the Geological Society of London, and positions on the boards of editors of *Palaeontology*, *Journal of Micropalaeontology* (including Chief Editor), and *Journal of Foraminiferal Research*.

John W. Murray is, without doubt, a worthy recipient of the prestigious Joseph A. Cushman Award, but it is the Cushman Award that will benefit most from the inclusion of Murray amongst the list of recipients.

See also:

Whittaker, J.E. 2001. The 2001 Joseph A. Cushman Award. *Journal of foraminiferal Research* **31**: 171-2.

The Joseph A. Cushman Award was established in 1979 to honour researchers who have made outstanding contributions in the field of foraminiferology.



Meeting REPORTS



The Lyell Meeting 2002: Approaches to Reconstructing Phylogeny
Geological Society of London, Burlington House 5 June 2002

The Lyell Meeting attracted an international audience to the Geological Society this past June for the 13 British and American researchers discussing the latest approaches to phylogenetic reconstruction. The diversity of papers, ranging from critiques of the treatment of temporal data to statistical methods for hypothesis testing, was an adequate indication of the breadth and depth of current investigations.

Initiating the meeting, **Jonathan Adrian** of the University of Iowa presented his paper explaining his objections to the use of temporal order in phylogenetic analysis. Using the Sunwaptan Laurentian trilobites—one of the richest and well studied invertebrate marine records—Jon illustrated his position of the “absurd” alteration of biology-based hypotheses of relationship in order to conform to the fossil record. **Mark Wilkinson** of the Natural History Museum in London gave a valuable survey of consensus methods, cautioning for their appropriate use governed by a method’s properties and the investigator’s aims. Particular focus was given to the supertree methods and the propriety of supertree methods to particular problems.

Before the lunch break, **Chris Paul** of the University of Liverpool and **Andy Gale** of the University of Greenwich returned to variations on the theme of time by discussing the utility of the fossil and rock-record. Chris Paul’s defence of using the fossil record in phylogenetic reconstruction showed that 1) fossil morphospecies identification is 85% efficacious when tested with extant non-marine record, 2) periods of stasis dominate the rate of morphological change and 3) the stratigraphic record is a reliable data set in reliable stratigraphic fossil distributions. Andy Gale with coauthor Andrew Smith provided a cautionary note to interpreting mass extinctions and radiations by illustrating the sampling and preservation bias in the rock-record as exemplified by the correspondence of sea-level change and fauna preservation.

After the break, **John Callomon**’s paper discussed the well documented record of Jurassic ammonites, indicating this record preserves morphological change approaching a microevolutionary level. Callomon demonstrated the multidirectional changes among the Jurassic ammonite but concluded with the longing for an answer as to why.

From the Field Museum of Natural History in Chicago, **Peter Wagner** presented a sharp, skilful paper on the likelihood tests of phylogenetic hypotheses. Using bellerophonid molluscs as an example, Wagner explained an approach that tests the likelihood of conflicting hypotheses of phylogeny where numerous parameters (e.g. different assumptions of character evolution and stratigraphic data) affect data distributions. In the case of bellerophonitids, Wagner’s approach tested and rejected the best hypothesis of character evolution supporting a monophyletic relationship.

Paul Upchurch and **Craig Hunn** of the University of Cambridge gave a presentation on a statistical application of palaeobiogeography, stating that the history of a particular area may

be viewed as a network rather than a simple branching pattern. Thus comparing geographic history with phylogenetic history cannot be seen as simply comparing dendrograms, emphasizing the concept that biogeographic processes are likely to produce reticulate patterns.

Jen Jackson, with coauthors Jan Strugnell, Richard Fortey and Alan Cooper, emphasised the importance of using molecular data and the use of dating cladogenesis using molecular clocks. The main aim of the talk was to examine some of the limitations of using molecular rate estimations, notably the use of unreliable calibration points, confidence intervals and ambiguities linking sequence change to rate variation. It was also pointed out that these effects are cumulative and so dates obtained for cladogenetic events in the deep past, such as within the Precambrian, should be looked at within this light. Work is in progress to improve the accuracy of data gained from these methods.

Paul Kendrick, from the Natural History Museum, London, enlightened us on the use of molecular and biostratigraphic data in the quest to gain an understanding of the phylogeny of land plants. He mentioned the recent results of a molecular analysis of the phylogeny of angiosperms, which has greatly improved our understanding of this group. He stated, however, that there are still discrepancies between molecular and morphological results, and some parts of the phylogenetic tree of land plants that are still unresolved. He stressed the importance of the use of the spore and pollen record in the calibration of molecular clock data.

After the afternoon tea break **Paul Pearson** pondered on the problem of ancestry in phylogenetics and the use of stratophenetics to reveal evolutionary lineages. He talked of the concept that a species can only be considered the potential ancestor of another if it lacks apomorphies (a “meta-species”) and is derived from an older stratum.

Philip Donoghue presented the advantages of using the microfossil record when looking at conodont phylogeny. Conodonts have an extensive fossil record, long stratigraphic range (Middle Cambrian to end of the Triassic), although their phylogeny is poorly understood and attempts to compare phylogeny with stratigraphy have not been undertaken. He illustrated his point with the use of the conodont family *Palmatolepidae*, comparing the cladistic analysis with the stratigraphic record. The results showed differences at the Frasnian-Famnenian boundary, where the biostratigraphic data suggest an extinction event. This may be due to low taxon sampling density or problems with the phylogenetic reconstruction.

Jeremy Young (with coauthors Paul Brown, Ian Probert, Linda Medlin and Alberto Saez) provided an example of where palaeontological, biological and molecular data can be combined in elucidating phylogeny, using coccolithophores. Coccolithophores have a good fossil record and moderate modern biodiversity, which should make them good examples for phylogenetic research, using both morphological and molecular techniques. However, due to variable preservation of fossil taxa, conservative morphology and limited numbers of species currently in cultivation for use of cytogenetic and molecular studies, there are imperfections in the constructed phylogenies. Even so, combining results from different methods has been informative, especially with respect to the Liassic radiation of coccolithophores and the K-T extinctions and subsequent Palaeocene radiation.

The final presentation of the day, by **Matt Wills** from the University of Bath, was on the stratigraphic congruence of cladograms, asking the question “are some groups more congruent with the fossil record than others?” He demonstrated how the Stratigraphic Consistency Index

(SCI), Gap Excess Ratio (GER) and Relative Completeness index (RCI) can be used to judge how well data fit with the stratigraphic record.

Rudyard W. Sadleir & Jolyon Parish

Department of Zoology, University of Oxford, UK.

<jolyon.parrish@oriel.oxford.ac.uk>



Sex, violence and death at the BA festival of Science

Leicester University 13 September 2002

Each year the British Association holds a Festival of Science; this year's was based at the University of Leicester. After a week of fascinating talks ranging from esoteric ponderings on the religious implications of extraterrestrial life to topical discussions on climate change, the final day of the Festival included a session with the populist theme of ‘Sex, violence and death in the history of life’, co-sponsored by The Palaeontological Association.

First up was **Nicholas Butterfield** (University of Cambridge), starting his talk with the (slightly disturbing?) finding of 3,170 Google hits for the keywords sex + violence + death + Leicester. He examined where the three former topics relate to the grand scheme of evolution, particularly their biotic origination during the Proterozoic, by illustrating the surprising physical size and diversity of eukaryotes from around 2.5 Ga. We were also privileged witnesses to the first sex(ually differentiated structures) on Earth in a 1.2 Ga fossil, exceptionally preserved in silicified carbonate and interpreted as a red alga. Could this time represent a eukaryotic ‘big bang’ that produced all the major clades? Finally, he asked the question: Why have sex? His conclusion: to produce complexity, leading to feedback responses in other organisms to do the same (it seems one thing did lead to another).

After sex, of course, comes the morning after and specifically, the fertilised egg, as **Stefan Bengtson** (Swedish Museum of Natural History) reminded us. Moving from the Proterozoic to just post-Cambrian Explosion, he first noted the infamous disparity between molecular and palaeontological estimates for the origin of non-Ediacaran metazoans. The prevalence of phosphatisation after the Explosion resulted in some rocks being full of phosphatised ‘round thingies’. Based on analysis of SEM images, these are interpreted as cleavage embryos of early metazoans, such as annelids and scyphozoans. For the taphonomists among you, they are produced via encrustation of the embryo boundary by crystalline calcium phosphate. Phosphatisation is much scarcer before the Explosion, but some 570 Ma embryos, *sans* adults, have been found in China, offering the possibility of testing molecular estimates of metazoan origins palaeontologically.

David Siveter (University of Leicester) examined sex in the Phanerozoic itself. First task: identify sexual dimorphism. This is rare and often subtle, not always corresponding to population morphological bimodality. Hermaphrodites are a further problem. After running through some of the clear invertebrate examples of sexual dimorphism—ammonoids, euryterids, trilobites and spiders—he discussed the lurid world of ostracod sex. With a sperm:body length ratio of 10:1, the males require an intromittent organ occupying one third of their body volume, caught in action in a video of two mating ostracods (imagine a pair of amorous butter beans, if you will). Sex isn't everything though (no, really); asexual ostracod lineages can be traced back 100



Ma. The talk finished appropriately enough with serial grinding—of fossils—which, combined with digital photography, produced spectacular rotating 3D CGIs of the famous Herefordshire biota, possibly including the first ostracod soft parts from the Palaeozoic.

Introducing some welcome phytocentrism into the proceedings, **Peter Crane** (Royal Botanic Gardens, Kew) discussed the angiosperm paradox: why is the last plant group to evolve by far the most diverse? Recent advances in molecular phylogenetic systematics and improvements in the angiosperm fossil record are providing the rigorous information on the eco-evolutionary pattern of angiosperm radiation necessary to deal with this issue. Flowers are the site of angiosperm sex, so is this the answer? Firstly, the complexity of the match between angiosperm flowers and their pollinators means that any morphological change will lead to reproductive isolation and speciation. Secondly, mobile insect pollinators also allow sparse, isolated populations to survive, decreasing extinction. The result: evolutionary persistence and expansion. This would seem to be the answer only in some plant species (dependent on the exact plant-pollinator relationship), since the bennettitales, gnetales and cycad gymnosperm groups all appear to have flower-like structures and be insect pollinated.

Scott Sampson (Utah Museum of Natural History) gave the day's first lecture on vertebrates, illustrating the weird and wonderful forms dinosaur ornamentation can take: ceratopsian frills and horns, hadrosaur crests and theropod eye horns. He asserted that most of these structures are maladapted for functions that have been hypothesised for them, for example defence or thermoregulation; rather, they are primarily sexual characters involved in recognition, display and competition. Can we test this? Using modern analogues, a consistent pattern emerges in both extant and extinct species: secondary sexual ornamentation develops at sexual maturity, differs interspecifically (with the rest of the body fairly uniform between related species) and is usually, but not always, better developed in males. So how did it happen? Again, it appears to be complexity from isolation, also seen in extant cichlids. In North American Cretaceous dinosaurs, this resulted from population fragmentation by transgression and regression of the inland sea and the expansion of closed canopy angiosperm forest.

Following lunch, there was some violence; specifically, predation, and the question of whether it is a driving force in evolution. Most would say obviously, yes, but *ad hoc* adaptationism looms large; can the claim be tested? **Liz Harper** (University of Cambridge) showed how shellfish can come to our aid here, owing to their good fossil record, their common role as prey and their extant relatives for use as handy analogues. Predator morphology and prey damage are usually the only way to tell who ate whom, and it is the failed attacks that count; these are the individuals who survived and passed on their successful genes, contributing to evolution. Unfortunately, starfish predation and whole animal ingestion leave little fossil trace, but a variety of other examples were shown, from the angular growth line disruption caused by crabs to the distinctive drill holes produced by gastropods and octopuses.

Despite embarking on his first PowerPoint Presentation, **Richard Aldridge** (University of Leicester and President of the BA Geology section) gave a fine account of how the vertebrate got its skeleton. Initially it was thought that vertebrate biomineralisation was first obtained as a defensive exoskeleton in the armoured jawless vertebrates. As apparent from earlier talks, such *ad hoc* adaptationist explanations must be tested. Tracking the history of conodonts, from the initial discovery of phosphatic elements and natural assemblages, to the Carboniferous Granton

Shrimp Bed animal and the Ordovician Soom Shale, through to modern cladistic hypotheses and element functional studies, he showed that in actuality vertebrate hard parts (if you hold that conodonts are vertebrates) were first developed as an endoskeletal feeding apparatus.

Picking up the story, **Mark Purnell** (University of Leicester) looked at the subsequent evolution of feeding structures in armoured jawless vertebrate groups. Recent cladistic hypotheses indicate that vertebrate characters appear to have been acquired in mosaic fashion along the tree. Many of the characters are cranial, functionally related to feeding strategy; did this behaviour follow a similar gradation? For conodonts, microwear and element occlusion geometry implies predation, but what about the more derived jawless vertebrates? Using talents doubtless gained from years of watching Blue Peter, he used a skilfully constructed model heterostracan head shield and a pair of rubber gloves (hopefully someone took a picture) to illustrate hypotheses of tooth plate function. These could be tested by more conventional methods, namely SEM examination of plate microwear and microstructure. His conclusion: heterostracans, and probably other jawless vertebrates, were filter feeders; there is no trend in feeding strategy along the vertebrate tree.

After coffee came death. Death, followed by exceptional preservation, so providing a window through the taphonomic bias seen in most other deposits. **Sarah Gabbott** (University of Leicester) returned us to the Soom Shale lagerstätten of conodont fame, to examine its taphonomy and chemistry, and determine how this window came about. It seems that the exceptional conditions that preserved soft parts also favoured dissolution of hard parts; here, most preservation is moldic. The chemical conditions seem to be strongly acidic waters, probably owing to decaying algae producing weak acids then oxidised to stronger sulphuric acid. This precluded scavengers and allowed early mineral replacement of soft tissues with clay minerals, through bacterial precipitation.

Closing the session, we moved from local death to global mortality. **Richard Twitchett** (University of Bristol), battling initial technical difficulties, made the interesting (and perhaps worrying) comparison between the P-Tr extinction and modern events in the oceans. Consistent isotopic, geochemical and GCM evidence show that then, as now, Earth was in a phase of global warming, resulting in oceanic anoxia from the decreased temperature gradients and circulation. This caused very rapid biotic collapse, manifested in the record by dwarfed 'Liliput faunas' (a response to decreased productivity) and a significant reduction in bioturbation and tiering, both measures of ecological complexity. The biotic recovery from this was much slower. On a smaller scale, similar patterns are manifesting themselves in some modern settings; if such trends continue, are we ready to deal with a possible P-Tr level event?

All the day's speakers produced talks that were suitably accessible for those non-professionals in the audience, and covered sufficiently current material to interest the academics. Indeed, the unifying themes for the day have some relevance for all professional palaeontologists: first, the idea that a major consequence of sex is the production of complexity, and that this may be reason for its emergence, rather than to allow rapid evolution, and second, the Gouldian caveat of avoiding overzealous adaptationism and the consequent need to prove function rather than inductively assume it from form.

David Jones

Department of Geology, University of Leicester, UK
<doj2@leicester.ac.uk>



Association Meeting

Lyell Meeting 2003: The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis

Burlington House

24 February 2003

Organised by: Dr D. McIlroy

In recent years, sedimentologists in the petroleum industry and academia have increasingly turned to ichnology to improve their facies models, to help identify key surfaces of relative sea level change and in some cases to date their strata. The aim of the symposium is therefore to provide a critical review of the ichnology of all the major depositional environments and the use of ichnology in ichnostratigraphic and sequence stratigraphic analysis as well as high-resolution palaeoenvironmental studies.

Provisional Programme

- 09.45-10.30 Registration, Tea, Coffee and Biscuits, poster viewing.
- 10.30-10.40 Introduction.
- 10.40-11.00 **Dr D. McIlroy** and **A. Taylor** (Ichron Ltd., Cheshire, UK): Review of concepts, recent advances and frontiers.
- 11.00-11.30 **George Pemberton** (University of Alberta, Canada): Stratigraphic applications of substrate-specific ichnofacies: delineating discontinuities in the rock record.
- 11.30-12.00 **Alfred Uchman** (Jagiellonian University, Krakow, Poland): Palaeoenvironmental and evolutionary problems of deep-sea trace fossils.
- 12.00-12.30 **Kerrie Bann** & Fielding, C.R. (University of Queensland, Australia): Ichnological distinction between non-deltaic shoreface and delta front facies.
- 12.30-13.30 Lunch and poster viewing.
- 13.30-14.00 **María Gabriela Mángano** & **Luis Buatois** (Tucumán, Argentina) Ichnology of Carboniferous tide-influenced environments and tidal flat variability in the North American Midcontinent.
- 14.00-14.30 **Jorge Genise** (Museo palaeontológico, Trelew, Chubut, Argentina): The role of ichnofossils in assessing palaeoenvironments of palaeosols.
- 14.30-15.00 **Roland Goldring** (University of Reading, UK), Pollard J., Cadeé, G., D'Alessandro, A., Gibert, J. & Gostin, V.: Climatic controls on trace fossil distribution in the marine realm.

- 15.00-15.30 Tea, Coffee and Biscuits, poster viewing.
- 15.30-16.00 **Richard Bromley** (Copenhagen Geological Institute, Denmark): A stratigraphy of borers and borings.
- 16.00-16.30 **Mary Droser**, Jensen, S. (University of California, Riverside, USA) and Gehling, J.G. (south Australian Museum, Adelaide, Australia).
- 16.30- 17.00 **Richard Twitchett** & Barras, C. (University of Bristol, UK) Trace fossils in the aftermath of mass extinction events.

Poster presentations

- Bann, K.L., Tye, S.C. & Fielding, C.R. "Ichnofacies analysis and High-resolution sequence stratigraphy of a complex coastal and shallow marine succession, the Early Permian Pebley Beach Formation, Sydney Basin, Australia".
- McIlroy, D. "A comparison of the ichnology of estuarine and non-estuarine tide-dominated depositional systems".
- McIlroy, D. "Stratigraphic ichnology of the Neoproterozoic-Cambrian transition in Finnmark, Norway".
- Manning, P.L. "Vertebrate palaeoichnological approaches to palaeoenvironmental and palaeobiological analysis and interpretation of vertebrate ichnocoenoses".
- Schlirf, M. "The characterization of depositional environments and identification of key surfaces of relative sea level change with the help of trace fossils: examples from the Upper Jurassic of the Boulonnais (northern France)".

More information

For further details, please contact the organiser, <dmc@liv.ac.uk>.

This meeting is sponsored by: Amerada Hess, BP, Exxon Mobil, Shell, Statoil, Total Fina Elf, the Geological Society of London and the Palaeontological Association.

To register for this meeting please contact the Conference Office as detailed below:

Lydia Dumont,
The Geological Society of London, Burlington House,
Piccadilly, London W1J 0BG (<lydia.dumont@geolsoc.org.uk>)
Tel: + 44 (0) 20 7432 0989 Fax: + 44 (0) 20 7494 0579

SYLVESTER-BRADLEY AWARD REPORT

Phylogenetic significance of the dicynodont basicranium

Anomodonts are herbivorous therapsids which arose in the Late Permian and widely spread over the world. Development of specialized mastication allowed them to consume vegetation much more effectively than other competitors and remained as major herbivores during the Late Permian and most of the Triassic. Specialized mastication was correspondent with appearance of a number of unique synapomorphies such as posterior expansion of premaxillae, development of edentulous beak formed by premaxillae and dentary, lateral expansion of dorsal process of the squamosal for extensive attachment of external adductor musculature, antero-posteriorly convex lateral articular facet of articular bone (Hopson, Barghusen, 1986). These synapomorphies gave dicynodont skull very distinctive appearance, but development of the universal type of mastication in the group also contributed to many convergences and obscured many evolutionary trends. This is probably one of the reasons that no consensus in dicynodont relationship has been reached in previous phylogenetic studies (e.g. Cox and Li 1983; King 1988; Angielczyk 2001) which were based mostly on superficial cranial characters with little reference to postcranium and inner cranial structures such as the basiptyergoid articulation and braincase. Phylogenetic significance of basicranial characters has been tentatively revealed during investigation of dicynodont basicranium of the Late Permian genera *Kingoria*, *Diictodon*, *Dicynodon*, and Triassic *Lystrosaurus*, *Rechnisaurus*, *Tetragonias*, *Kannemeyeria*, *Angonisauros*, *Stahleckeria* and *Rhadiodromus*. This research showed principally similar construction of braincase and basiptyergoid articulation in all investigated Triassic dicynodonts (clade Kannemeyeriinae *sensu* King 1988) and the Late Permian genus *Dicynodon*, but also revealed significant difference in appearance of these structures among Permian forms.

In attempting to determine phylogenetic significance of basicranial characters and obtain more specific data on basicranial evolution in dicynodonts, investigation of the basiptyergoid articulation and braincase among the Late Permian primitive toothed dicynodonts *Eodicynodon*, *Emydops*, *Pristerodon*, *Robertia* and advanced toothless *Aulocephalodon*, *Dicynodon* and *Diictodon* has been undertaken in the collection of the South African Museum in Cape Town. These data were combined with results of previous investigations on the Late Permian and Triassic forms that allowed completing of the data matrix of 19 genera (*Angonisauros*, *Aulocephalodon*, *Dicynodon*, *Diictodon*, *Eodicynodon*, *Emydops*, *Kannemeyeria*, *Kingoria*, *Lystrosaurus*, *Pristerodon*, *Robertia*, *Placerias*, *Rechnisaurus*, *Rhadiodromus*, *Sangusaurus*, *Shansiodon*, *Stahleckeria*, *Tetragonias*, *Uralokannemeyeria*) and 17 basicranial characters. The data matrix included representatives of all main clades of the Late Permian and Triassic dicynodonts recognized in the most recent systematics (King 1988; Angielczyk 2001) except clade *Endothiodon*+*Chelydontops* (Angielczyk 2001) which specimens didn't provide sufficient basicranial data due to incomplete material or preparation. Parsimony analysis and the

character compatibility permutation test of 99 random sets (PTP=0.01) suggested at the highest possible confidence level that the data set contains significant hierarchical structure, interpreted as a result of phylogeny. After safe taxonomic reduction (Wilkinson 1995) of the data set and deletion of *Shansiodon* and *Uralokannemeyeria* the branch and bound search, with *Eodicynodon* treated as outgroup, yielded a single most parsimonious tree (MPT; L = 30; CI = 0.633; RI = 0.814; Fig. 1 A). This tree broadly agrees with most recent hypotheses on the relationships among dicynodonts, but conflicts with some, that *Lystrosaurus* is part of a clade of Middle-Late Triassic anomodonts (King 1988, Angielczyk 2001) and supports early branching of *Kingoria* clade (King 1988). Topological constraints with inclusion of *Lystrosaurus* as a monophyletic taxon in the clade of the Middle and Late Triassic dicynodonts, and excluding *Sangusaurus* and *Rechnisaurus* (*sensu* King 1988, Angielczyk 2001), yielded a slightly shorter MPT (L = 29, CI = 0.655) with lower retention index (RI = 0.792). Application of constraint with offshoot of *Kingoria* clade later than *Pristerodon* and monophyletic *Robertia* and *Diictodon* (Angielczyk 2001) yielded longer MPT (L = 34, CI = 0.559, RI = 0.746), than just the monophyly for *Robertia* and *Diictodon* (King 1988): L = 31, CI = 0.613, RI = 0.797. Heuristic bootstrapping (1,000 replicates) and estimation of decay indices showed moderate to strong support for clades of *Pristerodon*+*Robertia*+*Diictodon*, *Kingoria*, *Dicynodon*+*Lystrosaurus*, and all Middle-Late Triassic forms including separate clade of *Angonisauros*+*Tetragonias* (Fig. 1 B). Consideration of the homoplasy level and fraction of synapomorphic changes in the basicranium revealed that the most informative characters concern the construction of the basiptyergoid articulation and inner braincase structures—widening of processus cultriformis, overlapping of posterior part of the interptyergoid vacuity, separation of the canalis vidii from the carotid canals, posterior termination of the interptyergoid vacuity by basitrabecular processes and exit of the canalis vidii there, shape of the dorsum sellae, presence of the longitudinal ridge on the braincase floor, position of the fenestra basicranialis, presence of distinctive pila antotica and reduction of floccular fossa (CI, RI = 1.00). At the same time features reflecting mostly superficial appearance of the basicranium—closely situated carotid canals on the ventral side of the parabasisphenoid, presence of double exit of carotid canals in the sella turcica, height of the dorsum sellae, presence of the ridge between tubera fenestrae ovaes and connection between petiotic and parietal, ridge along the junction of the pterygoids, swollen edges of the interptyergoid vacuity—tend to be less informative (CI, RI ≤ 0.75).

This work is the direct result of the Sylvester-Bradley award which allowed visit of the South African Museum and INTAS fellowship N° YSF 2001/2-046 as well as Royal Society/NATO fellowship of the year 2001 which allowed collecting basicranial data on some Permian and most Triassic dicynodonts.

Mikhail Surkov

Geology Institute of the University of Saratov, Moskovskaya 161, 410075, Saratov, Russia
<SurkovMV@info.sgu.ru>



References

Angielczyk, K.D. 2001. Preliminary phylogenetic analysis and stratigraphic congruence of the dicynodont anomodonts (Synapsida: Therapsida). *Palaeontologia Africana*, 37, 53-79.

Cox, C. B. and Li, J.-L. 1983. A new genus of Triassic dicynodont from East Africa and its classification. *Palaeontology*, 26, 389-406.

Hopson, J.A., Barghusen, H.R. 1986. An analysis of therapsid relationships. In: N. Hotton III, P.D. MacLean, J.J. Roth and E.C. Roth [eds] *The ecology and biology of Mammal-like Reptiles*. pp. 83-106. Washington and London: Smithsonian Institution Press.

King, G.M. 1988. Anomodontia. *Handbuch der Paläoherpetologie*, 17. Gustav Fischer, Stuttgart, 175 pp.

Wilkinson, M. 1995. Coping with missing entries in phylogenetic inference using parsimony. *Systematic Biology*, 44, 501-514.

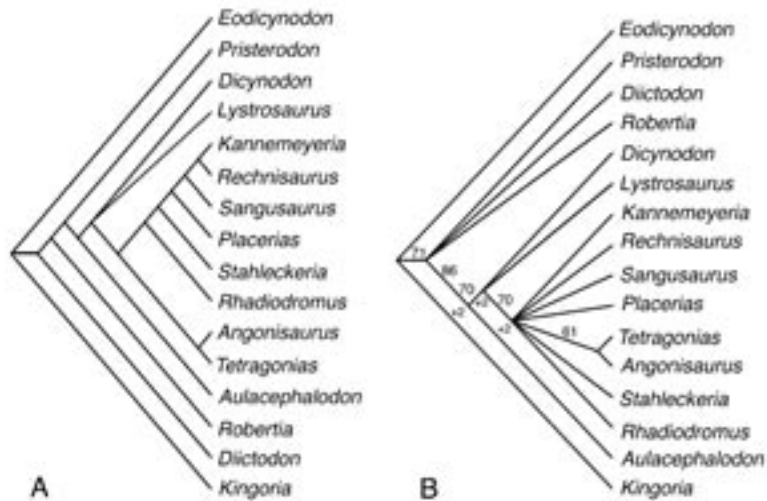
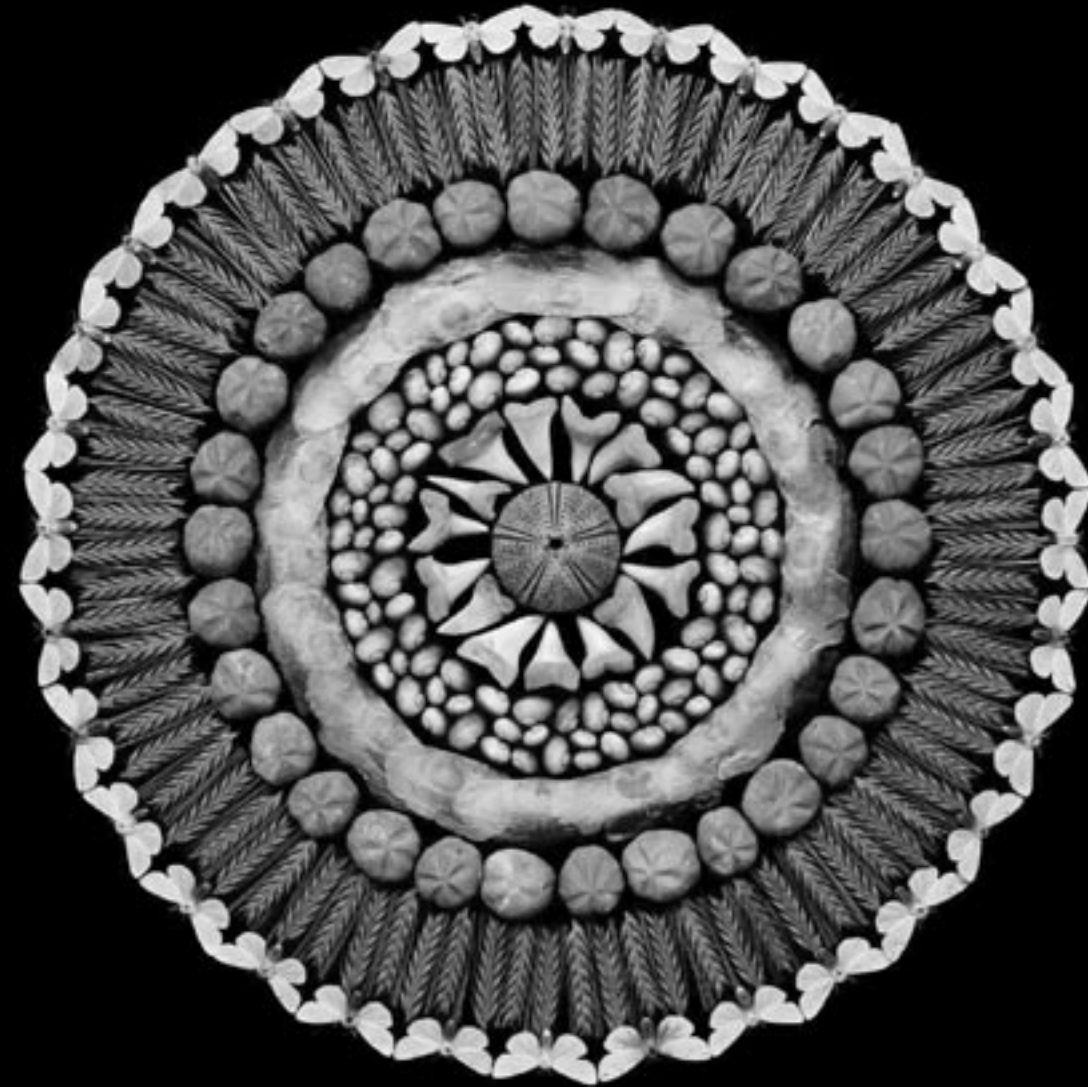


Figure 1. Most parsimonious hypotheses of the relationships of selected Late Permian and Triassic dicynodonts based only on data on braincase morphology. A, the most parsimonious tree after safe reduction (deletion of *Shansiodon* and *Uralokannemeyeria*). B, Heuristic bootstrap tree (1,000 replicates), bootstrap (only values > 50%) and Bremer support values (only indices >1) are shown.



systematics

Fourth Biennial Conference of the Systematics Association



Trinity College, Dublin, Ireland, 18-22 August 2003

INTERNET: www.systass.org EMAIL: systematics.conference@tcd.ie FAX: +353 (0)1 608 1147



CORRESPONDENCE

Technophilia and the black box

When I was asked to write this column I already had a topic in mind that I thought would be of interest to a broad audience of palaeontologists and biologists. I am particularly interested in the deep history of the Metazoa, and so far my research has focused on the use of morphological evidence and associated methodological aspects of using such data for reconstructing metazoan phylogeny. This is by no means a new field of research, and in many ways I continue to struggle with much the same issues that occupied the minds of the first generation of evolutionary biologists in the late 19th century. It is fascinating to realize that rather than Darwin's theory of natural selection, it was Darwin's theory of common descent that had the greatest impact upon biological practice in his own time (Bowler, 1996). This contrasts rather sharply with traditional historiography that came to conceptualize the Darwinian revolution in almost strict reference to debates about the mechanisms of evolution, in particular the theory of natural selection. In contrast, in the period immediately following the publication of *The origin of species*, attempts to reconstruct life's genealogy became the most popular research program in biology, initially flowering under the name 'evolutionary morphology' (Nyhart, 1995). For the first evolutionary biologists an interest in the processes of evolution appears to have been subsidiary to their chief focus on the reconstruction of the branching pattern of evolution, including the major branching points within the Metazoa. Interest in the reconstruction of the deep history of the Metazoa has never ceased since the early efforts in the 19th century, although at times it became a less visible part of zoology, notably with the rise of an experimental approach to biology at the end of the 19th century. Since the discipline of metazoan phylogenetics is rooted in such a rich historical matrix I intended to use this opportunity to dig up some conceptual fossils, not to reveal the undeniable value of past efforts for modern scientific progress, but to point out how past concepts can impede current progress in understanding animal evolution. However, the intended essay has to wait because two articles that I read this week unleashed some bottled emotions.

A technological advance unleashed a massive renaissance of interest in metazoan phylogenetics in the late 1980s and early 1990s when the development of computer software allowed for the analysis of comprehensive molecular and morphological data sets. Today phylogeneticists can choose from a wide variety of sophisticated techniques for the analysis of their data, including maximum-likelihood, Bayesian inference and the construction of a multidimensional vector space with species as end points. Although my recent move to a molecular lab now also opens these technological delicacies for my own delectation, my continuing interest in the use of morphological data guarantees that I will not entirely escape from the grip of maximum parsimony.

My continued reliance on PAUP and MacClade in this sophisticated age created somewhat of an identity crisis when I was a graduate student. The dismissal of cladistic parsimony in a citationless footnote in a major recent textbook of molecular systematics (Hillis *et al.*, 1996: 426) didn't help either! Being interested in reconstructing phylogenies I considered myself a

cladist. But when challenged to defend my intellectual commitment to others, I felt uncertain what it meant exactly to *be* a cladist. After all, cladists did not baptize their own discipline; instead cladistics received its name from the premier evolutionary systematist Ernst Mayr, and philosopher of science David Hull has branded words such as "cladistic" as 'weasel words' in reference to their remarkable conceptual plasticity that makes their precise meaning very difficult to pinpoint. Although I had taken several courses in phylogenetic systematics, including an advanced graduate level course, the philosophical underpinnings of the adopted methods received remarkably short shrift. Most of the time was spent on understanding the technicalities of the methods, and how to operate different computer programs. Consequently, I had to dig rather deeply into the literature on the epistemological foundations of cladistic analysis in search of some much craved intellectual *terra firma*. To render a long story short, I proceeded the way of most scientists according to Bowler (2000): we typically engage in methodological debate only when challenged to defend our views to others with differing approaches. My reading exercise restored my confidence in the logical soundness of doing low-tech cladistics with parsimony (in contrast to methods like maximum-likelihood that are impressive in the technicalities). Finding myself on firm epistemological ground, I could rejoice in the procedural simplicity of the method. This created some welcome peace of mind, because palaeontologists and biologists alike have no choice but to use standard cladistic analysis using parsimony for the analysis of morphological data sets.

However, unfounded doubts reappeared when I read two book reviews earlier this week. Sean Nee (2002) in a review of *The Nature of Diversity: An Evolutionary Voyage of Discovery* by D.R. Brooks and D.A. McLennan in *Nature* deplored the lack in this book of sufficient attention to "modern techniques" of phylogeny reconstruction such as maximum-likelihood and Bayesian inference. Nee states that he "did not carefully study the author's preferred recipe for phylogeny reconstruction; suffice it to say that it has such ingredients as 'Hennig's auxiliary principle' and 'Remane's criteria.' *Nature* readers will rarely encounter such arcana." In similar vein Peter Forey (Pal. Ass. Newsletter 50) commented in his review of *Fossils, phylogeny, and form. An analytic approach* on a chapter by McLennan and Brooks, taking issue with the "old fashioned Hennigian argumentation" presented in the chapter, including "characters viewed as transformation theories." Some readers may now think that I'm begging a bit too much from their indulgence in taking exception to some short dismissive comments in two book reviews. These short statements are either just that, not closely reasoned opinions, or else they are expressive of deep-seated convictions about something more important. I believe the latter.

Nee's qualification of Hennig's auxiliary principle and Remane's criteria as "arcana" of phylogenetic reconstruction reveals nothing more than his own ignorance of the fundamentals of parsimony analysis as practised by scores of biologists and palaeontologists using both morphological and molecular data sets. Translated into vernacular language, Hennig's auxiliary principle states simply that for the sake of phylogenetic analysis, observed similarities should be considered as potential homologies rather than being accepted *a priori* as parallelisms or convergences, while Remane's criteria are even more fundamental because they are criteria for the recognition of potential homologies in the first place (in this case morphological features). Without these fundamental ingredients phylogeny reconstruction becomes impossible in principle, irrespective of the nature of the evidence (molecular or morphological) or the methods employed (e.g. maximum likelihood or parsimony).

The fact that “readers of *Nature* will rarely encounter such arcana” has more to do with the policy of that particular journal than with anything else. Severe space limitations in journals such as *Nature* and *Science* do not allow any comprehensive discussion of data set compilation. Instead, the data sets are taken as given and at most a link is given to an appendix published online containing information about the nature of the data set. Forey’s labelling of “characters as transformation theories” as “old fashioned” is unintelligible in view of his use of standard cladistic software packages in his own work. Standard cladistic analysis is operationalized by the quantification of character state transformations, i.e. steps on a cladogram. Character states within a character are seen as different manifestations of the same homologous thing (character). Programs such as PAUP, MacClade, and Hennig86 are predicated upon this logic.

My major motivation for writing this piece, however, is that I consider the comments of Nee and Forey to be reflective of a deplorable attitude towards the only empirical anchor of phylogenetic studies, the data matrix. The following comments should not be taken as a critique of Nee’s and Forey’s own work, but workers in different fields have noted a recent shift from the attention directed towards construction of a robust data set towards the phylogenetic analysis of a given data set (e.g. Rieppel & Kearney, 2002). Recent practice in my own field of higher-level metazoan phylogenetics provides some striking illustrations.

The self-evident fact that the structure of the data matrix predominantly determines the outcome of a cladistic analysis hardly needs mentioning. Data matrix construction arguably is also the most difficult step of a cladistic analysis, and it is the only anchor that connects a cladogram to the empirical world. However, a remarkable paradox of cladistic practice then becomes apparent. This most important and difficult aspect of cladistic analyses has received strikingly little explicit attention, either theoretical or practical, especially when compared with the attention directed towards the extraction of phylogenetic signal from a given matrix. Typically we are presented with variations upon the minimally transparent statement that “the morphological matrix was compiled from various sources from the literature.” A larger section of the paper subsequently discusses aspects of cladogram construction, and finally the resulting topology is discussed with respect to topologies supported by other analyses. Character reassessment after tree building is an equally ignored aspect as data set compilation. This attitude is forcefully epitomized by a recent paper in *Nature* on the phylogenetic relationships within the Arthropoda. The authors (Giribet *et al.*, 2001) found it worth mentioning that they performed 120 independent phylogenetic analyses by varying sets of parameters and data partitions, “executed in parallel in the 256 processors, totalling two months of intense computation time using extremely effective tree search algorithms and an aggressive search strategy, equivalent to 42 years of computing time if analyses had to be conducted in a single-processor machine.” Strikingly, not a single character or character state transformation is mentioned in their paper! Instead, the characters are listed only in a supplementary appendix that can exclusively be accessed online. Although in this case space limitations may largely explain the adopted strategy, a study of data quality of five comprehensive phylogenetic analyses of the Bilateria or Metazoa published in the new millennium suggests there is reason for some concern.

The most striking conclusion of a study of all 604 characters included in the morphological data matrices of these five analyses is that the “absence” character states of almost 40% of the

characters are not properly defined (Jenner, in press). In all these cases, taxa with dissimilar morphologies were improperly united under the same character state, with the result that it is impossible meaningfully to interpret character state transformations on the resulting cladograms. These results signal that insufficient attention is directed towards insuring the quality of the phylogenetic data sets. One example illustrates the point.

One of the four unambiguous synapomorphies of the Bilateria in Nielsen (2001) is the reversal of a character coding the absence or presence of an adult brain derived from, or associated with, the larval apical organ. Comparison of the nervous system morphologies of the bilaterian phyla, however, clearly reveals that there is no empirical basis for this transformation. Among the phyla scored as lacking an adult brain derived from, or associated with, the larval apical organ are a) taxa without adult brains but with larval apical organs, such as Echinodermata; b) taxa with adult nerve concentrations that are formed separate from the larval apical organ, such as Chaetognatha and Gnathostomulida; and d) taxa with a larval apical organ and a brain derived from it, such as Cephalochordata. It can only be concluded that the reversal of this character to an unspecified character state in taxa with very dissimilar nervous system ontogenies and morphologies cannot be a reliable bilaterian synapomorphy.

Examples such as this indicate that the compilation of a data matrix should receive more attention that is current practice. Several past and present workers have levelled the criticism against cladistic analyses, that it allows one to produce results without careful character study. Obviously, you cannot blame the car for being driven by a bad chauffeur, for the explicitness of a cladistic data matrix should be a spur to careful morphological study.

Unfortunately, research into the phylogeny of the Metazoa has become unbalanced by the treatment of the data matrix as too much of a black box, while some of the most sophisticated techniques are subsequently employed to extract phylogenetic signal from the data set. Technological advances are one of the major driving forces of scientific progress, as is amply illustrated by the field of molecular systematics in which major efforts are exerted in the development of ever more powerful computers and software for the analysis of exploding data sets. The development of an immense parallel computing cluster in the molecular systematics laboratory of the American Museum of Natural History is a perfect example of the focus on such technological advances. However, there can also be too much of a good thing. The focus on technological advances is sometimes taken too far so as to become both a milestone and a millstone around our neck, as Richard Lewontin noted for his own development of gel electrophoresis used as a method for assessing intraspecific genetic variation (Lewontin, 1991). Population biologists promptly dropped many of their research topics to pursue the study of variation. However, the problems addressed by earlier research in population biology were not resolved. Whenever a workable technological advance is made available, researchers often jump on the bandwagon while dropping previous research concerns from consideration. Sometimes older techniques are simply superseded by the superiority of the new technology. However, in other cases an unwarranted “find ‘em and grind ‘em” mentality may arise, yielding plentiful results the significance of which may remain uncertain at best. The recent trend of crunching ever larger data sets to produce cladograms, the ‘quality’ of which is strictly assessed through quantitative support measures, indicates to me a technophilia taken too far.

References and further readings

- Bowler, P.J. 1996. *Life's splendid drama. Evolutionary biology and the reconstruction of life's ancestry, 1860-1940*. Univ. Chicago Press, Chicago.
- Bowler, P.J. 2000. Philosophy, instinct, intuition: what motivates the scientist in search of a theory? *Biol. Philos.* **15**: 93-101.
- Giribet G., Edgecombe G.D. and Wheeler W.C. 2001. Arthropod phylogeny based on eight molecular loci and morphology. *Nature* **413**: 157-161.
- Hillis, D.M., Moritz, C. and Mable, B.K. 1996. *Molecular systematics*. Sinauer Associates, Sunderland.
- Hull, D.L. 1988. *Science as a process. An evolutionary account of the social and conceptual development of science*. Univ. Chicago Press, Chicago.
- Jenner, R.A. in press. Boolean logic and character state identity: pitfalls of character coding in metazoan cladistics. *Contr. Zool.*
- Kluge, A.G. 2001. Parsimony with and without scientific justification. *Cladistics* **17**: 199-210.
- Lewontin, R.C. 1991. Electrophoresis in the development of evolutionary genetics: milestone or millstone? *Genetics* **128**: 657-662.
- Nee, S. 2002. Shaking the tree of life. *Nature* **419**: 435.
- Nielsen, C. 2001. *Animal evolution. Interrelationships of the living phyla*. Oxford Univ. Press, Oxford.
- Nyhart, L.K. 1995. *Biology takes form. Animal morphology and the German universities, 1800-1900*. Univ. Chicago Press, Chicago.
- Rieppel, O. and Kearney, M. 2002. Similarity. *Biol. J. Linn. Soc.* **75**: 59-82.
- Siddall, M.E. and Kluge, A.G. 1997. Probabilism and phylogenetic inference. *Cladistics* **13**: 313-336.

Ronald Jenner

University Museum of Zoology, University of Cambridge, U.K.
 <raj35@cam.ac.uk>

Sinking Teeth into Morphology through Cell Homology

Development is increasingly viewed as a panacea, the keystone that will unlock secrets of evolution that palaeontology alone cannot reveal. In this column we illustrate that, even if taxa known only as fossils were alive today, developmental data could only partially aid in determining the identity and affinities of both structures and taxa. The taxa we have chosen are conodonts, the fossil structures are conodont elements, and the developmental data include Raff's (1987) criteria for identification of cells as homologues and whether conodont elements are exo- or endoskeletal.

Conodonts are enigmatic creatures and conodont elements are enigmatic structures. On the basis of possible homologies of jagged fossilised elements that resemble aschelminth worm dental apparatus, gastropod radular teeth, hagfish teeth, coelacanth gill bar filter appendages, or teeth from beasts as yet unperceived, conodonts have been reconstructed as a bedazzling variety of invertebrates and vertebrates (Purnell 1999). Putative phylogenetic positions that conodonts might occupy could discombobulate traditional perspectives on skeletal development and evolution (Hall 1999; Donoghue and Aldridge 2001). For example, if conodonts were stem gnathostomes within jawless vertebrates (Donoghue *et al.* 2000), then enamel originated twice. Disconcertingly, the serrated elements provide almost exclusively the data with which cladistic analyses involving conodonts can be conducted (but see Aldridge *et al.* 1993 and Gabbott, Aldridge, and Theron 1995 for evidence concerning conodont notochord, segmented muscle, tail fin, and paired eyes).

Conodont elements are generally agreed to be skeletal, but both invertebrates and vertebrates contain exo- and endoskeletons. Were living conodonts available for study, could researchers assign conodont elements as exo- or endoskeletal, and would this identification aid in resolving the identity of conodont elements and affinities of conodonts? (This scenario might be considered less fanciful, if the reader recalls that coelacanths, which are hypothesised to possess larger bodies, once were thought to be extinct). We present briefly the techniques by which developmental biologists identify cell types and the interpretations that evolutionary developmental biologists would formulate on the basis of those identifications and homology considerations. Surprisingly, even with modern techniques, determining cell homology unambiguously is an arduous task. We suggest that, even with real specimens, the 'element enigma' would remain controversial, but the additional data that would be provided would elucidate greatly the 'conodont conundrum.'

As an intellectual exercise, we herein imagine that we have access not only to a living conodont, but to a well established, thriving breeding colony of living conodonts. We assume that we have at our disposal a complete molecular "toolkit," including a full complement of conodont-specific tracers, markers, and gene sequences, as well as data from microarray analyses, gene knockout or knock-in experiments, and so forth. We also assume, at the outset, that conodonts are vertebrates. How would we, as developmental biologists, go about analyzing whether conodont elements are exo- or endoskeletal?

The vertebrate skeletal system is developmentally composite. The exoskeleton is derived from neural crest cells. Exoskeletal elements develop in association with a basement membrane complex, are not preformed in cartilage, and share a phylogenetic history with dentine/enamel/oid coated elements of non-tetrapod craniates. The endoskeleton, on the other hand, derives from either neural crest or mesoderm. Endoskeletal elements arise secondarily, in that (developmentally) they are typically preformed in a non-osseous connective tissue (generally cartilage), which is then replaced by bone. In some endoskeletal elements, the cartilaginous precursor may have been lost phylogenetically (e.g. a membrane bone in a descendant with homology to an endochondral bone in an ancestor).

We cannot rely solely on position or gross histology. Positional data (superficial/external vs. deep/internal) can be misleading, and even in fresh tissue, exo/endoskeletal elements can be indistinguishable histologically and macroscopically. Certain aspects of exo- and endoskeletal development also may be similar. For example, according to current criteria, presence of a cartilaginous precursor (which is then replaced by bone) would identify the element as endoskeletal, but absence of such a precursor is less informative. Similarly, an exclusively mesodermal origin would exclude affiliation with the exoskeleton by definition, but a neural crest origin could indicate either. Furthermore, exoskeletal elements often develop in close association with the endoskeleton, as seen in the exoskeletal bones of the lower jaw which develop in the vicinity of, but are in no way causally connected to, Meckel's cartilage of the endoskeleton.

Thus, the first step in our developmental analysis would be to determine which cells give rise to the conodont elements, specifically (for the sake of illustration), whether they are neural crest derivatives. Raff (1987) outlined four criteria to identify homology at the cellular level:

1. Cells must come from the same precursor, germ layer (ectoderm, endoderm, mesoderm, neural crest) or embryonic region.

In theory, cell lineage analyses are straightforward. The four germ layers are established by the end of the neurula stage of craniate development. One must merely label cells from each region (either with vital dyes or genetic markers) and follow all of their descendants through each round of cell division, until the desired developmental stage is reached. Given the vast number of cells in most organisms, dilution of signal poses a significant problem. Vital dyes fade with each subdivision, and genetically marked cells are rapidly outnumbered (and effectively hidden) by unmarked cells. Another complicating factor is that neural crest cells migrate vast distances, arising in the embryo in a location that is not the final site of development of the skeletal element(s). Tracking neural crest cells is fairly straightforward during early migration but becomes increasingly difficult with increased time and distance from the neural tube.

2. Cells must have shared characteristics.

Cells are characterized by their morphology (shape, structural organization, composition), function (metabolism, synthesis and deposition of extracellular matrix) and behaviour (migration, interaction with other cells). All of these characteristics can be assessed by biochemical, immunological or physical staining properties. Most cells change their morphology, function and behaviour over the course of development, as they migrate or undergo differentiation. Cell markers are thus stage- (and species-) specific.

Neural crest cells have a characteristic morphology only as they emerge from the neural tube. And because neural crest cells have connections (physical and developmental) to both ectoderm and mesoderm, markers for both tissue types are commonly present; no cell markers exclusively label neural crest cells. For example, HNK-1 (a cell surface adhesion molecule) is necessary for neural crest cell migration. It can be used to label premigratory and migrating neural crest cells, but it only works in some species and the signal is often lost once the cells start to differentiate. HNK-1 also labels non-neural crest cells in target tissues. Other common neural crest markers, such as *Splotch/slug*, *Msx*, *Dlx*, and *Sox10*, are not found in all neural crest cells, and, furthermore, are expressed in a wide variety of other cell types.

3. Cells must share patterns of cell lineage-restricted gene expression.

As gene expression data are in many ways an aspect of morphology, their use means that we run into the same problems mentioned in the previous section. Evolutionary and developmental co-option of genes and gene networks is common. Thus, the gene expression pattern of a mesenchymal cell undergoing skeletogenesis may be very similar, whether the cell is derived from neural crest or mesoderm. (Given the hypothesized phylogenetic position of conodonts and differences in *Pax* gene expression between "gnathostomes" and lampreys (Murakami *et al.* 2001), *Pax* would be especially interesting to examine in conodonts for a possible role in development of the oral apparatus.)

4. Cells must have similar fates.

With the exception of red blood cells, cells rarely are completely (terminally) differentiated. State of differentiation is strongly influenced by extracellular environment. Many cells retain the capacity to dedifferentiate then redifferentiate as something else or, purportedly, to undergo a direct metaplastic transformation into a different cell type. At best, we would hope to determine a suite of characters consistent with a particular cell type, whether or not it is the terminal differentiated state. Furthermore, identification of cell fate is necessarily limited by what may be incomplete knowledge of currently existing cell types and modes of differentiation. Cells evolve.

It is possible that, using Raff's four criteria, we could identify whether conodont elements were derived from neural crest cells. If we alter our focus and apply these criteria to the level of tissues and organs, we may even be able to identify conodont elements as "teeth" (if they develop in association with a basement membrane complex, have the characteristic dentine/enamel/oid structure, etc.). But this is as far as development takes us.

The addition of phylogeny transforms this into an evolutionary developmental analysis. If conodont elements are homologous to vertebrate teeth, then they are exoskeletal regardless of where they occur in the body. Vertebrate teeth are never endoskeletal, though they may attach to endoskeletal bone. Interestingly, teeth (neural crest derivatives) only attach to endoskeletal elements that are also neural crest derived. Four interesting possible outcomes for conodont elements would be that they are:

- a) mesodermal or ectodermal (i.e. not derived from neural crest);
- b) not derived from neural crest but still homologous to teeth;
- c) that they are "true" teeth attached to a non-neural crest derived endoskeletal element; or even

d) that they are “homologous” to vertebrate teeth, but that other characters place conodonts well outside Craniata (teeth having evolved independently in conodonts and vertebrates).

Conclusions

Development does not release us from the muddle, it puts us into a muddle of a different sort. Developmental biology really only addresses cell lineage homology, and cell lineage homology does not translate directly to a statement of developmental, morphological or taxic homology. All other levels, including (ironically) developmental homology, can only be assessed through phylogenetic analysis. Potential for conflict abounds.

As stated at the outset, development is increasingly viewed as a panacea, the keystone that will unlock the secrets of evolution. But it isn't and it won't. Even if we had access to a complete genotype-phenotype map (which does not exist for any taxon), we still could not identify cells, tissues or organs in any evolutionary sense, because ontogeny does not (necessarily) recapitulate phylogeny! So although developmental analysis of our hypothetical breeding colony would not provide “the answer” to the conodont problem, the existence of such a colony might. Characters from living specimens could be used to increase robustness of phylogenetic hypotheses, and increased phylogenetic resolution strengthens assessment of homology at all levels.

References:

- Aldridge, R.J., D.E.G. Briggs, M.P. Smith, E.N.K. Clarkson, and N.D.L. Clark. 1993. The anatomy of conodonts. *Philosophical Transactions of the Royal Society, London*, **B340**: 405-421.
- Donoghue, P.C.J. and R.J. Aldridge. 2001. Origin of a mineralized skeleton. In *Major Events in Early Vertebrate Evolution*. (P.E. Ahlberg, ed.) Taylor & Francis, London. pp. 85-105.
- Donoghue, P.C.J., P.L. Forey, and R.J. Aldridge. 2000. Conodont affinity and chordate phylogeny. *Biological Reviews* **75**: 191-251.
- Gabbot, S.E., R.J. Aldridge, and J.N. Theron. 1995. A giant conodont with preserved muscle tissue from Upper Ordovician of South Africa. *Nature* **374**: 800-803.
- Hall, B.K. 1999. *The Neural Crest in Development and Evolution*. Springer-Verlag, Inc., New York.
- Murakami, Y., M. Ogasawara, F. Sugahara, S. Hirano, N. Satoh, and S. Kuratani. 2001. Identification and expression of the lamprey Pax6 gene: evolutionary origin of the segmented brain of vertebrates. *Development* **128**: 3521-3531.
- Purnell, M.A. 1999. Conodonts: functional analysis of disarticulated skeletal structures. In: *Functional Morphology of Invertebrate Skeletons*. (E. Savazzi, ed.) John Wiley & Sons Ltd., New York. pp. 129-146.
- Raff, R. 1987. Constraint, flexibility and phylogenetic history in the evolution of direct development in sea urchins. *Developmental Biology* **119**: 6-19.

Tim Fedak, Brian Hall, Wendy Olson,* Jon Stone, Matt Vickaryous

* Lead author for correspondence on this column

The Hall Lab, Department of Biology, Dalhousie University, Canada

<wolson@is.dal.ca>

Survival of the fittest... .. looking presenter?

Another academic year begins. I watch the dreadlocked, dungaree-clad mohair jumper-ed archaeology graduates from the University of York file past my window. I admire their fresh enthusiasm for a splendid subject, a subject whose success has often been fuelled, stoked and fanned by the media. I wonder at the subject's proficiency at capturing massive media coverage almost every week of the year, providing the public with a regular diet of human history. The archaeological media engine has been so thoroughly successful that at public lectures, newspaper, radio and television interviews I often find my archaeological viewpoint being sought! Methinks I am not alone?

I agree with Ed Jarzembowski (Newsletter, **49**) that the BBC's computer-generated leviathans have done much to enhance the public awareness of the palaeontological cast. However, the producers, directors and stage managers who generate the underpinning science are often an unseen component, given they might get in the way of a good story. It is sad that the TV sitcom 'Friends' has possibly done more for the public awareness of palaeontologists, but in this case, not palaeontology. It is clear that a balance between the data producers and their end science 'product' might provide a more complete view of the subject by the media.

There is certainly a thirst for palaeontological news stories and documentaries, but this is often tempered by the proviso of a dinosaurian or hominid spin on the story. Fish, amphibians or reptiles are often introduced as our, or the dinosaur's ancestor, descendent, missing-link, foodstuff or nemesis. It seems that the media often condemn many vertebrate groups to second-class 'medialutionary' significance when compared to dinosaurs and hominids. The inferiority complex felt by invertebrates does not even bear thinking about... or is that what dinosaurs ate?

The outlook is not too bleak; palaeontology will continue to find its way into the media. The Ten O'clock News still needs its '*and finally*' stories, as do the science pages of the broadsheets and plethora of remaining media. It seems ironic that the most recent media phenomenon, the Internet, is possibly the subject's greatest success story. The vast tracts of cyberspace occupied by palaeontological information is truly breathtaking, but so too are some of the inaccuracies!

It is clear that promotion of palaeontology can be effectively achieved via the diverse media available today; archaeology has already provided us with many working examples. '*Eduainment*' has its place, but this does not mean that the science and the scientists have to be removed from the final cut. If palaeontologists do not take part in the media, the television documentaries, newspaper articles or radio programmes will still be made, 'THEIR' way! Palaeontologists work hard to enhance our knowledge and understanding of the subject; we should also continue to work towards translating this science to a much wider, non-specialist audience.

As I sit and watch another Mick Aston clone pass my office window, closely followed by a Baldric, I wonder why palaeontology has been dealt such an apparently difficult hand. A

point on which I often reflect was raised at the Natures Treasurehouses (April, 2000) meeting at the Natural History Museum by Professor Richard Dawkins, '*Science doesn't have to be made fun, it already is*' and he went on to quote Einstein, saying that '*Science should be made as simple as possible, then simpler*'. Do the media only want the 'fun' elements of the subject, made as simple as possible for all to understand? If this is the case, is that such a terrible thing? The raw material of palaeontology is naturally written in stone, but its interpretation is often open to long debate and revision. With this in mind, to accuse the media of poor or rendered science is possibly not a useful approach, given the shifting sands of our subject. As Mark Twain so eloquently put it, '*There is something fascinating about science. One gets such wholesale returns of conjecture out of such a trifling investment of fact*'.

There is also something fascinating about the media. Palaeontology could gain such wholesale returns of public understanding for the science from such a trifling investment of collaboration. Ten years from now I might hope to see graduate palaeontologists filing past my window (who knows, even in York!), but will they be clones of Dave Martill, Mike Benton, Bill Oddie or does it really matter?

Dr Phil Manning

Keeper of Geology, Yorkshire Museum, York

Lecturer in Vertebrate Palaeontology, University of Liverpool

Publicity Officer, The Palaeontological Association

<palaeomedia@tiscali.co.uk>



An amateur palaeontologist, Brian Foster, unearthing a splendid Ichthyosaur for the cameras (Raising the Sea Dragon, BBC Knowledge)

Palaeontological Association Review Seminar

‘British Dinosaurs’

Convened by:

- **D.M. Martill (Univ of Portsmouth)**
- **M.C. Munt (Dinosaur Isle)**

To be held in:

- **Dinosaur Isle Museum, Isle of Wight**

Dates:

- **Wed 5th Nov 2003 (talks)**
- **Thurs 6th Nov 2003 (fieldtrip)**

More details in the next *Newsletter*.

>>Future Meetings of Other Bodies



Evolution and Development: interdisciplinary approaches
 Zoological Society of London, Regent's Park, London 21 November 2002

This workshop is sponsored by the Centre for Ecology and Evolution (UCL). For a map of the area please visit <<http://www.zoo.cam.ac.uk/ioz/location.htm>>. Organised by Dr Kevin Fowler <ucbhkof@ucl.ac.uk> and Dr. Hazel Smith <ucbhks@ucl.ac.uk>. Admission will be £6 (£3 for students and unwaged) payable on the door. Coffee and tea will be provided during the morning and afternoon breaks. The meeting will end with a wine reception. Evolutionary developmental biology is a wide-ranging research area of increasing activity and importance. This workshop brings together researchers from diverse backgrounds to highlight the most exciting current trends and consider future directions. Keynote speakers are Prof Paul Brakefield (University of Leiden, the Netherlands), Dr Anthony Graham (King's College London, UK) and Dr Andrew Hudson (University of Edinburgh). Other speakers include Dr Per Ahlberg (Natural History Museum, London, UK), Dr Martin Carr (University College London, UK), Dr Marty Cohn (University of Reading, UK), Dr Michael Frohlich (The Natural History Museum, London, UK), Prof. Paul O'Higgins (University College London, UK), Dr Sebastian Shimeld (University of Reading, UK), and Dr Richard Thomas (The Natural History Museum, London, UK). Participants are strongly encouraged to bring posters, but please e-mail <ucbhks@ucl.ac.uk> by 7th November with the title of your poster. To assist us in estimating numbers, please pre-register by 7th November by e-mailing <ucbhks@ucl.ac.uk> to confirm attendance.



Organic-carbon burial, climate change and ocean chemistry (Mesozoic-Paleogene)
 Burlington House, Picadilly, London, UK 9 – 11 December 2002

Geological Society of London, Marine Studies Group. This conference seeks presentations (oral and poster) on the major palaeoceanographic phenomena that characterized the 'greenhouse' world of the Triassic, Jurassic, Cretaceous and Palaeogene. Among the themes addressed will be results of recent ODP legs and multi-institutional programmes such as the Kimmeridge Drilling Project and C/T (Cenomanian-Turonian) Net. We solicit contributions on organic geochemistry and novel isotope systems as well as more established proxies that address the controls on the global carbon cycle and help elucidate its relationship to climate and oceanographic change. New data on the causes and effects of oceanic anoxic events, putative episodes of gas-hydrate dissociation, palaeoproductivity changes and equatorial and polar climate variability are particularly welcome. It is hoped that a number of papers can be published as a thematic set in the Journal of the Geological Society. Deadline for submission of abstracts is 1st November 2002. Abstracts of not more than one A4 page should be sent to Juergen Thurow (e-mail <j.thurow@ucl.ac.uk>).

Contact Juergen Thurow, Hugh Jenkyns <hughj@mail.earth.ox.ac.uk>, and/or Thomas Wagner <twagner@uni-bremen.de> for further details. For a registration form see the website <<http://www.geolsoc.org.uk/template.cfm?name=MSG2447>>



Secondary Adaptation of Tetrapods to Life in Water
 University of Otago, in Dunedin, New Zealand 9 – 13 December 2002

This meeting follows on from previous conferences in Poitiers and Copenhagen. Unsurprisingly, past meetings have included contributions on living and fossil marine mammals, reptiles and birds. Most contributions concentrated on evolutionary aspects of secondary marine adaptations, but some dealt with ecological patterns and functional and physiological complexes in living species. Similar themes are solicited for the next meeting. Please contact Ewan Fordyce <ewan.fordyce@stonebow.otago.ac.nz>, or see <<http://www.otago.ac.nz/geology/>>.



Society for Integrative and Comparative Biology (SICB)
 Sheraton Centre, Toronto, Ontario 4 – 8 January 2003

Please see <<http://www.sicb.org/meetings/>>.



British Columbia Paleontological Symposium
 Nanaimo, Vancouver Island, British Columbia 2 – 5 May 2003

The fifth British Columbia Paleontological Symposium will be held May 2–5, 2003, Malaspina University-College, Nanaimo, Vancouver Island, British Columbia, Canada. An exciting variety of presentations, workshops and field trips will appeal to all members of the professional and amateur palaeontological community. The Symposium will feature renowned vertebrate palaeontologist Dr Betsy Nicholls, Royal Tyrell Museum, as the keynote speaker, presenting "Ichthyosaur Update—Current Research on the Ichthyosaur Fauna from the Triassic of Northeastern British Columbia". Registration fee for the Symposium is \$65.00 CAD + GST before 1st April 2003. This fee includes the Welcome Reception, banquet, nutrition breaks and the Symposium abstract booklet. For more information visit the website <<http://web.mala.bc.ca/faep/paleo.htm>>



Bioevents: their stratigraphic records, patterns and causes
 Caravaca de la Cruz, Spain 3 – 8 June 2003

Pre- and post-meeting field-trips will be organized, with geological and/or cultural interest. During the meeting there will also be other scientific-cultural activities, related to Caravaca and the geological setting of the Murcia region. For further details contact: Diego Marín Ruiz de Assín, Secretaría de Bioeventos 2003, Ayuntamiento de Caravaca de la Cruz, 30400 Caravaca, Spain, e-mail <BIOEVENTOS@telefonica.net>.



Second Symposium on Mesozoic and Cainozoic decapod crustaceans
Oertijdmuseum de Groene Poort, Boxtel/Natuurhistorisch Museum
Maastricht, the Netherlands 3 – 6 September 2003

All aspects of decapod crustacean palaeontology, palaeoecology and palaeobiogeography will be outlined and discussed in two days of oral and poster presentations, grouped according to subject matter covered. Added to this is a full day of field work in the type area of the Maastrichtian Stage (Late Cretaceous), during which the crab-rich type Maastrichtian strata and the peculiar K/T boundary section of the Geulhemmerberg nearby will be visited (Maastricht area, southern Limburg, the Netherlands). Type material of all Late Cretaceous decapod crustacean taxa described in recent years will be on display at the Oertijdmuseum de Groene Poort, north of Eindhoven in the southeast of the Netherlands, for the duration of the symposium.

The second circular, with a preliminary programme and details regarding accommodation and submission of extended abstracts, will be sent out late 2002/early 2003.

For further information please contact Dr René H.B. Fraaije, <info@oertijdmuseum.nl> or Dr John W.M. Jagt, <john.jagt@maastricht.nl>.



Mantle plumes: Physical processes, chemical signatures, biological effects
Cardiff University / National Museum, Cardiff, Wales 10 – 11 September 2003

The meetings will be convened by Andrew Kerr (Cardiff University), Richard England (University of Leicester), and Paul Wignall (University of Leeds). Mantle plumes potentially link the Earth's internal convection with the evolution of life. The ascent of hot asthenospheric mantle beneath the lithosphere can be the catalyst for the formation of ocean basins, reshaping the Earth's surface, and the massive outpouring of lavas, ashes and gas can have significant effects on climate, destabilising the ecosystem and thus having the potential to dictate the course of evolution.

This meeting will address the validity of these links by bringing together geophysicists, petrologists and palaeontologists to discuss the current state of knowledge of mantle plumes and their effects on the environment through geological time. A two-day meeting will be held at Cardiff University and the National Museum & Gallery Cardiff on 10–11 September 2003. The key themes of the meeting will include: What do plumes tell us about mantle circulation? Where do they originate from, 670km? Can present plumes be used to infer the nature of past plumes? What are the sources of plume material? What can the latest petrological results tell us? What is the geology of plume related magmatism? What can we deduce about the frequency and magnitude of eruptions and their potential effects, from the recent and the past? Does the formation of large igneous provinces cause mass extinctions? If so, what is the kill mechanism? Why do most large igneous provinces slightly postdate the start of associated mass extinction events? Are they the final straw?



Specialist keynote speakers will be announced in forthcoming circulars. It is anticipated that selected papers from the conference will be published as a Geological Society Special Publication. Those interested in contributing to the meeting should initially send a provisional title, and authors, to Andrew Kerr. Abstracts will be requested at a later date. To register for future e-mail circulars please contact: Dr Andrew C. Kerr, Department of Earth Sciences, Cardiff University, Main Building, Park Place, Cardiff, Wales, UK. CF10 3YE (tel +44 (0) 29 2087 4578; fax +44 (0) 29 2087 4326; e-mail <kerra@cf.ac.uk>). The meeting website is <http://www.earth.cf.ac.uk/news/kerr_meeting.htm>.



The Rhynie Hot Spring System: Geology, Biota and Mineralisation
Aberdeen, Scotland 17 – 20 September 2003

An international conference and workshop on the Early Devonian Hot Spring System will be convened in Aberdeen, Scotland, on 17–20th September 2003. This meeting will serve as a forum for discussion on all aspects of the Rhynie cherts, and will aim to produce a synthesis of our current understanding of this unique Early Devonian ecosystem. Descriptions of new plants and arthropods will be presented, and studies of modern hot springs will provide analogues to explain the exceptional preservation of such biota. Models outlining the geological evolution of the Rhynie area, and the origin of the cherts in particular, will also be presented.

For further details please contact the convenors, Dr Nigel Trewin and Dr Clive Rice, at Rhynie Chert Research Group, Department of Geology and Petroleum Geology, Meston Building, King's College, University of Aberdeen, Aberdeen, Scotland, AB24 3UE; e-mail <rhynie@abdn.ac.uk>. Information about the Rhynie chert can also be found on our website at <<http://www.abdn.ac.uk/rhynie/>>.



8th International Symposium on Fossil Algae
Granada, Spain 18 – 20 September 2003

Following the decision of the closing meeting of the 7th International Symposium on Fossil Algae in Nanjing, the 8th ISFA will be held in Granada (Spain) from Thursday 18th to Saturday 20th September 2003. The aim of the Symposium is to provide a forum for all researchers interested in any aspect of the palaeobiology, biology and geological significance of calcareous algae and bacteria. Contributions on the biomineralization, taxonomy, evolutionary history, biogeography, ecology and palaeoecology, sedimentology and biostratigraphy of these groups will be welcome.

16–17 September: Pre-Symposium Field Excursion, Alicante.

18–20 September: Sessions, Granada.

21–22 September: Post-Symposium Field Excursion, Almeria.

The Pre-Symposium Field Excursion will focus on Cretaceous and modern Charales and Cretaceous dasycladaleans. Leaders: Bruno Granier and Carles Martin-Closas. The Post-Symposium Field Excursion will be devoted to Miocene microbial carbonates and Halimeda

bioherms, and Pliocene coralline red algae. Leaders: Julio Aguirre, Juan C. Braga, Jose M. Martin and Robert Riding.

For further details contact Juan C. Braga or Julio Aguirre, Departamento de Estratigrafía y Paleontología, Facultad de Ciencias, Universidad de Granada, Campus Fuentenueva s/n, 18002 Granada, Spain; e-mail <jbraga@ugr.es>, <jaguirre@ugr.es>.



International field seminar

Kerman, Iran 14 – 18 April 2004

Iran has a rich and varied geology, but much of it remains little-known outside the country. In Kerman Province (east-central Iran) there are especially well exposed and extensive sequences of Cambrian-Ordovician-Silurian-Devonian rocks, Jurassic-Cretaceous sediments, and Cenozoic rocks including sediments, metamorphic complexes and extensive volcanics. This notice is the first announcement of plans to hold a field-based seminar programme centred at the University of Shahid Bahonar, Kerman City. Estimated costs are US \$950 to include registration, accommodation, all meals and field transportation (students US \$600). Day 1: Introductory lectures on the geology of Iran. Days 2,3,4,5: Fieldwork covering four separate themes (Lower Palaeozoic-Devonian stratigraphy and faunas; Jurassic-Cretaceous geology and faunas; Cenozoic sediments, volcanics and structure; Economic geology including ore mineralogy and regional metamorphism). Each theme will run separately over the full four days of fieldwork, with co-ordination and guidance by local experts. For further details contact either Assoc. Prof. Mohammad Dastanpour (Department of Geology, Shahid Bahonar University, P O Box 76169-133, Kerman, Iran, Fax: [+] 98 341 2267 681, <dastanpour@mailuk.ac.ir>), or Prof. Michael G. Bassett (Department of Geology, National Museum of Wales, Cardiff, CF10 3NP, Wales, U.K. Fax: [+] 44 2920 667 332 <Mike.Bassett@nmgw.ac.uk>). For those who express an initial interest in participating in this programme, we anticipate sending a full circular and registration details in early January 2003. In responding to this first announcement, please state your specific area(s) of interest.



Ichnia 2004: First International Congress on Ichnology

Trelew, Patagonia, Argentina 19 – 23 April 2004

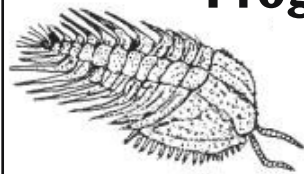
Aims and Scope: we have foreseen the necessity and convenience for convening a large, international meeting where researchers with a bewildering variety of backgrounds and interests gather to exchange their different views of Ichnology. It is expected that this exchange will strengthen our discipline and enhance its recognition from the scientific and technical community. We intend to trace, extend and fortify existing bridges between different fields of Ichnology, e.g. between palaeoichnology and neoichnology, vertebrate and invertebrate ichnologists, benthic ecologists and palaeoichnologists, soft and hard substrate ichnologists, etc. We strongly encourage the participation of a wide variety of non-ichnological scientists in the meeting. Should a soil scientist working on the micromorphology of modern earthworm

burrows and its destruction by trampling attend this meeting? What about a biologist or palaeontologist that works on biomechanical interpretation of extant or fossil organisms? Will an anthropologist contribution on human faeces or footprints be welcomed? Could a zoologist working on bioerosion or benthic bioturbation contribute to this meeting? The answer to all these questions is YES and we wish further to extend the invitation to petroleum geologists/engineers, wildlife biologists, reef biologists, trackers, entomologists, and any other scientist working on Ichnology-related issues.

The meeting will be held at the Museo Paleontológico Egidio Feruglio (MEF), located at the city of Trelew, in the Argentine Patagonia. The MEF is a modern Museum engaged in research and educational activities essentially related to the rich paleontological content of the Patagonia. Congress sessions will be held from 19 April to 23 April 2004. Pre, intra, and postcongress trips are scheduled. Preliminary symposia (to be confirmed) include: trace fossils and evolutionary trends; bioerosion in time and space; vertebrate ichnology; biomechanical and functional interpretation of trace fossils; the ichnofabric approach; applications of trace fossils in facies analysis, sequence stratigraphy and reservoir characterization; trace fossil taxonomy; ichnology and benthic ecology.

Visit the conference website for further details, at <<http://www.ichnia2004.com/>>.

Please help us to help you! Send announcements of forthcoming meetings to <newsletter@palass.org>.



Progressive Palaeontology GLASGOW

10 – 11 June 2003

Division of Earth Sciences,
University of Glasgow

- **Progressive Palaeontology is for postgraduates who wish to give presentations at any stage of their research.**
- **Any aspect of palaeontology welcomed.**
- **Oral and poster presentations**
- **Field trip and social events.**

Organisers: Alison Bowdler-Hicks, Jennifer England,
Claire Pannel, David Parkinson, Sarah Stewart

Division of Earth Sciences, Gregory Building,
Lilybank Gardens, University of Glasgow,
GLASGOW G12 8QQ

email: J.England@earthsci.gla.ac.uk
C.Pannel@earthsci.gla.ac.uk
D.Parkinson@earthsci.gla.ac.uk
S.Stewart@earthsci.gla.ac.uk

Book Reviews

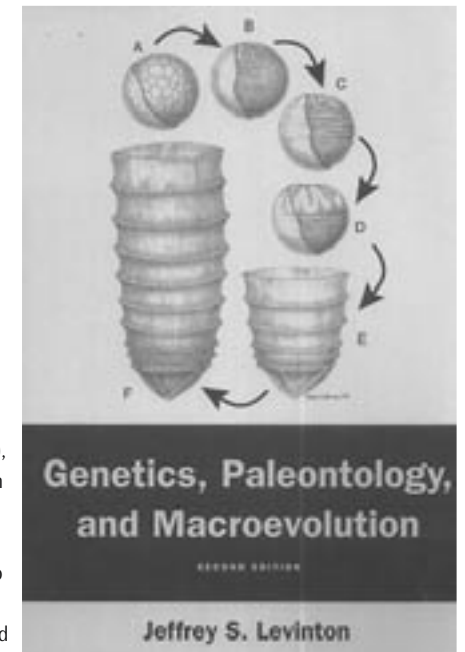
Genetics, Paleontology, and Macroevolution

Jeffrey S. Levinton (2001) Second Edition. 617 pp., Cambridge University Press. £ 37.95.

For a fossils lover like me to see that palaeontological evidence is taken seriously by a biologist is enough to make me happy. Jeffrey S. Levinton's book offers such a rare pleasure. The author does not seem bound by his disciplinary or methodological affiliation but uses a great variety of data to restore, interpret, and explain biological evolution, honestly selecting evidence solely on the basis of its heuristic value. Such an eclectic approach looks quite out of date (or rather *démodé*) in our days of extreme professional specialisation and probably it would be difficult to find anything comparable in the world's literature published in the last half century. Such was the situation when the first edition appeared in 1988 and not much has changed since.

It is hard not to sympathise with Jeffrey S. Levinton's commonsense attitude to science. Instead of just reviewing, classifying, and modifying concepts of other authors he seems to be interested in constructing a consistent and simple explanation for the structure of the living world. The integrative value of the concept of Darwinian evolution is self-evident in such a context. As long as evolution is explained by selection and random mutations, no difficulty emerges with applying to palaeontological research

the same methodological background of chemistry and physics which is the basis of inference in neontology. However, we have to be aware that whenever evolution is seen as a process extended in geological time, that changes dramatically. One enters then the field of phylogeny that refers to the unique history of life, and prone to all the weaknesses of historical sciences. Fortunately for the author, he does not attempt to make any practical use of his bold claim that "we have a set of physical and biological laws that might be used to construct predictions about the outcome of the evolutionary process" (p. 6), which sounds like a good piece of Hegelian historicism. In fact, Jeffrey S. Levinton seems largely uninterested in phylogeny, the subject offering a rather specific way to explain the complexity of the living world, not necessarily consistent with the standard



methods of natural sciences. He apparently prefers to avoid all those problems with entropy and laws of history.

This departure from the traditional approach to palaeontological evidence on evolution unavoidably influenced presentation of facts and ideas in the book. In old textbooks of palaeontology data on fossils are usually organised according to their phylogenetic meaning, and in principle any new fact could find immediately its precise place in a particular branch of the evolutionary tree (or a classificatory scheme). In the frame of a phylogenetic tree there is no difficulty with evaluating the importance of a discovery: either it represents a new branch derived from an earlier known evolutionary sequence or it offers a connecting link within a lineage. Its geological age, geographic location, and morphological traits are then all of equal importance. But, if one is not satisfied with such historical attitude, it remains just to illustrate a specific thesis with arbitrarily chosen case studies, paying little attention to their time-and-space coordinates. This is the way textbooks of ecology are written and Jeffrey S. Levinton's book has a similar organisation.

Regarding the palaeontological evidence presented in the book, the author's choice could easily be disputed especially with respect to the exaggerated (if existing at all) problem of stasis and sudden change. Haldane's paradox (that the palaeontologically documented rate of evolution is too slow to make natural selection the only driving force of morphological evolution) is the core of the problem. The author apparently failed to notice that this particular feature of the fossil record contradicts his claim that "the process of speciation [...] occurs on a timescale that is inaccessible to [...] paleontology" (p. 155). In fact, this is a misunderstanding of the fossil record equally clear as common. Speciation is truly a problem for palaeontologists but for completely different reasons—these are the geographic dimension of the process, which makes it impossible to document splitting of lineages in a single geological section, and a generally poor correspondence between the genetic isolation of populations and their morphology. Paradoxically, only phyletic evolution is directly observable in strata. However, speciation is nothing more than a divergent evolution of geographically separated populations, and eventually their genetic isolation must result in a morphologic distinction even in cases of initially undistinguishable sibling species (note that morphologic distinctions may also precede development of a genetic barrier). Jeffrey S. Levinton's claim that Haldane's paradox "is solved completely" because "slow change is rather a net effect of longer-term shifts and evolutionary reversals, which may or may not lead to a net change" (p. 301) is simply not true. To the best of my knowledge, there is enough evidence from bed-by-bed sampling of various fossil organisms that their evolution remains directional (although not necessarily linear) irrespective of the achieved time resolution. Probably we have to accept that a supply of evolutionary novelties is truly the limiting factor of the morphologic change.

I wholeheartedly concur with the core ideas of the book that:

1. There is no macroevolution. All phenomena of evolution are explainable within the same framework of theories connected with, or derived from, the Darwinian theory of evolution by natural selection.
2. Taxa are human concepts, not objectively existing entities. "The deep-seated belief in types derived from an essentialist philosophy" (p. 13; one may perhaps add that the human mind works easier while classifying and has difficulty with visualising processes of a smooth transformation).

Nevertheless, as Jeffrey S. Levinton admits, "to this very day, the taxic approach rules" (p. 25) and a significant part of the book relies on it, referring mostly to data assembled by followers of the school of quantitative palaeobiology. One may thus wonder why implications of the recent revolutionary changes in the philosophy of taxonomy, so destructive to the "taxic approach", are virtually ignored by the author. Readers have to be satisfied with a brief note that "current studies of taxonomic survivorship or diversity [...] could benefit from the retention of the evolutionary systematics' frame of reference" (p. 67).

Actually, not much space was offered in the book to "macroevolution", if it is understood as a large-scale morphological change, apart from its title and introductory definitions. The avoidance of phylogeny spoils especially the newly added chapter on the Cambrian "explosion". Much of it is a presentation of the history of Burgess Shale research and a polemic on contemporary authors. Fossils appear to be of little importance in argumentation and the author seems to be just satisfied that they are not too much different from Recent animals. Implications from the recent discoveries of the most ancient animals to the understanding of their phylogeny are barely mentioned. No comment is given on the fact that the discoveries of Cambrian embryos (one of them presented on the book's cover) support the idea that planktonic larvae (and consequently Lophotrochozoa) are phylogenetically late, that the concept of Ecdysozoa has good palaeontological support, that taphonomy may be of more importance than evolution in explaining the distribution of Precambrian and Cambrian faunas, and so on.

Even though Levinton avoids dealing with the historical aspects of evolution, his book is a good and helpful historical review. A review of the evolution of evolutionary biology in the last three decades (most publications referred to are from the seventies and eighties of the last century). Probably without at least a superficial knowledge of the disputes which stimulated development of our branch of science in those days, it is not possible to understand its present status. Jeffrey S. Levinton was at the centre of discussions all that time. Few people have enough knowledge of such diverse areas of science to compete with him in an authoritative presentation of these matters. The book is thus worth reading and having on the desk.

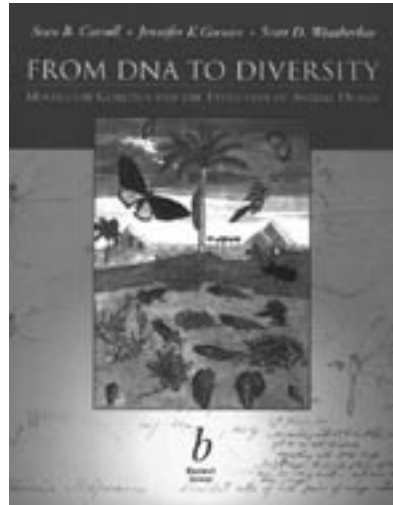
Jerzy Dzik

Instytut Paleobiologii PAN, Twarda 51/55, 00-818 Warszawa, Poland
<dzik@twarda.pan.pl>

From DNA to Diversity. Molecular Genetics and the Evolution of Animal Design

Sean B. Carroll, Jennifer K. Grenier and Scott D. Weatherbee. 2001.
Blackwell Science, Inc. xvi + 214 pp. Paperback. ISBN 0-632-04511-6. £33.95

The field of animal evo-devo serves its many fans well. Within the last two years three major new books have been published on the intricacies of animal evolution as seen from a molecular developmental genetic perspective. In 2001 Eric Davidson published his *Genomic Regulatory Systems*, and Sean Carroll and co-authors published *From DNA to Diversity*. This year Adam Wilkins' *The Evolution of Developmental Pathways* appeared, and next year another major publication is planned by Alessandro Minelli to be titled *The Development of Animal Form*. One might wonder whether this publication wave may not over-saturate the prospective audience,



but such a fear would be ungrounded. Although Wilkins' book so far sits mostly unread on my bookshelf, and although I have only seen the planned list of contents of Minelli's book, the field of evo-devo offers enough ground to cover and new developments worth reporting that these four books will be largely complementary to each other, or at least provide differing perspectives on interesting issues.

From DNA to Diversity is an attractive book, richly illustrated, and truly an 'easy' read. The book is a perfect introduction for students interested in evolution and development, and for those possessing already some background in molecular and developmental biology the modular nature of the book makes it perfectly suited for intermittent readings. That is not

a trivial thing to mention because I find texts on developmental genetics notoriously difficult to read. The main messages of such works have to be extracted from dense narratives strewn with scores of different gene and protein names and their abbreviations that often hold no relationship to the molecules' functions. Not surprisingly, students may see their enthusiasm for developmental genetics shrinking when confronted with the memorization and understanding of the myriad details of animal development as reported in such works as Adam Wilkins' *Genetic Analysis of Animal Development* (as happened to more than a few students during the course of developmental genetics that I took as an undergraduate). Carroll *et al.* keep technicalities to a bare minimum, and it is therefore a delight to read this book and have the general messages served to you on a plate. However, there is enough detail in the book to prevent it from being a boring read. Given the frantic pace of our modern lives combined with the almost universal complaint that there is simply not enough time even to keep up with what is published in one's own field of expertise, let alone to read broadly into other areas of science, this book presents a perfect solution for those interested in the link between DNA and diversity.

The book is divided into seven chapters with a short list of selected readings at the end of each chapter. Chapter one presents a "Brief History of Animals," introducing the metazoan fossil record, animal phylogeny, some basic characteristics of animal design, and it ends with the posing of the question how the evolution of animal diversity can be related to evolutionary changes in developmental programs that are hardwired in the DNA of animals.

Chapters two and three successively introduce the fundamental components of the genetic toolkit for animal development, and how this toolkit is employed to orchestrate the development of animal design. The examples are mostly taken from the detailed research that has been performed on model systems such as the fruit fly *Drosophila*, and the mouse and chicken. Homeobox genes, *Hox* genes, other transcription factors, signalling pathways, pleiotropy, organizers, morphogens, and the development of animal backs and bellies and anteroposterior axes, insect wings, and vertebrate limbs all pass in review. After reading these



two chapters the reader is equipped with some basic understanding of the general toolkit components that animals use to build their bodies, and the general logic of how gene expression is controlled in the differentiation of cell types, tissues, organs, and overall body organization.

Chapter four discusses "Evolution of the toolkit" to show how developmental regulatory genes and their function may change during evolution. Chapters five and six are concerned with how gene regulation, including the level, timing and pattern of gene expression, may evolve, and how this relates to changes in the morphology of organisms, including the origin of morphological novelties. A wide range of examples is discussed where changes in the gene expression patterns and their regulation are correlated with changes in morphology, ranging from the evolution of insect wing numbers and butterfly wing coloration patterns, to the evolution of paired appendages and neural crest cells in vertebrates. However, in some instances the added value of a genetic perspective for understanding the evolution of animal design may appear rather limited. For example, the development of vertebrate scales, hairs, and feathers show differing activities of several signalling pathways, but does that really help us understand the evolution of morphology better? In many cases, research has simply not yet progressed far enough or deeply enough to provide more than a translation of a vexing problem in the evolution of morphology into molecular terms. If we learn that the development of different morphologies is associated with different timing, patterns, and levels of expression of the same genes, but if we lack any data on the actual regulation of the expression of these genes, then our conceptual gain is limited. However, Carroll *et al.* treat enough different examples to flesh out some genetic rules of development across the animal kingdom, and at least their suspected role in the evolution of phenotypes.

The final chapter concludes the book by taking a look at the nature of raw genetic variation underlying morphological variations found within species, and that may be offered to the scrutiny of natural selection. Particular attention is paid to variation in the *cis*-regulatory sequences of genes, which are the sites for the binding of transcriptional regulators of genes. Carroll *et al.* conclude by stressing the importance of changes in regulatory DNA for the evolution of animal morphology.

Although "poetic," "stunning," "excellent," "crisp," "exciting," and "outstanding" are some of the telltale (and largely deserved) adjectives characteristic of the "incandescent praise" for this book offered by several "noteworthy luminaries," this common man nevertheless feels that a few critical comments can be made. Apart from a few typing errors in the text, 'metazoan' is frequently written with a capital 'M,' while the status of the 'Onychophora' as a 'minor' phylum appears to be endorsed by the consistent failure to use a capital 'O' (including in the glossary). One is reminded of Cuvier's embranchements when echinoderms are described as radially symmetric. When the paralogous *engrailed* 1 and 2 genes are discussed, the *engrailed* 1 genes are considered to be "more closely related to one another" than to the *engrailed* 2 genes from the same paralogy group because they share a "more recent common ancestry." Such a short statement on the difficult issue of relating gene histories and species histories is more likely to yield confusion than enlightenment. In terms of recency of common ancestry, as for example defined by cladogenesis during evolution, paralogs resulting from a single duplication event are by definition equally closely related because they arose at the same moment in time. However, the authors appear to reify the *engrailed* gene tree as a species tree, an extrapolation that



cannot be upheld because the *engrailed* paralogs did not originate through cladogenesis. This difficult issue could have benefited from a more detailed discussion. I consider this example as symptomatic of the overall flavour of the book, especially with respect to the treatment of subjects that are not developmental genetics. Although a lot is included in the book, a lot is left out, and not all with equal justification. For a book that recognizes the merit of “integrating the study of palaeobiology, comparative embryology, and developmental genetics,” rather short shrift is given to several important subjects, including metazoan phylogenetics, information from the fossil record about body plan evolution, and an explanation of systematic methods used to extrapolate from particular examples to the general significance of regulatory changes during animal evolution. A few examples follow.

At a general level the attention given to explaining the nature and importance of outgroups for evolutionary comparisons is minimal. Onychophora and Cephalochordata are demoted to the role of “outgroups” of Arthropoda and Vertebrata respectively, and it is concluded that the “resemblance of these animals to their extinct ancestors has led them to be called ‘living fossils.’” Consequently, the genetic toolkit these taxa possess is supposed to be reflective of the state of the toolkit before the radiation of arthropods and vertebrates respectively. Although the importance of nearest relatives for deducing ancestral characters in diverse taxa is undisputed, the adopted reasoning comes perilously close to considering recent onychophorans and cephalochordates as stand-ins for Uarthropoda and Uvertebrata. Of course, the authors will immediately counter by saying that this is merely a simplification, but it nevertheless may seriously distort the views of the uninitiated. The problem is that Onychophora and Arthropoda, and Cephalochordata and Vertebrata are considered sister taxa. Without a third group to root the direction of evolutionary change one might argue with equal justification that a given extant vertebrate could stand as a model for the ancestral cephalochordate, and that a given extant arthropod can inform the characters present in the ancestor of the Onychophora. The use of the vague term “basal” throughout the book also indicates the need for a more rigorous discussion of phylogenetic concepts. Carroll *et al.* call echinoderms basal deuterostomes. Given the supplied phylogeny, one could with equal justification call urochordates basal deuterostomes, or arthropods basal ecdysozoans. The addition of a few sentences to the discussions would make these issues much clearer to a novice, and for a book of just over 200 pages, space limitations appear not to be an issue.

The role of fossils in understanding animal body plan evolution is also effectively ignored. Of course, the author’s aim is to illuminate animal evolution from a gene’s eye perspective, but some omissions are striking. In a paragraph entitled “Evolution of the echinoderm body plan” no mention is made at all of the extensive echinoderm fossil record, including the controversial but vitally important carpoids. The preceding paragraph about the evolution of the snake body plan only provides the thinnest veneer of an ecological and palaeontological context. By stating that “body elongation and limblessness are associated with burrowing,” and by the inclusion of two fossil snakes in the accompanying cladogram, the authors apparently consider both bases sufficiently covered. Here, I think the authors forego a precious opportunity for exciting students by introducing some of the “messiness” that is science in action. Throughout the last five years, there has been a vigorous debate about the evolutionary origins of snakes, primarily motivated by new fossils and their phylogenetic systematization. One prominent new hypothesis is that



snakes are not the descendants of small burrowers, but instead they are the closest relatives of some of the largest predators that have ever roamed the Earth: the mosasauroids. This evidence and recent new evidence for the cladistic placement of fossil snakes basal to extant snakes (work by Michael Lee and John Scanlon) instead argue for the evolution of an elongate snake body and the loss of limbs as taking place in a marine or at least semi-aquatic setting, of primitively large animals. The hypothesized re-evolution of hindlimbs in the fossil snakes as depicted in the cladogram in the book would then be an unnecessary hypothesis. These findings provide an entirely different context for the discussion of the origin of snakes than the classic scenario. For a book with the “evolution of animal design” in the title such additions to those parts of the text where discussions are not strictly limited to model systems could make for a more interesting read.

The preface of a popular textbook in developmental biology states that doing developmental biology is a reward for students who have done well in molecular and cell biology. With the addition of phylogenetic and palaeontological perspectives to the synthetic discipline of evolutionary developmental biology, teachers would do well to provide a balanced treatment. I think the book reads like a textbook, which reflects both a strength (concise, clear exposition) and a weakness (some topics are overly simplified). However, despite the fact that some readers may find the book a bit scrawny as a meal, it is most definitely a tasty appetizer.

Where Edward O. Wilson spoke of taxonomists as “stewards and spokesmen” for the biodiversity on our planet, so have Carroll, Grenier and Weatherbee effectively disseminated the importance of regulatory evolution for the evolution of animal body plans to a wider audience. Their simplest take-home message can be epitomized in the words of the eminently paraphrasable Dobzhansky: “nothing in evolutionary biology makes sense, except in the light of changes in regulatory DNA.” If you want more, read the book.

Ronald Jenner

University Museum of Zoology, University of Cambridge, UK

<raj35@cam.ac.uk>

The Primate Fossil Record

ed Walter C. Hartwig. Cambridge University Press, Cambridge.

ISBN: 0 521 66315 6. £120.

In 1979 Fred Szalay and Eric Delson published a comprehensive review of the fossil record of primates, *Evolutionary History of the Primates* (Academic Press, San Diego). To the growing dismay of a great many students, it was to remain the only such treatment for more than 20 years. During that time, the number of known species of fossil primates more than doubled, new finds, notably from Asia, but also from North Africa, vastly increased our insight into the early evolution of anthropoid primates, while, in Africa, the race to find the earliest members of the human lineage has taken us ever further back in time and is now establishing itself in the Late Miocene. *The Primate Fossil Record*, edited by Walter C. Hartwig, is the long awaited up-to-date review of these and the many other significant developments of the past 20 years. For the production of this volume, Hartwig succeeded in securing the participation of many of the world’s leading authorities on particular aspects of primate evolution.

Following a summary of current hypotheses on the origin of the order Primates, *The Primate Fossil Record* is structured into five main parts: “The earliest primates and the fossil record of prosimians”, “The origin and diversification of anthropoid primates”, “The fossil record of early catarrhines and Old World monkeys,” “The fossil record of hominoid primates” and finally “The fossil record of human ancestry.” Each part contains several chapters, which review a specific group of fossil primates. These chapters all follow the same framework and include an Introduction, followed by sections on the History of discovery and debate, Taxonomic framework and Evolution of the group. There is an introductory chapter for each major radiation of fossil primates.

The History of discovery and debate sections are a great success. By including them, Hartwig hands the reader a tool to form a personal judgement regarding the soundness of past and current interpretations of the fossil record. The sections are informative throughout and many of them make for enjoyable and entertaining reading. The Taxonomic framework sections include the list and descriptions of the taxa. Inevitably, as an edited volume, *The Primate Fossil Record* is not as coherent throughout as a single author treatment would have been, and this is particularly apparent in the Taxonomic framework sections, where various contributors use different taxonomies. In his introductory chapter, Hartwig states that (p. 1) “Although classifications are presented ... we stress that they are means to the end of putting the genera into context, rather than ends in themselves. We encourage students to arrive at their own taxonomic frameworks by using this book to assemble the primary literature and understand what has been debated until now.” This is a fair point. However, readers should be aware that the ensuing lack of uniformity can be confusing. Chapter 20 (European hominoids), for example, lists *Griphopithecus africanus*, a new combination, as a member of the hominoid family Griphopithecidae. The same species is discussed in Chapter 22 (Middle and Late Miocene African hominoids) under its usual name, *Equatorius africanus*, and as a member of the hominoid family Hominidae. An associated example is the definition of Hominidae, which varies widely between chapters. The Evolution section gives authors the opportunity to focus on a particular aspect of the evolution of a group based on their particular area of interest and the specific characteristics of the group. In their excellent chapter on

Quaternary Malagasy lemurs, for example, Godfrey and Jungers concentrate on the factors that may have driven the dramatic extinctions which Malagasy lemur faunas have suffered since the arrival of humans on the island 2,000 years ago. In contrast, Gebo provides a substantial discussion of adapiform post-cranial adaptations. Not all the Evolution sections are equally strong, however, and some do not go much beyond reiterating suggested taxonomic relationships.

An important attribute of a reference volume is how much information it contains and how easily it can be accessed. *The Primate Fossil Record* contains an enormous amount of information



both in the text and through its literature citations. It includes all species of fossil primates known at the time of submission, nearly all of them accompanied by anatomical descriptions and many of them illustrated. The drawings and photographs of specimens are generally both good quality and informative. A weakness is perhaps the absence, in the form of a list of synonyms, of a systematic reference to taxa that are no longer considered to be valid. This can make it difficult to square the content of this current review with the earlier literature, without first reviewing the systematic history of a taxon. However, the sections on the History of discovery and debate do go some way towards filling this gap. And, of course, with its substantial list of references, *The Primate Fossil Record* provides the student with an ideal starting point for a full-scale investigation into a taxon's history.

I can recommend *The Primate Fossil Record* to students and professionals alike. Besides aiding in their research, it will also, in particular thanks to its History of discovery and debate and Evolution sections, be a great resource to those who teach primate evolution. Unfortunately, those operating on a limited budget may find its price a bit painful. Students should be warned, however, that although the primary references (those describing new fossils) are listed at the end of each relevant chapter, all other references (60 pages of them!) are combined at the end of the book. Photocopying of individual articles will therefore only be of limited use. Libraries may need to obtain multiple copies!

Looking ahead, I hope we will see another update of the primate fossil record before its species diversity doubles again. As it currently stands, the rate of discovery of new species of fossil primates shows no sign of slowing down and some pretty phenomenal gaps remain to be filled in the primate fossil record. For example, at least 20 and possibly more than 30 million years of the evolution of the Malagasy lemur lineage are virtually uncharted, as is indicated by the age of the oldest known representatives of their sister group, the lorisiforms. In another important example, there is a complete lack of fossil evidence regarding where or when the order Primates originated. Articles published since *The Primate Fossil Record* went to press have already shed some light on both these issues. First, the presence of a putative lemur in the Oligocene of Pakistan (Marivaux *et al.* 2001) is set, if confirmed, to challenge traditional views of primate evolution. And second, the results of a recently developed statistical approach suggest that the last common ancestor of living primates lived more than 80 million years ago, some 25 million years before the first known primate fossils (Tavaré *et al.* 2002). Not all the existing gaps will eventually get filled, but I hope that many of them will and the omens are good for a lot more exciting material to be discovered in the near future.

Christophe Soligo

Human Origins Group, Department of Palaeontology, The Natural History Museum, UK
 <C.Soligo@access.unizh.ch>

References Cited

Marivaux, L., Welcomme, J.-L., Antoine, P.-O., Métais, G., Baloch, I. M., Benammi, M., Chaimanee, Y., Ducrocq, S., and Jaeger, J.-J. (2001). A fossil lemur from the Oligocene of Pakistan. *Science* **294**: 587-591.

Tavaré, S., Marshall, C.R., Will, O., Soligo, C., and Martin, R.D. (2002). Estimating the age of the last common ancestor of extant primates using the fossil record. *Nature* **416**:726-729.

Exceptional Fossil Preservation. A unique view on the evolution of marine life

Eds. David J. Bottjer, Walter Etter, James W. Hagadorn and Carol M. Tang. Columbia University Press. 2002, 512pp. ISBN 0231102550 £32.50 (pbk); ISBN 0231102542 £71.50 (hbk)

If you were asked to pick your top dozen exceptional faunas of all time, which would you include, which would you omit, and on what criteria would you justify your choice? It's probably not as straightforward as it sounds. This well produced book provides case studies of the palaeobiology, palaeoecology and taphonomy of eighteen exceptional faunas, ranging in age from the Vendian to the Eocene. The inclusion of some faunas, Burgess Shale, Chenjiang, Mazon Creek, Solnhofen, would probably make everyone's top dozen; the inclusion, and exclusion, of others would probably provoke more discussion. Perhaps some less obvious choices merit inclusion simply to bring them to wider attention? The unifying theme in the choice of faunas for this book is their preservation within marine environments; the emphasis on European and North American examples reflects the geographic focus of most research to date. There is, however, probably sufficient known about other important faunas that a case could be made for their having been included; for example, the importance of those from the late Neoproterozoic Doushantuo Formation of China is acknowledged.



The book itself is an extremely readable synthesis of the information currently available on each fauna, including balanced reviews where interpretations of the available evidence conflict. Both the volume of literature cited and how up to date it is are particularly impressive. The quality of illustrations is high, particularly the photographic images; the ornamentation used in a minority of the line drawings is a little overpowering. The photographic illustrations are exclusively of representative taxa from each fauna; complementing these with high resolution images of the detail in which tissues can be preserved in some of these faunas would have conveyed a stronger impression of what the term 'exceptional' includes. These quibbles are minor: the stated goal was "to present an easily accessible casebook of marine Lagerstätten with exceptional macrofossil preservation, outlining and illustrating the great variety in styles of preservation, the types of organisms preserved, the mechanisms that led to such preservation, and the lessons to be learned from this type of fossil deposit." The editors (who individually also contributed the majority of the chapters) and publishers have succeeded admirably, and at £31.50 sterling the book represents good value for money to boot.

Who should buy it then? In recent years significant advances in our understanding of exceptional fossil preservation have been made by experimental simulation of the processes

involved in both tissue degradation and mineral authigenesis. It is this aspect of the book that is the least fleshed out. These research areas are not covered in depth in the introductory chapter, although the concept of taphonomic windows (what controls the environmental and temporal distribution of conservation Lagerstätten?) does receive fuller treatment. This absence, and the restriction of the book to faunas preserved in marine environments limits its usefulness as a course textbook; the latter criterion automatically excludes coverage of, for example, any of the important Tertiary lacustrine faunas. I suspect courses themed on "Exceptional preservation" may be better served by the relevant parts of, for example, Palaeobiology I, and Palaeobiology II, simply because of their greater breadth. The particular strength of this book is that it is an alternative to the growing number of volumes dealing with individual conservation Lagerstätten; anyone interested in this expanding area of palaeontological research will benefit from having the summaries of each biota, and the comprehensive reference lists, to hand. Palaeontological libraries should definitely have reference copies; the book clearly demonstrates how important faunas such as these are to our understanding of the history of life on Earth, and how innovative palaeobiological research interprets the information contained within them.

One theme emerged as I read the book: the relatively limited amount of literature available on the taphonomy of many of these faunas, compared to that covering their palaeoecology or the systematic biology of taxa: "we still do not completely understand all the causes that led to the preservation of Ediacara organisms" (Bottjer, Chapter 2); "taphonomic study of this deposit is still in a nascent state" (Hagadorn on Chenjiang, Chapter 3); "a systematic taphonomic analysis of the deposit has not yet been published" (Hagadorn on Bear Gulch, Chapter 9). As both a stimulus and a starting point for further research the book is an invaluable source of information: as summarised by Bottjer on p. 29, "we are only just beginning to understand how to investigate Lagerstätten".

Patrick Orr

Department of Geology, NUI: Galway, Galway, Ireland.

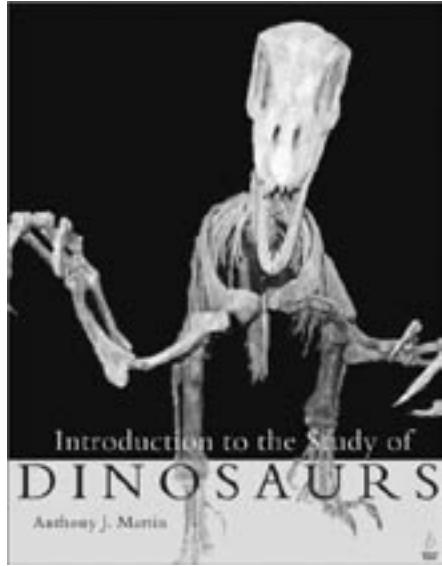
<Patrick.Orr@nuigalway.ie>

Introduction to the Study of Dinosaurs

Anthony J. Martin, 2001, Blackwell Science. Paperback. 440 pages, 184 illustrations. \$74.95. ISBN 0-632-04436-5.

This is another Dinosaur 'textbook', intended for those taking a basic course in dinosaur studies. The author aims to deliver a comprehensive guide to the study of dinosaurs, and as such the book deals with the basic requirements to study vertebrate palaeontology. The book covers the applications of chemistry, geology, biology and physics to palaeontology in a clear and concise way. Examples are given which relate to dinosaurs so that the reader may understand the application of various disciplines to the subject.

Each chapter begins with a short introduction entitled "Dino Thoughts" provided to set the reader thinking about the topic. The diagrams, mostly in colour, are clear and easy to understand, although some of the line drawings are poorly done or inaccurate. The numerous photographs, also in colour, are, on the other hand, good, and it seems that the author has used



his own pictures taken in various museums and institutions around North America and Europe, as well as pictures from the field and other sources. The book is up-to-date in terms of discoveries and ideas, and also has Web page references where further investigation into the topics discussed can be carried out (this has advantages over non-Web-based references, which might not be as accessible to those to whom the textbook would be of interest).

The book covers a wide range of dinosaur-related topics, including the history of dinosaur research, anatomy, taphonomy, ichnology, feeding habits and evolution. It also gives a brief introduction to the main clades of the Dinosauria. The last chapter provides information on the dinosaur-bird relationship and dinosaur extinction.

There is also a glossary and comprehensive index.

In general the information given on the various clades is well set out and covers the main points, including a brief history of the research done on the group, palaeobiogeography, evolutionary history, and synapomorphic features of the clades. Unfortunately the cladograms given do not have any characters labelled on them, which might have been useful.

The book, however, does contain some inaccuracies; for example the figure depicting the body armour of an ankylosaurian (fig.14.2, p.328) shows the skull of an ankylosaurid attached to the body of a nodosaurid (*Edmontonia*). Some of the information given is incorrect; returning to the chapter on Thyreophora it is stated that *Pinacosaurus* is a nodosaurid and *Silvisaurus* an ankylosaurid, where in actual fact the reverse is the case. There are also a few errors in the spelling of taxonomic names.

Compared with other dinosaur “textbooks,” such as Lucas (1994) and Fastovsky & Weishampel (1996), this volume is directed more towards the application of scientific disciplines to the study of dinosaurs, and focuses less on individual dinosaur clades. This book, however, does have more colour pictures, both diagrams and photographs, than the above volumes.

In my view this book should be useful as a foundation guide to the study of vertebrate palaeontology, however, it should not be used as a reference for detailed information on dinosaurs. I would recommend the book for anyone who wishes to begin a study of dinosaurs and needs guidelines, and as such the book fulfils the intentions of the author. The questions, “Dino Afterthoughts”, given at the end of each chapter, provoke thought, not only drawing upon recalled information from the chapter, but also making the student think about the answer. There are also some practical tasks to allow direct observation. The book could be improved by some collaboration with dinosaur specialists, at least to make sure all the information is correct

and up-to-date. In my opinion the book is a little expensive (\$74.95) for its content, but would be useful to high school and college students.

Extracts from the book, including some of the images, can be found at:

<<http://www.blackwellscience.com/dinosaurs/>>

Jolyon Parish

Department of Zoology, University of Oxford

<jolyon.parish@oriel.oxford.ac.uk>

References:

Fastovsky, D.E. & Weishampel, D.B. 1996 *The Evolution and Extinction of the Dinosaurs*, Cambridge University Press.

Lucas, S.G. 1994 *Dinosaurs. The Textbook*, Wm. C. Brown Publishers.

Eocene Biodiversity – Unusual occurrences and rarely sampled habitats

ed Gregg F. Gunnell. 2001. Kluwer Academic/Plenum Publishers New York, Boston, Dordrecht, London, Moscow xxi plus 442pp. ISBN 0-306-45628-0 (hbk) £65.55

This is the 18th volume in *Topics in Geobiology*, an ongoing series of almost exclusively multi-authored compilations initiated by Plenum Press over 20 years ago. Since 1998, when Plenum Press was acquired by Kluwer Academic, the series has been published under the joint imprint. There can hardly be a palaeontologist who has not consulted these volumes—since the first on Skeletal growth of aquatic organisms (edited by Rhoads and Lutz), they include Animal-sediment relations (McCall and Tevesz), Heterochrony in evolution (McKinney), Taphonomy (Allison and Briggs), Organic geochemistry (Engel and Macko), and Ammonoid palaeobiogeography (Landman, Tanabe and Davis). Although extracting citation data for the series is not straightforward, there is no doubt that it has had a substantial impact on research in the broad field of geobiology.

There are many reasons to open *Eocene Biodiversity*. The Eocene (34-55 mya) is certainly one of the most interesting intervals in the Tertiary. It witnessed the first appearance of many modern mammal orders. It was a period of dramatic global climate change. Rich faunas are known from nearly every continent, so there is the potential to consider the impact of environmental change on extinction, origination, overall diversity, community structure and geographic distribution. There are some spectacular examples of exceptional preservation, and a number of the stratigraphic units have just the kind of names—Gnat-out-of-Hell, Grizzly Buttes, Red Hot—that attract the compulsive browser.

The book grew out of a symposium at the 1998 Society of Vertebrate Paleontology meetings in Snow Bird, Utah. Forty authors from USA, Canada, Argentina, France, Germany, Tanzania and Pakistan contributed 16 chapters, the whole edited by Gregg Gunnell, an expert on Tertiary primates at the Museum of Paleontology, Ann Arbor, Michigan. The preface states that the book ‘was conceived as an introduction to non-traditional Eocene fossil samples, and as a place to document and discuss features of these fossil assemblages that are rare or unique’. The focus is



on Lagerstätten, deposits that yield exceptional morphological information, and/or significant insights into Eocene biodiversity. The coverage, however, is selective, with an emphasis on vertebrates, and especially mammals. You will search in vain for the spectacular fishes from Monte Bolca in northern Italy, the extraordinary cellular preservation at Geiseltal in eastern Germany, the silicified flora of the Princeton Chert or the lacustrine assemblage of fishes, insects and plants at Horsefly, both in British Columbia.

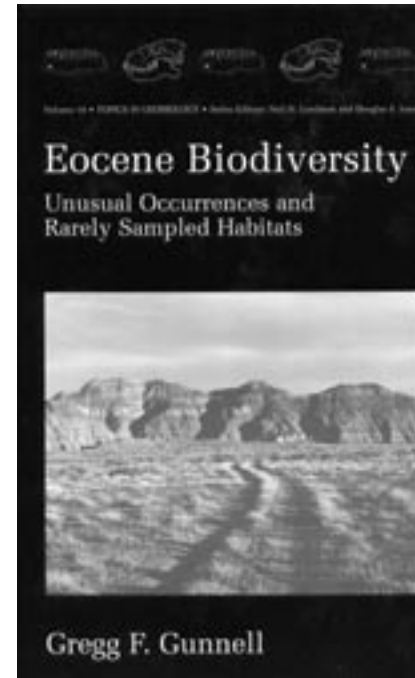
The classic Konservat-Lagerstätten of Green River and Messel are treated here. Green River lake deposits have been mined for fossils for about 150 years and have yielded well over a million vertebrates, the majority of them fishes. Lance Grande provides the first comprehensive account of the fish fauna since the second edition of his book on the Paleontology of the Green River was published in 1984. This is a systematic review, family by family, with 29 illustrations of spectacular specimens with complete body outlines.

The Messel vertebrate fauna is reviewed in two well illustrated chapters, by Jens Franzen and Gerhard Storch. Franzen considers the taphonomy, including the soft-tissue outlines, which sometimes preserve even internal organs such as intestine, liver, and veins. The relatively high abundance of birds and bats at Messel is explained by asphyxiation due to CO₂ (possibly volcanic) from the lake. Large mammals were rarely transported into the lake and the small number of primates (only eight known specimens) may have been victims of predation. Storch analyses the functional morphology and mode of life of a range of Messel taxa. He considers the niches occupied by the mammals as well as their reproduction and ontogeny.

A little known biota from Mahenge in Tanzania (described by Harrison *et al.*) also preserves soft parts. It provides data from a geographical province and time period for which there is almost no other record. The biota was deposited in a stratified crater lake above a kimberlite pipe. Previous reports on Mahenge are confined almost exclusively to Greenwood's investigations of the fishes in the 1960s but the locality has also yielded frogs, insects and plants (no mammals as yet).

Most of the deposits described in the volume yield just bones and teeth. A common technique for collecting such microvertebrate material is surface prospecting. The method is illustrated by a picture of a prone palaeontologist: "as recommended by 19th century paleontologist O.C. Marsh, Miller keeps her nose about six inches above the ground, pointed down not up!". Surface prospecting has been applied extensively to the early Eocene Willwood Formation of the Bighorn Basin, Wyoming, which includes over 1,500 fossil mammal localities. Silcox and Rose's study of four quarries in alluvial sediments shows that surface prospecting yields fewer taxa than excavating and screen washing. The smallest fossils are under-represented as a result of weathering and collection bias. The Willwood Formation also includes freshwater limestones, described by Bloch and Bowen, that accumulated on a distal flood plain, some in hollow tree trunks, others as ponded water at the surface of palaeosols. Acid preparation has produced over 50 species of mammals and birds. Faunas from unusual environments increase the sample of Eocene biodiversity: small mammals are much better represented in these limestones than in mudstones.

Aspects of vertebrate taphonomy are an emphasis of many of the contributions. Grizzly Buttes, a major locality in the Bridger Formation of southwestern Wyoming, yields plentiful mammal remains, including ancient primates. Since first collected by Marsh and Cope in the 1870s it



has been the source of a substantial fauna investigated by the American Museum of Natural History. Alexander and Burger demonstrate that predation by raptorial birds is an important agent in generating accumulations. A second chapter on the Bridger Formation in southeastern Wyoming, by Murphey *et al.*, provides a comprehensive analysis of the *Omomys* Quarry. The entire biota associated with the dominant primate is described and a range of taphonomic agents considered. The history is complex, and includes the effects of attritional accumulation as well as nesting (there are large numbers of bird bones and egg fragments), and predation by owls. Predators are also implicated in accumulating the small mammals at Gnat-out-of-Hell, in the Uinta Formation of northeastern Utah, investigated by Thornton and Rasmussen. The assemblage, which includes occasional concretions of crushed mammal remains, is unique taphonomically in the Uinta

Formation. The predators have not been identified with certainty—no direct modern analogue has been established—but may have been diurnal raptorial birds.

Some chapters focus on less well documented geographic areas, including the Gulf Coast Plain of the United States. Beard and Dawson describe the Wasatchian Red Hot local fauna from Mississippi, the most diverse mammalian assemblage from the early Cenozoic of the southeastern United States. Twenty-four species of land mammals are represented mainly by isolated teeth and jaw fragments. Westgate considers the palaeoecology and biostratigraphy of marginal marine deposits in Texas, Arkansas, Alabama and Georgia. The focus is mainly on fishes, but important accumulations of mammals are also described, particularly in the Casa Blanca local fauna in Texas, which represents a mangrove community. Farther afield Hartenberger *et al.* review the mammalian fauna preserved in palustrine limestones at Chambi, central Tunisia, and compare its stratigraphic position and ecology with faunas from elsewhere, particularly in Europe. Gingerich *et al.* report on the newly discovered Ghandera Quarry in Baluchistan, Pakistan, which provides the most complete information to date on mammalian communities on the Indo-Pakistan subcontinent during the Eocene. The biota is remarkably diverse for one so early in the Eocene.

Two chapters deal with mass mortalities. McGee records hundreds of bones of *Coryphodon* in the Wasatch Formation of the Washakie Basin, Wyoming. This large herbivorous browser perished catastrophically in a fluvial environment, and some reworking followed. Williamson compares three mass death deposits of herds of the condylarth *Meniscotherium* in proximal fluvial settings, in Wyoming and New Mexico.



Gregg Gunnell, with his colleague William Bartels, contribute the final chapter—on the South Pass area of southwestern Wyoming. They comment on unusual and unique taxa, consider the impact of sampling and time averaging, discuss immigration, speciation and their impact on diversity, and interpret the structure of the assemblages in the area and how and why they differ from those in coeval basins. Here, perhaps, was Gunnell's blueprint for the book, but few of the other chapters on mammals could address this range of questions.

Eocene Biodiversity contains much of interest, both primary data on taxon occurrences, and insights on taphonomy (of vertebrates in particular) that could be applied more widely. But the overall organization of the book, or lack of it, is disappointing. This is a collection of papers that loosely targets an important issue. The subject matter and nature of the treatment vary significantly from chapter to chapter (so that the lack of abstracts is an irritation)—some are reviews of well documented biotas, others almost preliminary reports on relatively new discoveries. While this was perhaps inevitable, the chapters are not grouped into sections and there is little apparent logic to the order in which they appear. There is no introductory chapter to provide a context, nor any summary to pull the threads together. The significance of the deposits as a whole to our wider understanding of the Eocene is only considered in very general terms. In the editor's own words "the book demonstrates that, despite being one of the best sampled intervals of the Cenozoic, there is still much to be learned about the organisms that lived during the Eocene." While *Eocene Biodiversity* will be an essential purchase for libraries that serve vertebrate palaeontologists, I suspect that only those individuals working on Tertiary mammals will buy it.

Derek E.G. Briggs

Department of Earth Sciences, University of Bristol, UK.

<d.e.g.briggs@Bristol.ac.uk>

Late Ordovician articulate brachiopods from the Red River and Stony Mountain formations, southern Manitoba

Jin Jisuo and Zhan Ren-bin. 2001. NRC Research Press, Ottawa, Ontario, Canada, 117 pp., 23 pls. US\$ 42.95.

The late Ordovician brachiopod faunas of the North American Mid-Continent include some of the most interesting and spectacular taxa of the entire period. Many species are endemic, and scattered across a number of palaeocommunities are some of the larger individuals of the phylum recorded from Lower Palaeozoic rocks. Literature on these faunas is, nevertheless, dispersed and many taxa are in need of revision. Jin and Zhan have produced a beautifully-illustrated monograph of the well-preserved and numerous late Ordovician brachiopods from the Red River and Stony Mountain formations in Southern Manitoba. Here in the north-eastern part of the Williston Basin giant orthide, strophomenide and rhynchonellide brachiopods coexisted in a range of relatively shallow-water communities in predominantly carbonate environments.

The systematic section includes the detailed description of 16 rhynchonelliform genera (one, *Nasutimena* is new) together with 22 species, of which two are new. The descriptions are

supported where relevant by bivariate graphs and serial sections. Both are useful but despite the large samples available of many of the taxa, there are no statistical data that might in the future be used for multivariate comparisons with other similar faunas. Description and discussion of the Manitoba taxa have, none the less, helped clarify a number of wider taxonomic problems. The orthide *Dinorthis* is quite different from *Plaesiomys*, whereas *Gnamptorhynchos* is clearly an aberrant platystrophiid. The sowerbyellid *Thaerodonta* can be separated from *Eochonetes* together with *Sowerbyella* and *Eoplectodonta* and the true identity and age of the type species of *Strophomena*, *S. planumbona*, have been clarified; it is in fact an Ashgill species from Richmondian strata in type Cincinnati area. The plates are generally excellent with very few poorly focused shots; uniformity of brightness and contrast has been maintained across all 23 plates including those shots of serial sections.



Sections on the biostratigraphy, biogeography and palaeoecology are developed from the core of systematic work. A number of local brachiopod biozones, previously established by the first author and his colleagues, are developed and refined. The biogeography of this unusual fauna is investigated in some detail and is compared statistically (with a useful appendix of raw data) with faunas elsewhere in North America together with coeval faunas from the Altai Mountains, Kazakhstan and south-east China. There are, not surprisingly, few similarities with those assemblages outside the Laurentian basins. It would have been interesting, however, to look also at some of the Laurentian marginal faunas such as those at Girvan, south-west Scotland. Moreover a number of Mid-Continent taxa do in fact appear in the North Estonian Confacies belt on Baltica during the later Ordovician, indicating interesting links between the two regions. The palaeoecology of the faunas is developed within the framework of a set of two palaeocommunities and linked to major transgressive-regressive cycles established in the region partly on the basis of rich coral faunas. Statistics are provided for the *Kjaerina hartae* and *Diceromyonia storeya* communities; the latter is lower-diversity assemblage with smaller individuals perhaps indicating more restricted environments whereas the former probably occupied more open-marine settings in Benthic Assemblage zones 2-3.

This is a carefully-researched and well-illustrated monograph fauna, clearly a must for researchers involved in the study of the Lower Palaeozoic and its faunas. The brachiopods are commonly large, reflecting the pleasant conditions in parts of the Williston Basin during the latest Caradoc and Ashgill prior to the end Ordovician extinction events. This monograph does considerable justice to these spectacular animals.

David Harper

Geological Museum, Copenhagen, Denmark

<dharper@savik.geomus.ku.dk>



Atlas of marine invertebrate larvae

Young, C.M. (ed.) with Sewell, M.A. & Rice, M.E. (assoc. eds). 2002. 621 pp. Academic Press, London. ISBN 0-12-773141-5 (hbk). £66.95.

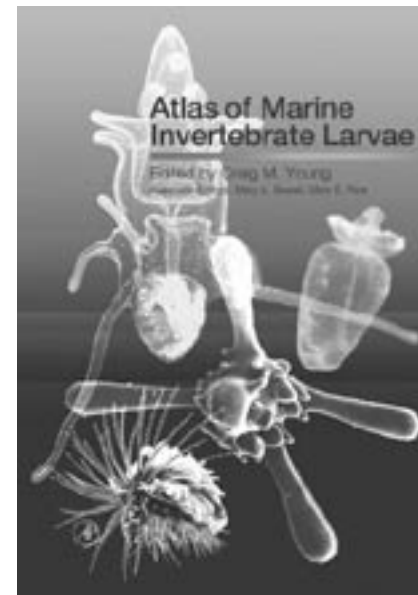
For over a century, attempts to uncover metazoan evolutionary history have been dominated by comparative embryology (e.g. Haeckel 1874; Jägersten 1972). This influence remains pervasive (e.g. Nielsen 2001), but new lines of evidence have begun to confront embryologically-derived phylogenies. Molecular phylogenetics provides a source of data that is quasi-independent of embryology and anatomy, and a means of testing embryology-based phylogenies through congruence. Palaeontology, too, has provided great insight into early metazoans through direct study, rather than through inference using more-or-less appropriate proxies amongst the living fauna and, crucially, providing access to early and/or primitive metazoans that have no living relatives that might serve as proxies for experimental analysis. Nevertheless, embryology remains central to our understanding of metazoan phylogeny, and through technological advances (developmental genetics) its sphere of influence has been extended from a study of evolutionary pattern, to providing knowledge of the underlying mechanistic basis of evolutionary change. But embryology-based schemes are often a stark contrast to molecular-based phylogenies and the reconciliation of the two remains a significant yet currently intractable problem. A key issue concerns one of the basic premises of evolutionary embryology which contends that early ontogenetic characters are more reliable indicators of phylogenetic relationships than are later and adult characters. This follows from the assumption that late development is contingent upon early development and, thus, early development must be least subject to adaptive change. And although some authors argue that there is phylogenetic evidence in support of this assertion, just as many have provided evidence against this hypothesis. A useful arbiter in this debate would be a rich fossil record of larvae and embryos that is as ancient as the phyla themselves, providing direct evidence of the early developmental stages of early metazoans, in place of living proxies. While this would have been wishful-thinking a few decades ago, there has been a steadily growing expectation of the data retrievable from the fossil record, with the discovery of Cambrian and Ordovician larvae of arthropods and, more recently, the discovery of Proterozoic, Cambrian and Ordovician embryos, from early cleavage stages, through to miniature adults. Although published records of such fossils remain sparse, it is as likely that their paucity results from the absence of an appropriate search image in the minds of palaeontologists, particularly given that the larvae are, by definition, morphologically alien to their more familiar adult counterparts.

Enter stage left the brand-spanking-new *Atlas of invertebrate marine larvae*. The brain-child of Professor Fu-Shiang Chia, this volume is replete with scanning electron micrographs collated by the venerable professor for just such a purpose, but commissioned and completed by a multinational group of embryologists and dedicated to Chia. And it is chiefly in the use of micrographs that the *Atlas* beats all the competition, including Brusca & Brusca's *Invertebrates*, and Gilbert & Raunio's *Embryology*, both of which have provided great service as introductory texts to metazoan embryology, but which simply cannot compete in terms of graphical documentation. The *Atlas* is precisely what it purports to be: each chapter is dedicated to a phylum (or sub-phylum in the case of the arthropods, echinoderms and molluscs) and includes a two- to six-page concise and well-referenced introduction to the morphology, development,

ecology and/or variation in larval development—but this is very much subordinate to the high resolution greyscale and colour plates in terms of space dedicated. The balance between space devoted to the different phyla is highly disproportionate in some instances: there is almost as much text devoted to the Phylum Cycliophora as to the polychaetes, despite the Cycliophora containing only a single microscopic species, *Symbion pandora*, that is restricted in its habitat to the mouthparts of decapod crustaceans and not described until 1995 (Loriciferans, another of Reinhardt Kristensen's 'new' phyla, also receive disproportionate attention). The emphasis on graphical representation over textual interpretation is welcome—there are few other contemporary volumes concerning comparative embryology that contain so few cladograms (there is just one, in the echinoid chapter), so the *Atlas* is very much a data repository that makes no apologies for an absence of debate over process, interrelationships, and character polarity. Rather, it is a (relatively) untainted data source from which such analyses may be built.

The apparent irrelevance of palaeontological data is betrayed by an almost complete lack of reference to the fossil record. Predictably, and quite justifiably, the remarkable arthropod larvae from the Late Cambrian Orsten deposits make a cameo appearance in the chapter dealing with crustaceans, including a micrograph of *Bredocaris admirabilis*, but they fail to form the basis of any discussion and appear to be included more as curios than as data. Stem-groups? Schlem-groups! However, *Acaenoplax*, the recently described aplacophoran-like beastie from the Wenlock Herefordshire Lagerstätte (Sutton *et al.* 2001), provides a more substantive basis for discussion over validity of the Amphineura (Aplachophora+Polyplacophora)—a brief evolutionary digression that provides an interesting primer for anyone wanting to define a 'hot' research project in evo-devo.

While the book is very complete in its coverage of phyla that exhibit indirect development, I cannot help feeling that there are holes in this coverage. This stems from the rather arbitrary



nature in which both phyla and larvae are defined. Many of the phyla recognised in the book are classified at much lower rank in most current, and many older systematic treatments. Would anything have been lost by adopting either a rank-free approach, or one in which less controversial ranks were applied? Many of the so-called larvae are also not so morphologically dissimilar to their adult counterparts, which begs the question: why produce a book that is restricted in its content to just indirect development? Why not produce an atlas of embryology, period?

Given the general avoidance of phylogenetic matters, the overall structure of the book is somewhat biased towards being an embryological crowd-pleaser. Although there is no explicitly defined structure

to the ordering of the chapters, a retrospective overview reveals a *scala naturae* sequence of phyla that is compatible with metazoan phylogenies based upon comparative embryology, and incompatible with molecular phylogenies. No doubt this is entirely coincidental.

My flailing attempts at criticising the volume have plumbed new depths. This is a measure of the quality of a volume that achieves its aims precisely and will provide an invaluable introduction to the comparative embryology of indirect developers for years to come. It is even difficult to complain about the price; although £66.95 could not be considered bargain of the century, who, these days, could expect a technical volume of this size, scope and quality to cost so little? This book is only going to be bought by those directly interested in metazoan phylogeny, the evolution of life history strategies, and comparative embryology, but ensure that your library has a copy so that you can appreciate it as a work of art as much as hard-nosed science.

References

- Brusca, R.C. and Brusca, G.J., 1990. *Invertebrates*. Sinauer, Sunderland, MA, 922 pp.
- Gilbert, S.F. and Raunio, A.M. (Editors), 1997. *Embryology: constructing the organism*. Sinauer, Sunderland, MA, 537 pp.
- Haeckel, E., 1874. The gastraea theory, the phylogenetic classification of the animal kingdom and the homology of the germ-lamellae. *Quarterly Journal of Microscopical Science*, **14**: 142-165, 223-247.
- Jägersten, G., 1972. *Evolution of the metazoan life cycle: a comprehensive theory*. Academic Press, London, 282 pp.
- Nielsen, C., 2001. *Animal evolution: interrelationships of the living phyla*. Oxford University Press, Oxford, 563 pp.
- Sutton, M.D., Briggs, D.E.G., Siveter, D.J. and Siveter, D.J., 2001. An exceptionally preserved vermiform mollusc from the Silurian of England. *Nature*, **410**: 461-463.

Philip Donoghue

Department of Earth Sciences, School of Geography, Earth & Environmental Sciences, University of Birmingham, UK
<p.c.j.donoghue@bham.ac.uk>

Phylogenetic trees made easy: a how-to manual for molecular biologists

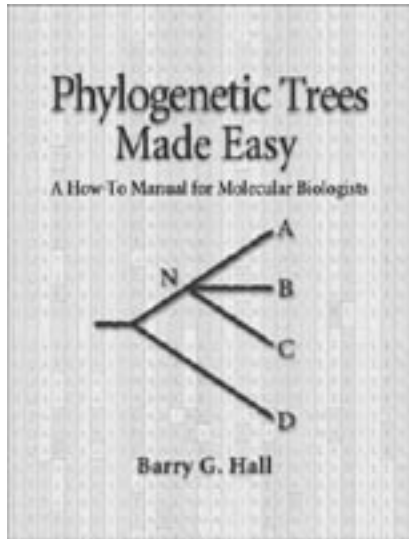
Hall, B. G. 2001. 179 pp. Sinauer Associates. ISBN 0878933115 (pbk). £18.99

I don't know about you but I have always found the basic premise on which palaeontology is based a little perverse. Why circumscribe your dataset on the rather arbitrary criterion that all the taxa you study are extinct—as ridiculous as only studying taxa that are extant. Since Patterson's (1981) seminal criticism of the role of palaeontological datasets in systematic biology, the integral importance of palaeontology to systematics (Donoghue *et al.* 1989) and biogeography (Lieberman 2001) has been well made. But the converse also holds: we cannot

hope to provide a complete understanding of evolutionary problems without a complete understanding of the dataset. Clearly, the answers to questions in evolutionary biology, big and small, often lie with an integrative approach. But one of the great barriers to this lies with mutually exclusive components of palaeontological and neontological datasets; many biologists find interpretation of palaeontological data deceptively simple—they interpret fossil remains as though they are merely petrified, rather than rotten and squished. For palaeontologists, dealing with that other world, molecular datasets, is the barrier, but perhaps it is only deceptively so. The basic problem is the wont of an introduction. As with cladistic analysis of morphological datasets, there is a dearth of learn-with-mother accounts of how to do your first analysis, and more often than not, unless you have access to a rabid cladist, or the time and money to go on a course, such as the three-week cladistics portion of the *Advanced Methods in Taxonomy* MSC course at the Natural History Museum, the only solution is to get down and dirty, to learn from your mistakes and hope that you recognise them before you commit yourself to publication! But in dealing with molecular datasets, many palaeontologists may be overcome by the sheer difference in the nature of characters and, above all, the nature of homology and its recognition, of which more later. But help is now at hand; *Phylogenetic trees made easy* is just that, a learn-with-mother guide to molecular phylogenetics that, with the help of on-line resources, including various bits of freeware, and public sequence repositories such as GenBank, takes the reader through the process of sequence retrieval, alignment, distance, parsimony, likelihood and Bayesian approaches to phylogenetic analysis and a neat guide to presenting and printing trees for character analysis and, ultimately, publication.

The book is supported by a series of pages on the publisher's website <<http://www.sinauer.com/hall/>> that include all of the files necessary to follow the alignment and phylogenetic analysis of exemplar protein sequences, as well as links to sites from which the freeware software (alignment and Bayesian analysis) can be retrieved. However, it is also possible to obtain and develop the files by retrieving them directly from GenBank using a Web interface to BLAST, which runs on US government computers. This was excellent when I first worked through the tutorials over a year ago, but the BLAST interface has changed subsequently such that the urls printed in the book are no longer immediately valid and it is no longer obvious how to retrieve the specific protein sequences used, at least to a buffoon like me. With the support of a website, such problems are easily overcome by placing new hyperlinks and addenda to the book such that it keeps apace with changes, but Sinauer and Hall have not yet realised this potential.

Even to the complete novice, the sequence alignment tutorials remain viable using the supporting files on the Sinauer website. Within ten minutes you can have aligned the sequences, performed a phylogenetic analysis and be well on your way to preparing tree files for publication. This is all very scary. Hall encourages the tutee to play around with the penalties imposed upon gap opening and gap closing in the search for homology between the sequences until the strongest signal is recovered. Thus, the value of the penalties is entirely arbitrary and is likely to vary, possibly even quite considerably, from one analysis to another. I'm not altogether naïve, and I was fully aware that alignment was both subjective and the blackest of boxes upon which all molecular analyses are based, but I still found this shocking and a positively metaphysical experience.



While the identification of homology amongst morphological data is a much greater intellectual challenge that can be more readily accepted or rejected by peers, molecular datasets are open to much more realistic models of evolution in phylogenetic analysis. The tutorials run through all the most popular methods of analysis, as well as one that is still only now coming into vogue, Bayesian analysis, and it is likely that its inclusion in the book will go some way towards its mainstream take-up.

Aside from these practicalities, the book also includes concise accounts of some of the theoretical foundations, including tree rooting, tree searching methods, and the different algorithmic methods of tree construction.

Thus, background information is provided on a need-to-know basis, rather than in any attempt to compete with textbooks such as Kitching *et al.* (1998) or Schuh (2000).

All in all, *Phylogenetic trees made easy* is a reasonably priced, well-written and well-executed tutorial-based introduction to the practicalities of molecular phylogenetic analysis that neatly bridges the gap between ignorant and novice. It will not turn you into a fully-fledged gene-jockey, but it will allow you to begin to test and assess the veracity of published analyses.

References

Donoghue, M.J., Doyle, J., Gauthier, J., Kluge, A. and Rowe, T., 1989. The importance of fossils in phylogeny reconstruction. *Annual Review of Ecology and Systematics*, **20**: 431-460.

Kitching, I.J., Forey, P.L., Humphries, C.J. and Williams, D.M., 1998. *Cladistics: the theory and practice of parsimony analysis*. Oxford University Press, Oxford.

Liebermann, B.S., 2000. Paleobiogeography: using fossils to study global change, plate tectonics, and evolution. *Topics in Geobiology* **16**. Kluwer Academic /Plenum, New York.

Patterson, C., 1981. Significance of fossils in determining evolutionary relationships. *Annual Review of Ecology and Systematics*, **12**: 195-223.

Schuh, R., 2001. *Biological systematics*. Cornell University Press.

Philip Donoghue

Department of Earth Sciences, School of Geography, Earth & Environmental Sciences, University of Birmingham, UK
<p.c.j.donoghue@bham.ac.uk>



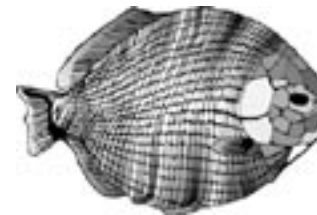
Pleuroceras



Calymene



Dalminites



Dapedium

Fossil Fun

By ROCKSCENE

8 Quality greetings cards featuring colourful fossil designs supplied individually wrapped with coloured envelopes. Each card is labelled with the fossil name and basic stratigraphy in stylish gold lettering.

Available from:
Amanda Jenkinson
19 Norton Street; Knighton
Powys; LD7 1ET
Tel: (01547) 520699
Amanda@rock-scene.co.uk

Visit
www.rock-scene.co.uk
for coloured images and
retail/wholesale prices.



Amaltheus



Callavia



Paradoxides



Cephalaspis & Bothriolepis

Post-graduate opportunities in Palaeontology

This is our second digest of career opportunities in palaeontology. Careers advice is available from the Palaeontological Association website <www.palass.org> and includes a series of biographies from Palaeo-MSc students through to Professors of Palaeontology, Museum Curators, Science Publishers, and workers in both Show- and Oil-business, all of whom have made their way through a career path in palaeontology. Descriptions of palaeontology, and palaeontology-related, MSc courses are listed below, along with a digest of all PhD projects currently open for applications to begin in October 2003.

M.Sc. in Palaeobiology: University of Bristol, Department of Earth Sciences

The M.Sc. in Palaeobiology offers a broad-based overview of modern approaches in palaeobiology. Students study nine out of 16 possible options, and topics range from taphonomy and palaeoecology to mammalian palaeobiology, dinosaurs to trace fossils, systematic methods to macroevolution. Then there is a six-month independent project, and students are offered a wide range of topics. The programme is designed for students with a BSc in either a biological or earth sciences subject, and conversion courses in evolution, basic palaeontology, and sedimentology are offered. Students also receive training in writing scientific papers, creating Web sites, applying for Ph.D.s and jobs (both in Britain and overseas).

So far, 60 students have graduated, and many have gone on to rewarding careers in palaeontology and related scientific areas. Full details of the programme, of former students, and how to apply are available on the Web site <<http://palaeo.gly.bris.ac.uk/opportunities/MSc.html>>. Application forms may be downloaded from the web site, or they can be provided by <shirley.sparks@bris.ac.uk>

M.Sc. Micropalaeontology: University College London

The science of Micropalaeontology studies the microscopic remains of animals, plants and protists belonging to biological groups mostly of simple organisation and less than 1mm in size. These organisms were extraordinarily abundant and diverse in the past and continue to be so in modern environments, in many cases forming the primary elements in marine, lacustrine and terrestrial organic productivity cycles and food chains. The production of these organisms is a basic component of the global biogeochemical system, intimately linked to present and past environmental change. In this way microfossils are keys to palaeoceanography and palaeoclimatology and to understanding the evolution of the biosphere. Our ability to use the pattern of evolution of microfossil groups during the last 400 million years as a means of ascribing relative ages to sedimentary rocks and reconstructing their environmental histories is of great value for understanding global sedimentary geology, and has especially important

applications, for example, in the hydrocarbon industry.

The M.Sc. and Diploma course in Micropalaeontology was founded in 1959, was the first of its kind in Britain and was specifically designed to train professional micropalaeontologists. The importance of the subject for biostratigraphy and palaeoenvironmental interpretation is firmly established through its application to hydrocarbon exploration, and also as a key to understanding the history of the continental shelf and oceanic basins. A high proportion of graduates have entered the oil industry, either following the M.Sc. course or after further research. Close links are maintained with the hydrocarbon industry.

The course is broadly based and covers calcareous, organic-walled and siliceous microfossils. Great emphasis is placed on the biostratigraphy and spatial distribution of the organisms and their application to problems of zonation and correlation and to environmental analysis. All major post-Palaeozoic microfossil groups are covered in the M.Sc. curriculum. Individual and team project work forms an important part of the course.

The entry qualifications for the M.Sc. in Micropalaeontology are: at least a Lower Second Class Honours degree in Geology, although joint combinations with Geography, Biology and Oceanography may be acceptable. We welcome enquiries from graduates with experience in oil companies who wish to obtain further qualifications.

Further details and application forms are available from:

Professor A.R. Lord

Department of Geological Sciences, University College London, Gower Street, London, WC1E 6BT, UK. Tel: (44) 020 7679 7131; Fax: (44).020 7388 7614
<micropal@ucl.ac.uk>

M.Sc. Advanced methods in taxonomy and biodiversity: Imperial College London

Imperial College of Science, Technology and Medicine and The Natural History Museum are jointly offering a Masters degree course in Advanced Methods in Taxonomy and Biodiversity.

The one-year full-time M.Sc. course provides essential skills for all concerned with taxonomy and biodiversity. The course is composed of ten taught modules followed by a four month research project. The series of modules seeks to provide as wide as possible an overview of the theory and practice of modern taxonomy and systematics, with associated biodiversity studies. During their four-month research project, students can specialise in their chosen area.

The course is based at The Natural History Museum, London, one of the world's premier institutions for research on the diversity of the natural world. The collections include over 68 million specimens, 800,000 of which are type specimens, and the Museum houses a world class library covering all areas of taxonomy and systematics. The Museum is situated next to the main South Kensington campus of Imperial College, and there are close research and teaching links between the two establishments. Students will therefore be situated in the heart of London, and are able to make full use of the facilities at both institutions.

Students are trained to a high level of competence in systematics and a detailed understanding of the various uses and problems involved. The course provides methodological background,



including quantitative skills, computer applications and practical skills in morphological and molecular techniques of taxonomy and systematics. The most up-to-date ideas and research in taxonomy and biodiversity are taught, to a large extent from primary literature. Hands-on training in conducting research in this area will be provided by project supervisors, with specialisation in the student's field of choice. After completing the course, students will be able to:

- apply a wide range of techniques to the study of systematics, including collections management, identification, key construction, taxonomic revision, phylogeny reconstruction and comparative methodologies;
- understand the diversity of living organisms in space and time and be familiar with methods for measuring this diversity and monitoring changes due to both anthropogenic and natural factors, and in Earth history;
- select appropriate methods to solve taxonomic and biodiversity problems, and be able to acquire and analyze taxonomic data, including both traditional and molecular data;
- understand fully the conceptual basis of taxonomy and phylogenetics and in particular, cladistics, and to understand "biodiversity" within this framework;
- apply these concepts to issues of biodiversity and conservation management and research, to set priorities for sustainable development, environmental assessment and inventories; apply these concepts to other areas of biology such as parasitology and epidemiology.

Who is this course aimed at?

The course is aimed at anyone concerned with taxonomy and biodiversity. It is relevant to those involved with biodiversity assessments, conservation and sustainable development, from biomedical sciences to agriculture and fisheries, as well as to those intending to pursue academic careers in systematics and related fields.

Entry requirements

Applicants should normally either have or expect to gain at least a lower second class honours degree (or equivalent) in a biological or environmental subject (e.g. zoology, botany, microbiology, agriculture and veterinary science). Exceptionally students with different backgrounds or with related work experience will be considered.

Further details are available from:

Ms Amoret Brandt

Department of Entomology, Natural History Museum, London SW7 5BD tel: +44 (0)20 7942 5036; fax: +44 (0)20 7942 5229
<a.brandt@nhm.ac.uk>

Ph.D. Palaeo projects for 2003

The following is a digest of the PhD projects and MSc courses offered to commence in October 2003. This is by no means an exhaustive list and the institutions listed, plus others that are not listed, may well extend this list over the next few months. Further details for many of these projects are already available on institutional Web sites (url supplied); details for all will be available shortly. An email address is included for first point of contact for expressions of interest in any of the titles and it is advisable to make your interest known as soon as possible. Application deadlines can be as early as January 2003, and interviews usually take place during the period January–April. Funding for subsistence and tuition fees is usually awarded on a competitive basis.

University of Birmingham: Department of Earth Sciences

Palaeobiology of primitive armoured vertebrates.

Supervisors: Dr Philip C.J. Donoghue and Prof. Philippe Janvier (MNHN, Paris).

Contact Phil Donoghue for further details <p.c.j.donoghue@bham.ac.uk>.

Cambrian-Ordovician development of the Iapetus passive margin in NW Scotland—an integrated sedimentological, palaeontological and sequence stratigraphic analysis.

BGS CASE award (pending)

Supervisors: Dr M.P. Smith and Dr M. Krabbendam (British Geological Survey).

Contact Paul Smith for further details <m.p.smith@bham.ac.uk>.

Architectural development of Silurian reefs.

Supervisors: Dr Alan Thomas, Dr Paul Smith, Dr Don Mikulic (Illinois State Survey, USA) and Dr Joanne Klussendorf (University of Wisconsin, USA).

Contact Alan Thomas for further details <a.t.thomas@bham.ac.uk>.

The micropalaeontology and ichnology of the Triassic-Jurassic boundary interval, Southern UK.

Supervisors: Dr I. J. Sansom, Prof. A. Hallam and Dr C. Elliott (NAMS).

Contact Ivan Sansom for further details <i.j.sansom@bham.ac.uk>.

Further information can be obtained from <<http://www.earthsciences.bham.ac.uk/>>.

University of Bristol: Department of Earth Sciences

Diagenesis of foraminifer shells and the retention of palaeoclimate information in deep-sea cores.

Supervisors: Dr Paul N. Pearson and Prof. Bernard Wood.

Contact Paul Pearson for further details <paul.pearson@bristol.ac.uk>.

The taxonomy, ecology and evolution of Oligocene planktonic foraminifera.

Supervisor: Dr Paul N. Pearson.

Contact Paul Pearson for further details <paul.pearson@bristol.ac.uk>.

A mathematical and computational analysis of walking in sauropod dinosaurs.

Supervisors: Prof. Mike Benton and Dr Don Henderson.

Contact Mike Benton for further details <m.benton@bristol.ac.uk>.

Collector curves, study time, and the quality of the fossil record.

Supervisor: Prof. Mike Benton.

Contact Mike Benton for further details <m.benton@bristol.ac.uk>.

Further information can be obtained from <<http://www.gly.bris.ac.uk/>>.

University of Cambridge: Department of Earth Sciences

Early evolution of the zooplankton.

Supervisor: Dr Nicholas Butterfield.

Contact Nick Butterfield for further details <njb1005@esc.cam.ac.uk>.

Convergence and historical trajectories.

Supervisor: Prof. Simon Conway Morris.

Contact Simon Conway Morris for further details <sjl11@esc.cam.ac.uk>.

Palaeobiology of giant inoceramid bivalves.

Supervisors: Drs E.M. Harper and J.S. Crampton.

Contact Liz Harper for further details <emh21@cussam.ac.uk>.

Biominalization of molluscan shells.

Supervisors: Drs E.M. Harper and E. Salje.

Contact Liz Harper for further details <emh21@cus.cam.ac.uk>.

Animal mechanics and engineering design in large fossil vertebrates.

Supervisor: Prof. David Norman.

Contact David Norman for further details <dn102@esc.cam.ac.uk>.

Further information can be obtained from <<http://www.esc.cam.ac.uk/>>.

Cardiff University: Department of Earth Sciences

Reassessment of biodiversity among Jurassic shelf communities.

Supervisors: Dr Lesley Cherns and Professor V. Paul Wright.

Contact Lesley Cherns for further details <Cherns@Cardiff.ac.uk>.

Geobiology of Mid-Palaeozoic terrestrial ecosystems as determined from palaeosols (Fossil Soils).

Supervisors Professor Paul Wright and Professor Dianne Edwards.

Contact Paul Wright for further details <wrightvp@cf.ac.uk>.

Algae and mass extinction events.

Supervisor Dr Robert Riding.

Contact Robert Riding for further details <riding@cf.ac.uk>.

Algae as palaeoclimate indicators.

Supervisor: Dr Robert Riding.

Contact Robert Riding for further details <riding@cf.ac.uk>.

An exploration of the chemistry and physics of pattern formation in microfossils.

Supervisors Dr Alan Hemsley and Dr Peter Griffiths (Chemistry).

Contact Alan Hemsley for further details <hemsleyar@cf.ac.uk>.

Origin of life.

Supervisors: Dr Ian Butler and Professor David Rickard.

Contact David Rickard for further details <rickard@cf.ac.uk>.

Fossil bacteria.

Supervisors: Professor David Rickard and Dr Brian Dancer (Biosciences).

Contact David Rickard for further details <rickard@cf.ac.uk>.

Further information can be obtained from <<http://www.earth.cardiff.ac.uk/>>.

University of Dublin Trinity College: Department of Zoology

No distinct projects have yet been identified but students with a 2.1 or higher interested in graduate work in the general area of avian systematics and palaeontology are encouraged to make contact with Gareth Dyke <gareth.dyke@ucd.ie>.

Further information can be obtained from <<http://www.tcd.ie/Zoology/>>.

University of Durham: Department of Geological Sciences

Computer simulation modelling of the end Ordovician glaciation.

Supervisors: Dr H.A. Armstrong & Dr G.L. Milne (University of Durham).

Contact Howard Armstrong for further details <h.a.armstrong@durham.ac.uk>

Biosphere and geosphere dynamics during end Ordovician climate change.

BGS CASE AWARD (pending)

Supervisors: Dr Howard Armstrong, Alan Owen (University of Glasgow) and Mark Williams (BGS, Keyworth).

Contact Howard Armstrong for further details <h.a.armstrong@durham.ac.uk>.

Further information can be obtained from <<http://www.dur.ac.uk/geolsci/www/homepage.htm>>.

University of Edinburgh: Department of Geology and Geophysics

Quantifying Heterogeneity: Modelling of Carbonate Platforms & Reefs.

CASE studentship with Schlumberger.

Supervisors: Drs Andrew Curtis (Edinburgh & Schlumberger), Sandy Tudhope (Edinburgh) and Rachel Wood (Schlumberger & Cambridge).

Contact Andrew Curtis for further details <curtis@cambridge.oilfield.slb.com>.

Further information can be obtained from <<http://www.glg.ed.ac.uk/>>.

University of Glasgow: Division of Earth Sciences

Origin and environmental significance of Beach Rocks in Scotland.

Supervisors: Drs G.B. Curry (Earth Sciences, University of Glasgow), J. Hansom (Geography & Topographic Sciences, University of Glasgow) & Professor A.E. Fallick (Scottish Universities Environmental Research Centre, East Kilbride).

Contact Gordon Curry for further details <g.curry@earthsci.gla.ac.uk>.

Further information can be obtained from <<http://www.earthsci.gla.ac.uk/>>.

University of Leeds: Department of Earth Sciences

Exceptionally preserved Tertiary fossil plants from Antarctica: climatic, environmental and evolutionary significance.

(A CASE project with the British Antarctic Survey).

Supervisors: Jane Francis, Earth Sciences, University of Leeds; Alistair Crame, British Antarctic Survey; Collaborator: David Cantrill, Swedish Natural History Museum.

Contact Jane Francis for further details <J.Francis@earth.leeds.ac.uk>.

Fossil preservation at hydrothermal vents and cold seeps: taphonomy in modern and ancient chemoautotrophic environments.

Supervisors: Dr Crispin Little, Dr Lianne Benning, School of Earth Sciences, University of Leeds, Dr Kathleen Campbell, Department of Geology, University of Auckland, New Zealand.

Contact Cris Little for further details <c.little@earth.leeds.ac.uk>.

Devonian cold seep communities from Morocco: palaeocology and palaeoenvironments.

Supervisors: Dr Crispin Little, School of Earth Sciences, University of Leeds, Dr Jörn Peckmann, Research Center for Ocean Margins, University of Bremen, Germany.

Contact Cris Little for further details <c.little@earth.leeds.ac.uk>, 0113 3436621.

Palaeocology of Jurassic Black Shale bivalves.

Supervisors: Dr Paul Wignall, Dr Crispin Little, School of Earth Sciences, University of Leeds.

Contact Paul Wignall <p.wignall@earth.leeds.ac.uk> or Cris Little <c.little@earth.leeds.ac.uk> for further details.

Further information can be obtained from <<http://earth.leeds.ac.uk/earth.htm>>.

University of Leicester: Department of Geology

Enigmatic fossils from the Upper Ordovician Soom Shale Lagerstätte of South Africa.

Supervisors: Prof. Richard Aldridge and Dr Sarah Gabbott.

Contact Dick Aldridge for further details <ra12@le.ac.uk>.

Taphonomic, environmental, and stratigraphic biases in the fossil record of early vertebrates.

Supervisors: Dr Mark A. Purnell, Dr Sarah Davies, (University of Leicester) and Dr Alain Blicek (Université des Sciences et Technologies de Lille).

Contact Mark Purnell for further details <map2@le.ac.uk>.

Major ecological transitions in early vertebrate evolution.

Supervisors: Dr Mark A. Purnell, Dr Jan Zalasiewicz (University of Leicester) and Dr Jane Evans (NIGL).

Contact Mark Purnell for further details <map2@le.ac.uk>.

Further information can be obtained from <<http://www.le.ac.uk/gl/re/>>.

University of Newcastle: Fossil Fuels and Environmental Geochemistry

Biomolecular analysis of ancient tooth enamel: you are what you eat, even in the Pleistocene?

Supervisors: Matthew Collins (Newcastle), Mike Richards (Bradford) and Hervé Bocherens (Montpellier).

Contact Matthew Collins for further details <m.collins@ncl.ac.uk>.

Further information can be obtained from <<http://nrg.ncl.ac.uk/nrg/nrg.html>>.

University of Plymouth: Department of Geology

Maastrichtian Foraminifera from the chalk facies of N.W. Europe.

Supervisors: Prof. M.B. Hart and Dr G.D. Price.

Contact Malcolm Hart for further details <M.Hart@plymouth.ac.uk>.

Foraminiferal change across the Cretaceous/Tertiary boundary in Denmark.

Supervisors: Prof. M.B. Hart, Dr G.D. Price and Prof. E. Hakansson (Copenhagen).

Contact Malcolm Hart for further details <M.Hart@plymouth.ac.uk>.

Further information can be obtained from <<http://www.science.plym.ac.uk/DEPARTMENTS/GEOLOGY/>>.



Royal Holloway University of London: Department of Geology

Palaeogene micromammal assemblages: their accumulation and use as palaeoproxies.

(CASE with Natural History Museum).

Supervisors: Dr M.E. Collinson/Dr J.J. Hooker (NHM).

Contact Margaret Collinson for further details <m.collinson@gl.rhul.ac.uk>.

Ocean chemistry and planktic foraminifera evolution during the mid-Cretaceous.

Supervisors: Dr Darren R. Gröcke, Prof. Brian Huber, Dr Michal Kucera, Dr Sarah James.

Contact Darren Gröcke for further details <grocke@gl.rhul.ac.uk>.

Assessing rates of dispersal of evolutionary innovations in marine microplankton using the fossil record of planktonic foraminifera.

Supervisor: Dr M. Kucera.

Contact Michael Kucera for further details <m.kucera@gl.rhul.ac.uk>.

Late Carboniferous Fires—Can they be used as palaeoclimatic indicators?

Supervisor: Professor A.C. Scott.

Contact Andrew Scott for further details <a.scott@gl.rhul.ac.uk>.

Further information can be obtained from <<http://www.gl.rhnc.ac.uk/>>.



University of Southampton: School of Ocean and Earth Science

Micro-chemistry of Jurassic fossil wood.

Supervisors: Dr John Marshall, Dr Steve Roberts and Dr Stephen Hesselbo.

Contact John Marshall for further details <jeam@soc.soton.ac.uk>.

Mediterranean response to abrupt climate change.

Supervisors: Dr Eelco Rohling, Prof. Chris German and Dr John Thomson.

Contact Eelco Rohling for further details <ejr@soc.soton.ac.uk>.

Extreme climates in the late Cretaceous and early Cenozoic.

Supervisors: Dr Paul Wilson and Prof. Chris German.

Contact Paul Wilson for further details <paw1@soc.soton.ac.uk>.

Devonian charcoal and the evolution of the Carbon cycle.

Supervisors: Dr John Marshall and Dr Steve Roberts.

Contact John Marshall for further details <jeam@soc.soton.ac.uk>.

Giant volcanism, anoxia & ocean dynamics in the Cretaceous.

Supervisors: Dr Paul Wilson, Dr Damon Teagle and Prof. Jochem Marotzke.

Contact Paul Wilson for further details <paw1@soc.soton.ac.uk>.

Role of diatoms in Cretaceous biogeochemical cycling.

Supervisors: Prof. Alan Kemp, Dr Pat Simms and Dr Irena Strelnikova.

Contact Alan Kemp for further details <aesk@soc.soton.ac.uk>.

Further information can be obtained from <<http://www.so.es.soton.ac.uk/>>.



Palaeontology

VOLUME 45 • PART 6

CONTENTS

- Jurassic soft-bottom oyster *Crassostrea* from Japan 1037
TOSHIFUMI KOMATSU, KIYOTAKA CHINZEI, MOHAMED S. ZAKHERA *and* HIROSHIGE MATSUOKA
- The Rutland *Cetiosaurus*: the anatomy and relationships of a Middle Jurassic British sauropod dinosaur 1049
PAUL UPCHURCH *and* JOHN MARTIN
- The taxonomy and stratigraphical significance of the Anglo-Welsh Cryptolithinae (Trinucleidae, Trilobita) 1075
ALISON BOWDLER-HICKS, J. KEITH INGHAM *and* ALAN W. OWENS
- Poekilopleuron bucklandii*, the theropod dinosaur from the Middle Jurassic (Bathonian) of Normandy 1107
RONAN ALLAIN *and* DANIEL J. CHURE
- The first isophlebioid dragonfly (Odonata: Isophlebioptera: Campterochlebiidae) from the Mesozoic of China 1123
G. FLECK *and* A. NEL
- Heteromorph ammonites from the Tata Limestone Formation (Aptian–Albian), Hungary 1137
O. SZIVES *and* N. MONKS
- Chiniquodontid cynodonts: systematic and morphometric considerations 1151
FERNANDO ABDALA *and* NORBERTO P. GIANNINI
- Burlingiid trilobites from Norway, with a discussion of their affinities and relationships 1171
JAN OVE R. EBBESTAD *and* GRAHAM E. BUDD
- Sauropod dinosaurs from the Lower Cretaceous of eastern Asia: taxonomic and biogeographical implications 1197
PAUL M. BARRETT, YOSHIKAZU HASEGAWA, MAKOTO MANABE, SHINJI ISAJI *and* HIROSHIGE MATSUOKA
- Conulariid-like fossil from the Vendian of Russia: a metazoan clade across the Proterozoic/Palaeozoic boundary 1219
ANDREI YU. IVANSTOV *and* MIKHAIL A. FEDONKIN

The Palaeontological Association

46th Annual Meeting 15th–18th December 2002

University of Cambridge

ABSTRACTS



Oral presentations

Oral presentations will take place in the Physiology Lecture Theatre and, for the parallel sessions at 11:00–1:00, in the Tilley Lecture Theatre. Each presentation will run for a maximum of 15 minutes, including questions. Those presentations marked with an asterisk (*) are being considered for the President's Award (best oral presentation by a member of the Palaeontological Association under the age of thirty).

Timetable for oral presentations

MONDAY 9:00

Affinity of the earliest bilaterian embryos

Xiping Dong and Philip Donoghue

Calamari catastrophe

Philip Wilby, John Hudson, Roy Clements and Neville Hollingworth

Tantalizing fragments of the earliest land plants

Charles H. Wellman

Use of Morphometrics to Identify Character States

Norman MacLeod

Constructional Morphology of Pelagic Crinoids

Adolf Seilacher and Rolf B. Hauff

Origins of teeth amongst jawed stem group gnathostomes

Moya Meredith Smith and Zerina Johanson

MONDAY 11:00—Marine Palaeontology A (parallel)

*Growth patterns in primitive hexactinellid sponges

Joseph P. Botting

Ichnology of the type area of the Maastrichtian Stage (Upper Cretaceous): burrowing and boring immediately prior to the K/T boundary event

Stephen K. Donovan and John W.M. Jagt

Phytoplankton diversity and distribution patterns in the Triassic: the dinoflagellate cysts of the upper Rhaetian Koessen Beds (Northern Calcareous Alps, Austria)

Susanne Feist-Burkhardt, Björn Holstein and Annette E. Götz

A new Locality for *Schizocystis armata* (Forbes, 1848)

William Fone and Christopher R.C. Paul

**Cornulites serpularius*—pursuing a Palaeozoic enigma

Liam Herringshaw

The evolutionary diversification of Palaeozoic echinoids

Charlotte Jeffery

Holocene reef structure and growth at Mavra Litharia, southern coast of Gulf of Corinth, Greece: a simple reef with a complex message

Steve Kershaw and Li Guo

New perspectives in palaeoscolecidans

Oliver Lehnert and Petr Kraft

MONDAY 11:00—Non-marine Palaeontology A (parallel)

Guts and Gizzard Stones, Unusual Preservation in Scottish Middle Devonian Fishes

R.G. Davidson and N.H. Trewin

*The use of ichnofossils as a tool for high-resolution palaeoenvironmental analysis in a lower Old Red Sandstone sequence (late Silurian Ringerike Group, Oslo Region, Norway)

Neil Davies

The harvestman fossil record

Jason A. Dunlop

A New Trigonotarbid Arachnid from the Early Devonian Windyfield Chert, Rhynie, Aberdeenshire, Scotland

Steve R. Fayers and Nigel H. Trewin

*Molecular preservation of upper Miocene fossil leaves from the Ardeche, France: implications for kerogen formation

S. Neal Gupta, A. Stott, D.E.G. Briggs, R.P. Evershed and R.D. Pancost

*A new archaeopteridalean progymnosperm from Venezuela

Susan Hammond

*Responses of paratropical vegetation over different time scales to climate changes in the Palaeogene

Guy Harrington

Bone invasion: Microbial focal destruction in Late Miocene mammal bone

George Iliopoulos

MONDAY 2:00—Precambrian/Cambrian A

Early diagenesis in a Lower Cambrian black shale: more than meets the eye

Uwe Balthasar

Signs of life in a desiccating, dysaerobic, upper Middle Cambrian lagoon

Nicholas J. Butterfield

*Census fossil assemblages from the Middle Cambrian Burgess Shale

Jean-Bernard Caron

Hallucigenia unveiled

Desmond Collins

The dawn of deuterostome evolution: red sky in morning, calcichordates warning?

Simon Conway Morris and Degan Shu

Palaeoecological distribution of Ediacaran fossils

Dima Grazhdankin

MONDAY 4:00—Precambrian/Cambrian B***Halkieriids in Middle Cambrian phosphatic limestones from Australia***Susannah M. Porter***Body building in *Halkieria* and comparisons with chitons and other possible stem-group molluscs***Bruce Runnegar****The Early Cambrian *Mickwitzia* from Greenland and Nevada and the origin of the brachiopods***Christian Skovsted, Lars E. Holmer and Alwyn Williams****Waptia fieldensis*, a possible crustacean from the Middle Cambrian Burgess Shale of British Columbia, Canada***Rod S. Taylor and Desmond H. Collins***Cambrian food chains: new perspectives***Jean Vannier, Chen Junyuan, Zhu Maoyan and Huang Diying***The origin of metazoan reefs: Neoproterozoic of the Nama Group, Namibia***Rachel Wood, John P. Grotzinger and J.A.D. Dickson***TUESDAY 9:00—Extinctions and Transitions*****Oceanographic changes during the Late Devonian mass extinction***David Bond***The palaeoclimatic significance of the Devonian-Carboniferous boundary***J.E.A. Marshall, T.R. Astin, F. Evans and J. Almond****A Global Overview of the lundgreni (Wenlock, Silurian) Graptoloid Extinction Event***Lucy Muir****Microfaunas across the Bathonian-Callovian boundary***K.J. Riddington***Significance of a recently discovered, exceptionally diverse, Early Triassic marine assemblage from Oman***Richard J. Twitchett***The end-Permian mass extinction: sudden or gradual?***Paul B. Wignall***TUESDAY 11:00—Marine Palaeontology B (parallel)****Hydrothermal vent and cold seep molluscs: view from the fossil record***Crispin T.S. Little and Kathleen A. Campbell***The morphology of hyolithids and its functional implications***Mónica Martí Mus and Jan Bergström***Microplankton associations and biofacies: testing Silurian palaeoenvironmental models***Gary L. Mullins, Richard J. Aldridge and David J. Siveter***A revised high-resolution ammonite time scale for the Lower Jurassic of Great Britain***Kevin N. Page***Palaeobiology of Carboniferous microcrinoids***George Sevastopulo***Composition, depositional setting and palaeoecology of Siphonodendron biostromes in the late Viséan of SE Ireland***Ian D. Somerville and P. Cózar****Calcareous nanofossil assemblages during the Messinian Salinity Crisis: evidence from the Polemi Basin, Cyprus***Bridget S. Wade and Paul R. Bown***Early ontogenetic development of blastoids***Johnny A. Waters and Sara A. Marcus***TUESDAY 11:00—Non-marine Palaeontology B (parallel)****The Middle Devonian Flora of Yunnan, China***Christopher M. Berry and Wang Yi****How to make dinosaur tracks: interpreting dinosaur footprint formation and preservation using laboratory controlled simulations***Simon Jackson****Application of high-resolution computed tomography in palaeontology: analysis of a Middle Devonian labyrinthodont tooth from New York State, USA***Vicky MacEwan****The influence of substrate consistency on footprint morphology: field experiments with an emu***Jesper Milàn and Richard G. Bromley***The cranial morphology and systematics of the enigmatic basal ornithischian *Heterodontosaurus tucki* Crompton and Charig, 1962***David B. Norman, Alfred W. Crompton and Alan J. Charig***Ancient weavers on the silk road: Jurassic spiders from China***Paul Selden and Dong Ren****Microevolution of the charophyte genus *Harrisichara* across the Eocene-Oligocene transition in the Isle of Wight, Southern England***Nick P. Sille, Michal Kucera, Margaret E. Collinson and Jerry J. Hooker****Trackways meet trackmakers: the composition of early tetrapod communities***Lauren Tucker*

TUESDAY 2:00—Palaeoecology***Tooth wear in Sticklebacks and the role of competition in speciation***David C. Baines, Mark A. Purnell and Paul J.B. Hart****Response of Late Carboniferous tropical vegetation to transgressive-regressive rhythms at Joggins, Nova Scotia***H.J. Falcon-Lang***Relating Sedimentological Context to Ecological Strategy: a method for examining disturbance in the fossil record***Walton A. Green and Dana Royer****Mid Cretaceous fossil forests from Alexander Island, Antarctica***Jodie Howe***The evolution of swimming among ammonoids***Christian Klug and Dieter Korn***Walking with Millipedes: Kinematics of Locomotion in *Polyxenus* and Implications for Reconstructing the Functional Morphology of the Palaeozoic Millipede *Arthropleura****Heather M. Wilson***TUESDAY 4:00—Concepts and Approaches****Paedomorphism in the Late Devonian tetrapod *Ichthyostega* from East Greenland***Henning Blom***Variation in trilobite terrace ridge patterns using extended eigenshape analysis***Abigail Brown and Norman MacLeod***Character concepts in arthropods: new perspectives for bridging morphological disparity***Ruth Ann Dewel, Jetta Eibye-Jacobsen, Muriel Walker and Richard H. Thomas****Marine invertebrate calcium carbonate—same old story?***Jennifer K. England, Maggie Cusack and Martin Lee***Phylogenetic Congruence Between Hard and Soft Part Data Sets: How Taphonomy Affects Ostracod Phylogenies***Lisa E. Park****Conodonts, cladistics and the fossil record***Linda M. Wickström***Abstracts of oral presentations*****Tooth wear in Sticklebacks and the role of competition in speciation**David C. Baines¹, Mark A. Purnell¹ and Paul J.B. Hart²¹Department of Geology and ²Department of Biology, University of Leicester, Leicester LE1 7RH, UK <dcb14@le.ac.uk> <map2@le.ac.uk> <pbh@le.ac.uk>

Some of the most exciting and widely cited recent work on the ecological controls on speciation focuses on members of the *Gasterosteus aculeatus* species complex. In Canadian lakes, these sticklebacks occur as two morphologically distinct forms or species, and experimental evidence indicates that the differences between them are the result of competition for food resources causing ecological character displacement. The role of competition in evolution is contentious, however, largely because of the fundamental difficulty of extrapolating from field or laboratory experimental results to the longer periods over which new species evolve. The hypothesis that speciation was caused by ecological character displacement driven by trophic niche differentiation is particularly difficult to test in fossils because feeding cannot be observed directly. Functional changes have to be inferred from changes in morphology, and determining whether morphological changes were caused by shifts in feeding thus becomes circular.

Analysis of tooth wear patterns offers a way out of this impasse. Wear on teeth, whether in living or extinct animals, provides direct evidence of tooth use and feeding habits. We have conducted quantitative analysis of tooth wear in laboratory populations of sticklebacks raised under controlled feeding regimes. This is the first quantitative analysis of microwear in non-tetrapods, and our results have important implications for understanding the role of niche differentiation in the evolution of fossil sticklebacks, and in aquatic vertebrates more generally.

Early diagenesis in a Lower Cambrian black shale: more than meets the eye

Uwe Balthasar

Department of Earth Sciences, University of Cambridge, Cambridge CB2 3EQ, UK <ubal01@esc.cam.ac.uk>

Cathodoluminescence and backscattered SEM analysis of shale-hosted organophosphatic and trilobitic fossils from the Lower Cambrian Mural Formation (Jasper National Park, Canadian Rocky Mountains) reveal a complex early diagenetic history leading to aluminosilicate replacement. In organophosphatic shells, aluminosilicate crystals initiate within the shell along originally organic lamellae of a few microns thickness. In the early stage of replacement these lamellae can be replicated with high fidelity, but during further diagenesis idiomorphic crystals initiate along these lamellae, penetrate the juxtaposed phosphatic layers, and thus destroy the original microstructure. Additionally, a prominent layer of silica occurs frequently at the interior edge of organophosphatic shells, which is often followed by a phosphatic zone up to one millimetre thick, typically with needle shaped aluminosilicate crystals floating in the matrix. Trilobite cuticles are pervasively replaced by aluminosilicates growing as idiomorphic crystals perpendicular to the surface of the cuticle, thereby destroying the primary calcitic shell

microstructure. Reworked specimens of trilobites and organophosphatic fossils in co-occurring limestones also show initial stages of aluminosilicate replacement, indicating its very early diagenetic occurrence. Insofar as these shelly remains co-occur with a range of Burgess Shale-type fossils, this study may shed light on the exceptional preservation seen in the Burgess Shale and Soom Shale, both of which have been reported as resulting from aluminosilicate replacement.

The Middle Devonian Flora of Yunnan, China

Christopher M. Berry¹ and Wang Yi²

¹ Department of Earth Sciences, Cardiff University, PO Box 914, CF10 3YE
<berrycm@cardiff.ac.uk>

² Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, China <ywangngs@hotmail.com>

The Middle Devonian Flora of Yunnan was first studied by Halle in 1936. Since then the few publications devoted to these plants have included monographs on large collections of individual plants or small amounts of diverse taxa from scattered localities. We are building up large collections from the Xichong Formation and its lateral equivalents, in order to understand better the nature of the flora as a whole as well as to provide monographic treatments of the individual plants. Floras of Middle Devonian age from Europe, North and South America are dominated by herbaceous lycopsids of widespread distribution, cladoxyloids, progymnosperms and iridopteridaleans in various proportions. Yunnan assemblages contain endemic herbaceous lycopsids and a moderate sized tree with very conspicuous terminal cones. The presence of cladoxyloids, progymnosperms and iridopteridaleans has not been confirmed, but rather there are a number of unusual, sometimes large plants which so far defy classification into the normal Middle Devonian groups. The palaeogeographical and evolutionary significance of this flora will be discussed. The assemblages are likely to be as dramatic for our understanding of early plant evolution as some of the other well publicised fossils that have emerged from China in recent years.

Paedomorphism in the Late Devonian tetrapod *Ichthyostega* from East Greenland

Henning Blom

University Museum of Zoology, Downing Street, Cambridge, CB2 3EJ, UK
<hb269@cam.ac.uk>

In the fossil record, analysis of paedomorphism—considered to be an important mechanism of evolutionary change—relies on the understanding and description of interrelationship, change in size and shape, and distribution. Partial growth series from two species of the Famennian (Late Devonian) tetrapod *Ichthyostega* from East Greenland allows comparison of two ontogenetic paths in skull and jaw morphology. Analysis of skull proportions shows that the *Ichthyostega* specimens from the younger Britta Dal Formation have proportionally broader skulls than those of the older Aina Dal Formation. Together with sculpture characters,

proportions have been used to separate these assemblages to two different species. Also the individual ontogenetic growth series are different and show that the juveniles of each species are more similar in proportions than the adults, suggesting that the stratigraphically younger *I. eigili* retained some juvenile characteristics of the stratigraphically older *I. stensioei*. Growth patterns and tooth differentiation in the upper and lower jaws also provide strong support for the hypothesis that *I. eigili* is paedomorphic. This suggests that paedomorphism may have played an important role in the evolutionary experimentation of structure, function and ecology that took place during the fish-tetrapod transition.

*Oceanographic changes during the Late Devonian mass extinction

David Bond

School of Earth Sciences, University of Leeds, Leeds LS2 9JT, UK
<d.bond@earth.leeds.ac.uk>

The extinctions at the Frasnian-Famennian boundary constitute one of the “big 5” crises of the fossil record. Numerous causes have been proposed for this mass extinction event including meteorite impact and global cooling. The extinction interval is associated with two organic-rich limestone beds, called Kellwasser beds, in the condensed, deep-water German boundary sections: consequently, marine anoxia has also been proposed as a cause of the extinction. Evidence for the global nature of the Kellwasser events has been sought in Late Devonian sections from Poland, France, Belgium and the United States using integrated techniques of pyrite framboid assay, gamma-ray spectrometry and traditional facies analysis. These reveal that only the Upper Kellwasser Horizon, of terminal Frasnian age, may record a truly global oceanic anoxic event. The manifestation of this event varies according to location. In basal locations anoxic-dysoxic deposition was persistent throughout much of the Frasnian with an intensification of anoxia to truly euxinic conditions occurring at the end of the Stage. In platform interiors and slope settings the anoxic event is a discrete pulse that punctuated oxic background conditions. The oxygenation changes have also been compared with the fossil record, particularly of the styliolinids, an enigmatic group of small, conical-shelled fossils that were probably planktonic. This group persisted in reasonable abundance until the very end of the Frasnian, but their reported persistence into the Famennian has yet to be confirmed.

*Growth patterns in primitive hexactinellid sponges

Joseph P. Botting

Department of Earth Sciences, Downing Street, Cambridge CB2 3EQ
<joseph00@esc.cam.ac.uk>

Detailed studies of the growth patterns of modern siliceous sponges are restricted to demosponges and theoretical models. It is generally assumed that sponge growth is essentially incremental, with completion of one arbitrary unit being followed by external addition. All recent species are thick-walled, but Lower Palaeozoic sponges are dominated by thin-walled hexactinellids, the earliest groups consisting of a single spicule layer. Large populations of a primitive dictyospongiid from the Caradoc of Mid Wales have allowed the reconstruction of



the growth patterns of its spicules and body morphology. The results indicate that growth occurred through continuous expansion of the globose body, accompanied by continuous enlargement of existing spicules, with a spicule size limit being reached only during the lifetime of a few individuals. One implication of this system is that the perfect quadrupled pattern of Protospongia, which is only known from specimens of very large size, could have resulted from the enlargement of a species which has tractose development in its early growth stages, or, alternatively, the tractose taxa evolved from quadrupled ancestors through paedomorphosis. This variation in spicule size and tract development should therefore be seriously considered when employed for taxonomic purposes.

Variation in trilobite terrace ridge patterns using extended eigenshape analysis

Abigail Brown^{1&2} and Norman MacLeod¹

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

²Department of Geology and Geophysics, University of Edinburgh,
Grant Institute, West Mains Road, Edinburgh EH9 3JW, UK
<Abigail.Brown@nhm.ac.uk> <N.MacLeod@nhm.ac.uk>

Many trilobites have cuesta-like structures, known as terrace ridges, on both the dorsal and ventral surfaces of the exoskeleton. These structures are relatively poorly studied and their function is controversial. Although terrace ridges all appear to have the same basic construction, they are highly variable and several types are known, including long, continuous forms with asymmetric profiles running subparallel to the margin and symmetrical forms which bear a qualitative similarity to fingerprints.

Research is underway investigating terrace ridge shape variation across the class Trilobita, using a recently developed morphometric technique, extended (landmark-registered) eigenshape analysis (MacLeod, 1999). Major trends in the variation of simplified terrace ridge arrays are currently being explored, both within and between the terrace ridge-bearing orders. Preliminary results show that analysis of pygidial doublural terrace ridge arrays gives good taxonomic separation and can differentiate both phylogenetically and ecologically coherent groups. In particular, this analysis appears to separate pelagic and benthic terrace ridge-bearing forms, potentially providing an independent morphological test for trilobite mode of life hypotheses based on other aspects of morphology.

Signs of life in a desiccating, dysaerobic, upper Middle Cambrian lagoon

Nicholas J. Butterfield

Department of Earth Sciences, University of Cambridge, Cambridge
CB2 3EQ, UK <njb1005@esc.cam.ac.uk>

An extensively mud-cracked black shale unit near the top of the upper Middle Cambrian (Bolaspidella zone) Pika Formation in Jasper National Park, Alberta, Canada, contains diverse range organic-walled microfossils and locally abundant patches of faecal pellets. The microfossils include *Wiwaxia* sclerites, both simple and jointed(?) polychaete-type chaetae, and



an eclectic assortment of spinose elements. These latter include short curved spines, usually with associated denticles and a subtending elongate pore (poison gland?), longer curved spines with a distinct basal attachment structure (broadly reminiscent of chaetognath grasping elements), and a highly variable array of triangular, setose, and occasionally paired sclerites. It is not clear whether these spinose elements are components of a single taxon; most, however are reliably interpreted as the sclerites of priapulid worms. Priapulids are unusually well represented in Burgess Shale-type assemblages, a pattern sometimes interpreted as characteristic of level-bottom ecosystems in the Cambrian. A more likely explanation, however, is found in the unique capacity of living priapulids to withstand relatively extreme dysaerobic and anoxic conditions. Insofar as dysaerobic/anoxic conditions are necessary (though certainly not sufficient) for Burgess Shale-type preservation, it is unlikely that Burgess Shale-type biotas represent "typical" Cambrian communities.

*Census fossil assemblages from the Middle Cambrian Burgess Shale

Jean-Bernard Caron

Department of Zoology, Ramsay Wright Zoological Laboratories, University
of Toronto, Toronto, ON M5S 3G5, Canada <jcaron@rom.on.ca>

A preliminary assessment of 20 fossil assemblages from the Middle Cambrian Burgess Shale has yielded more than 50,000 specimens, mostly of soft-bodied organisms. Royal Ontario Museum field parties collected the specimens from a series of discrete siliciclastic units in a section extending stratigraphically down through about 5 metres beneath the base of the Phyllopod Bed (Walcott Quarry) on Fossil Ridge. The assemblages include 95 of the genera known previously from the Phyllopod Bed, and at least 35 potential new genera representing a range of phyla. Despite variations in number of species and abundance of specimens, most individual fossil assemblages appear to retain high fidelity to the composition of the source community and represent potential census assemblages. Recurrence of species associations suggests seasonal, or shorter, episodes of burial, and provides an opportunity to study the natural temporal variation of the composition and structure of Burgess Shale communities at an ecologically meaningful scale. The application of multivariate statistical methods to the analysis and interpretation of the variations in these assemblages allows the integration and summary of large numbers of specimens and taxa, thereby providing a means of examining community associations.

Hallucigenia unveiled

Desmond Collins

Department of Palaeobiology, Royal Ontario Museum, 100 Queen's Park,
Toronto, Ontario M5S 2C6, Canada <desc@rom.on.ca>

Since Conway Morris named and redescribed *Hallucigenia sparsa* (Walcott, 1911) in 1977, it has been regarded as the weirdest of the Middle Cambrian Burgess Shale animals. Conway Morris' interpretation of the paired spines as legs, with a single row of bifid tentacles along the back, and with a globular head, began a topsy turvy succession of restorations: Ramsköld and Hou in 1991 turned *Hallucigenia* upside down, with the spines along the back; in 1992 Ramsköld

discovered claws from the second row of tentacles on the holotype, and turned *Hallucigenia* front to back, with the head at the narrow end; then, in 1995 Hou and Bergström returned *Hallucigenia* back to front, and revived the globular head of Conway Morris.

Examination of the original and newly collected specimens indicates that there are two different forms of *Hallucigenia*: a larger form with a robust, rigid trunk, a robust neck and a globular head; and a smaller form with a thinner, more flexible trunk, and a small head with two fang-like projections, two short horns and possibly a pair of eyes, connected to the trunk by a very thin neck. Both forms have seven pairs of robust spines along the back, and seven pairs of long, thin, flexible legs terminating in the large claw typical of onychophorans. The two forms may be either sexual dimorphs, or separate *Hallucigenia* species.

The dawn of deuterostome evolution: red sky in morning, calcichordates warning?

Simon Conway Morris¹ and Degan Shu²

¹ Department of Earth sciences, University of Cambridge, Cambridge CB2 3EQ, UK

² Early Life Institute, Northwest University, Xi'an, China

In contrast to our understanding of the early evolution of the ecdysozoans and lophotrochozoans, where the fossil record and molecular biology appear to be in fair agreement, the case for the deuterostomes is less resolved. Insights from the Chengjiang Lagerstätte, South China, however, may help in both defining and linking the otherwise notably disparate phyla. Here we report on two interesting discoveries; one confirmatory, the other controversial. The former concerns the discovery of an extensive suite of the fish *Haikouichthys*, hitherto known only from a single and incomplete specimen. The new material confirms its agnathan status, both with respect to the sensory apparatus and also key post-cranial features. The latter concerns a new yunnanozoan, a group with a chequered history in terms of phylogenetic placement. Here we present new evidence that casts serious doubt on the craniate hypothesis, and suggests a position as a stem-group deuterostome of broadly hemichordate grade. New information on the gills suggests that the evolution of the diagnostic pharyngeal openings may have been more complex than hitherto suspected. In addition the new material strengthens a proposed link to the vetulicolians. Chengjiang deuterostomes therefore provide historical data on body-plans that are in accordance with both Romer's somato-visceral hypothesis and Jefferies' calcichordates, specifically with respect to a bipartite body, the anterior of which bears pharyngeal openings and the posterior of which is segmented.

Guts and Gizzard Stones, Unusual Preservation in Scottish Middle Devonian Fishes

R.G. Davidson and N.H. Trewin

Department of Geology and Petroleum Geology, University of Aberdeen, Aberdeen AB24 3UE, UK <Bob.Davidson@uk.coflexip.com>

Relics of internal organs identified as kidney, liver, heart, ?spleen, and also eyes, have been recognised in several fish specimens from the Middle Devonian nodule bed localities of Tynet Burn, Gamrie and Lethan Bar, north-east Scotland. Internal organs are represented by dark red to black stains positioned where the organs were situated in life. This phenomenon has been observed in the acanthodians *Diplacanthus*, *Cheiracanthus* and *Mesacanthus*, and in the actinopterygian, *Cheirolepis*. In some specimens eyes are also preserved as dark stains.

The fossil bone of the fish in nodules from Tynet Burn is stained by iron oxide deposited by the action of chemotrophic bacteria during early burial. Concentration of iron deposition at haemoglobin rich organ sites in early diagenesis may provide the visible contrast which enables traces of these organs to be seen.

Two specimens of the Arthrodire *Cocosteus* display a fusiform mass of stomach contents, containing pebbles that acted as 'gizzard' stones and also fragmentary acanthodian material, providing dietary evidence for this predator.

*The use of ichnofossils as a tool for high-resolution palaeoenvironmental analysis in a lower Old Red Sandstone sequence (late Silurian Ringerike Group, Oslo Region, Norway)

Neil Davies

Earth Sciences, School of Geography, Earth and Environmental Sciences, University of Birmingham, Birmingham B15 2TT, UK <nsd073@bham.ac.uk>

The late Silurian Ringerike Group of southern Norway is an early Old Red Sandstone megasequence that marks the regressive culmination of Cambro-Silurian marine deposition in the Oslo Region. It has traditionally been divided into three formations—the Sundvollen and Stubdal Formations to the north of Oslo (representing muddy coastal plain and braided fluvial deposition respectively), and the Holmestrand Formation to the south (representing fluvio-deltaic deposition). A comprehensive ichnological analysis of the Ringerike Group has resolved many problems in the interpretation of the stratigraphical and palaeoenvironmental relationship between the northernmost and southernmost outcrop areas. To the north, various facies dependent ichnoassemblages are dominated by epifaunal arthropod trackways, with less abundant burrows, looping traces, escape structures, and ichnofossils of uncertain origin. In contrast, the Holmestrand Formation has more diverse ichnoassemblages dominated by burrow traces and arthropod resting traces, with less abundant arthropod trackways, escape structures, and looping traces. Other biogenic structures present in both areas include microbial matgrounds, medusoid imprints, and problematic impressions. The distribution of the ichnofauna in each area is clearly facies controlled and provides new insights into both the ichnological subdivision of nearshore environments and the variation in the palaeoenvironmental conditions of the Oslo Region during the latest Silurian.



Character concepts in arthropods: new perspectives for bridging morphological disparity

Ruth Ann Dewel¹, Jetta Eibye-Jacobsen², Muriel Walker³ and Richard H. Thomas⁴

¹Department of Biology, Appalachian State University, Boone, NC 28608, USA.

²Invertebrate Department, Zoological Museum, Universitetsparken 15 DK-2100, Copenhagen Ø, Denmark

³Department of Biology, University of Leicester, University Road, Leicester LE1 7RH, UK

⁴Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

The task of identifying phylogenetically useful characters for analyses combining fossil and extant taxa is difficult. Complex transformations can greatly modify characters and impede our ability to recognize homology across large gaps of time. The objective of this study was to examine living and fossil arthropods to determine if structures previously thought to be unrelated may actually represent different states of a drastically transformed character. Several characters of ecdysozoans, encompassing such prominent attributes of the Cambrian arthropod fauna as the “Peytoia”, frontal appendage, and biramous limb appear to fall into this category. Attention was paid to finding in living arthropods the homologues of characters present in Cambrian arthropods, many of which belong to the stem groups of extant forms. Putative homologues of these characters and others were assessed by standard criteria to identify primary homology. Criteria were relaxed for some characters, which were described with explicit *a priori* statements of putative homology. More broadly defined characters or characters comprised of new structurally and/or functionally discrete states were incorporated with characters from other analyses of ecdysozoans into a phylogenetic analysis using PAUP. The impact of the newly interpreted characters was substantial and yielded unexpected results including a lack of support for such widely accepted taxa as Mandibulata and Myriapoda.

Affinity of the earliest bilaterian embryos

Xiping Dong¹ and Philip Donoghue²

¹Department of Geology, Peking University, Beijing, 100871, P. R. China

²Lapworth Museum of Geology, University of Birmingham, Birmingham B15 2TT, UK

Classical attempts at unravelling the evolutionary history of metazoans have focused upon the early development of living organisms as an absolute guide to evolutionary relationships. Unfortunately, because the fossil record has been limited largely to the remains of adults and late juvenile stages it has had little to offer in this endeavour and, as a result, some of the basic assumptions of evolutionary embryology have escaped testing. Recent discoveries of fossil embryos from the terminal Neoproterozoic of China and Early Cambrian of Siberia provide the potential for such tests but, until the affinity of these embryos can be constrained further, their significance is mute.



New collections of embryos from the Middle and Late Cambrian of China, and Lower Ordovician of North America, include developmental stages from late cleavage through to much later developmental stages in which phylogenetically informative aspects of the organism's anatomy have begun to unfold. The embryos resemble strongly *Markuelia secunda*, described previously by Bengtson & Zhao (1997, *Science* 277: 1645-8), thus providing constraint over the affinity of these, the earliest unequivocal bilaterian embryos. *Markuelia* is a priapulid that underwent direct-development, a life history strategy rare amongst living priapulids. Phylogenetic analysis unequivocally resolves *Markuelia* as a stem-group priapulid and character optimisation suggests that the majority of fossil (stem group) were direct-developers.

Ichnology of the type area of the Maastrichtian Stage (Upper Cretaceous): burrowing and boring immediately prior to the K/T boundary event

Stephen K. Donovan¹ and John W.M. Jagt²

¹Department of Palaeontology, Nationaal Natuurhistorisch Museum, Darwinweg 2, Postbus 9517, NL-2300 RA Leiden, The Netherlands <donovan@naturalis.nnm.nl>

²Natuurhistorisch Museum Maastricht, Postbus 882, NL-6200 AW Maastricht, The Netherlands <john.jagt@maastricht.nl>

The Vaals, Gulpen and Maastricht formations (Campanian-Maastrichtian) of The Netherlands and Belgium have yielded an ichnofauna comprised of at least 33 ichnogenera of invertebrate burrows and macroborings, many of which still await formal documentation. These structures are indicative of a range of activities in various biotopes immediately prior to the K/T event, and give at least some indication of the presence of taxa lost due to poor preservation of unmineralised and aragonitic skeletons. Some recent discoveries add interesting and tantalizing ichnotaxa to an already diverse list. Enigmatic *Arachnostega gastrochaenae* Bertling in the internal mould of a bivalve represents unusual preservation of a burrow—or is it a boring? An unnamed ‘chambered’ boring in an oyster shell has a morphology strongly influenced by shell structure. *Radulichnus* Voigt, *Renichnus* Mayoral and *Centrichnus* Bromley and Martinell are three distinctive borings indicative of specific activities of benthic molluscs. Large, non-penetrative *Oichnus* isp. nov. borings infest irregular echinoids, and are distinctive in having concave walls and a large central boss. Internal blisters show that this infestation occurred when the echinoids were alive. Overall, the ichnotaxonomic composition of these formations is as reminiscent of a Cenozoic succession as one from the Mesozoic.

The harvestman fossil record

Jason A. Dunlop

Institut für Systematische Zoologie, Museum für Naturkunde der Humboldt-Universität zu Berlin, D-10115 Berlin, Germany

<jason.dunlop@museum.hu-berlin.de>

Harvestmen (Arachnida: Opiliones) are relatively rare as fossils, but current data on their fossil record is summarised here and superimposed on the most recently published phylogeny—(Cyphophthalmi (Eupnoi (Dyspnoi + Laniatores)))—to infer minimum times for cladogenesis.



The 'primitive' cyphophthalmids lack a fossil record, and thus express a ghost range of c. 400 million years. Fossils potentially referable to the familiar, long-legged eupnoid group occur in the Devonian of the Rhynie chert. Fossils assigned to the Carboniferous arachnid order Kustarachnida are simply misidentified eupnoid harvestmen. Putative members of the more cryptic dyspnoid harvestmen occur in the Carboniferous Coal Measures. The bizarre, spiny, mostly tropical laniatores are only known from Tertiary ambers (mostly Dominican) and thus express a c. 250 million year ghost range. The other major conclusion to be drawn is the relative modernity of almost all the fossil harvestmen. The earliest examples resemble living forms in gross morphology and most Tertiary fossils can be referred to extant genera. This implies an extraordinary degree of stasis within Opiliones throughout their evolutionary history.

***Marine invertebrate calcium carbonate—same old story?**

Jennifer K. England, Maggie Cusack and Martin Lee
Division of Earth Sciences, University of Glasgow, Glasgow G12 8QQ, UK
<J.England@earthsci.gla.ac.uk>

Biominerals perform a range of functions in nature and contribute greatly to the fossil record. Calcium carbonate is abundant in invertebrate systems and occurs in a wide range of ultrastructural forms as well as different polymorphs. Two species of living brachiopod, *Terebratulina retusa* and *Neocrania anomala* and the common mussel, *Mytilus edulis*, span a range of ultrastructural motifs as well as two calcium carbonate polymorphs; calcite and aragonite. The valves of *T. retusa* have a primary layer of acicular calcite underlain by calcite fibres of the secondary layer. The dorsal valves of *N. anomala* also have a primary layer of acicular calcite while the secondary layer consists of semi-nacre i.e. tabular calcite that grows by screw dislocations. *M. edulis* valves consist of an outer layer of prismatic calcite with a nacreous aragonite inner layer. Comparison of the major and trace elements as well as the amino acid composition of the three marine invertebrates allows an initial survey of the inorganic and organic components. This will begin to determine the extent to which similar processes have evolved to produce apparently different biominerals.

***Response of Late Carboniferous tropical vegetation to transgressive-regressive rhythms at Joggins, Nova Scotia**

H.J. Falcon-Lang
Department of Earth Sciences, University of Bristol, Bristol BS8 1RJ, UK
<falconlang@hotmail.com>

Fossil plant assemblages are described in their sequence stratigraphic context from the Upper Carboniferous (Langsettian) Joggins Formation of Nova Scotia to elucidate ecosystem response to transgressive-regressive rhythms. Results show that rising base-level resulted in retrograding submerged mires co-dominated by *Lepidodendron* and *Lepidophloios* lycopsids, which were subsequently replaced by short-lived *Paralycopodites* lycopsid communities following mire drowning. Extensive brackish bays existed during early highstand, distally fringed by progymnospermous and gymnospermous coastal/upland vegetation. Late highstand bay



filling generated prograding distributary wetlands dominated by flood-disturbed lycopsid-pteridosperm-sphenopsid communities and cordaite mangroves. As base-level fell, well-drained alluvial plains were dominated by fire-prone cordaite and/or *Sigillaria* communities, which persisted until the next phase of base-level rise resulted in a return to lycopsid-dominated coastal mires. Rhythmic ecosystem succession of this kind repeatedly occurred on a 100-500 ka timescale at Joggins. This is the first time ecosystem response to Late Carboniferous global change has been identified, a process which may have been very important in creating and maintaining high tropical biodiversity.

A New Trigonotarbid Arachnid from the Early Devonian Windyfield Chert, Rhynie, Aberdeenshire, Scotland

Steve R. Fayers and Nigel H. Trewin
Department of Geology and Petroleum Geology, Meston Building,
King's College, University of Aberdeen, Aberdeen, Scotland AB24 3UE

A new trigonotarbid arachnid is introduced from the Early Devonian (Pragian) Windyfield chert. The material comprises an almost complete, exceptionally preserved individual approximately 8mm in length, and fragmentary remains. The specimens occur in bacterially laminated chert. The box-like carapace has a projecting apically toothed clypeus displaying parallel ridges. Both lateral and median eye tubercles are present. The carapace surface has a distinctive lobation and is tuberculate. The lateral and posterior margins appear rebordered. The sternum is indented with a straight posterior margin. The ornament of the walking legs comprises longitudinal rows of thorn-like tubercles. The abdominal tergites and their lateral margins are tuberculate, and the ninth tergite is fused. The sternites exhibit tuberculation along their posterior borders, though laterally the tuberculate ornamentation hints at the presence of fused, relic lateral plates. Although similar in overall body plan, this new arthropod is quite distinct from *Palaeocharinus*, the common trigonotarbid of the Rhynie chert, in both its size and ornamentation. This animal is a palaeocharinid, although similarities may be tentatively drawn with the anthracomartids. Like the other Rhynie chert trigonotarbids, this animal appears to have been a terrestrial predator, and its discovery increases the faunal diversity of this remarkable deposit.

Phytoplankton diversity and distribution patterns in the Triassic: the dinoflagellate cysts of the upper Rhaetian Koessen Beds (Northern Calcareous Alps, Austria)

Susanne Feist-Burkhardt¹, Björn Holstein² and Annette E. Götz³

¹Department of Palaeontology, The Natural History Museum, Cromwell Road, London, SW7 5BD, England, UK <s.feist-burkhardt@nhm.ac.uk>

²Geologisch-Paläontologisches Institut, Johann-Wolfgang-Goethe Universität, Senckenberganlage 32-34, D-60325 Frankfurt, Germany <bholstei@stud.uni-frankfurt.de>

³Martin-Luther-Universität Halle-Wittenberg, Institut für Geologische Wissenschaften und Geiseltalmuseum, Domstr. 5, D-06108 Halle (Saale), Germany

The first unequivocal dinoflagellate cysts are known from the Upper Triassic, but the first relatively diverse assemblages in Europe occur in the uppermost Triassic, the Rhaetian. These assemblages are characterised by only a few species and genera belonging to many different families. The dinoflagellate cyst assemblages of the Koessen Beds from a key section in the Calcareous Alps (Eiberg section near Kufstein, Austria) are presented. Most samples are rich in well-preserved dinoflagellate cysts. For the first time, the species *Wanneria listeri* (STOVER & HELBY 1987) BELOW 1987, which was so far known only from the Norian of Australia and Indonesia, is recorded from European sediments. The dinoflagellate cyst assemblages change significantly in their quantitative and qualitative composition depending on the lithology of the samples and the position of samples in a sedimentary sequence. The observed distribution patterns are discussed in context with the cyclic sedimentation of the limestones and marls of the Koessen Beds. Moreover, we try to decipher the palaeoecological factors that are responsible for the distribution patterns recognised in the Rhaetian of the Northern Calcareous Alps.

A new Locality for *Schizocystis armata* (Forbes, 1848)

William Fone¹ and Christopher R.C. Paul²

¹Staffordshire University, Stafford, ST18 0DG, UK <W.Fone@Staffs.ac.uk>

²Department of Earth Sciences, University of Liverpool, Liverpool L69 3GP, UK

Cystoids of the Echinoencrinitidae are known from the Silurian rocks of Britain. However, with the exception of a small number of specimens, locality details are vague or absent for the material available to study. Newly collected samples of *Schizocystis armata* (Forbes, 1848) provide material whose exact provenance is known. A comprehensive review of the British Silurian cystoids has concluded that water depth restricted the distribution of the fauna (Paul, 1967). The British Silurian cystoid material is rare and only available in old collections. Old museum collections seldom record exact locality or horizon of specimens. The Holcroft collection in the Department of Geology, University of Birmingham is an exception. Holcroft was one of the few Victorian collectors to record exact localities. However the localities are no longer available for modern study. We report a new locality in Shropshire yielding articulated specimens of *Schizocystis armata* (Forbes, 1848) together with a rich benthic and nektonic fauna that includes

crinoids, trilobites, brachiopods and gastropods. The associated fauna provides insight to the lifestyle of the cystoids and the bio-facies they occupied.

Palaeoecological distribution of Ediacaran fossils

Dima Grazhdankin

Department of Earth Sciences, University of Cambridge, Cambridge CB2 3EQ, UK <dgra99@esc.cam.ac.uk>

A siliciclastic succession of the late Neoproterozoic Vendian complex, White Sea area, north-western Russia, demonstrates a wide range of sedimentary facies, some of them recurring in a vertical succession. Each lithofacies contains a distinct and separate assemblage of Ediacaran fossils preserved in life position. Facies-controlled distribution also characterizes other Ediacaran localities, so demonstrating for the first time that fossil assemblages occurring in similar facies are directly comparable at a global scale. Thus to a truly remarkable degree the Ediacaran biotas preserved in proximal prodelta settings in South Australia, in the White Sea area, and in Central Urals are closely parallel. The fossil assemblages found globally in fluviomarine facies are also directly comparable, as corroborated by a recent discovery of *Rangea* in a distributary-mouth bar lithofacies in the White Sea area. This in turn reveals a marked degree of environmental sensitivity and pronounced ecological specialization in these early communities. Based on the White Sea section, correspondence between depositional environment and taxonomic composition rules out hypotheses of biogeographic provinciality of the Ediacaran biotas, and also casts doubt on existence of evolutionary progression during Ediacaran times. What is evident is that Ediacaran organisms rapidly explored various environmental settings, ranging from shallow-water deltaic sandy shoals to deep-water aprons, and maintained this ecological disparity, with limited overall change, for more than 20 million years.

Relating Sedimentological Context to Ecological Strategy: a method for examining disturbance in the fossil record

Walton A. Green¹ and Dana Royer²

¹Department of Geology and Geophysics, Yale University, P. O. Box 208109, Yale Station, New Haven, Connecticut, 06520 USA <walton.green@yale.edu>

²Department of Geosciences, Pennsylvania State University, University Park, PA 16802, USA <droyer@psu.edu>

Too frequently, methods of analysis used by modern ecologists cannot be applied to ancient ecosystems because data of the right type or of sufficiently high quality are not obtainable from the fossil record. One such method is Grime's (1974) procedure for ordinating herbaceous plants in a ternary diagram in which the vertices represent three primary ecological strategies for sessile organisms (Competitor, Stress Tolerator, Ruderal). Here we suggest a method of plotting plant species on similar ternary diagrams based not on their morphology and physiology but on geographic or sedimentological contexts in which they are found. This will allow comparison of the ecological strategies employed by plants in modern and ancient terrestrial ecosystems and



can potentially be generalized to marine ecosystems dominated by sessile organisms in which disturbance is an important factor.

Work cited: Grime, J.P. 1974. Vegetation classification by reference to strategies. *Nature* 250:2631.

***Molecular preservation of upper Miocene fossil leaves from the Ardeche, France: implications for kerogen formation**

S. Neal Gupta^{1,2}, A. Stott², D.E.G. Briggs¹, R.P. Evershed² and R.D. Pancost²

¹Department of Earth Sciences, University of Bristol, Bristol, UK

²School of Chemistry, University of Bristol, Bristol, UK

Organic diagenesis is an important mechanism in fossilisation. Here we report the results of an investigation of the upper Miocene freshwater diatomite of St. Bazile, which yields diverse plants and arthropods. All the fossil leaves irrespective of plant type show characteristic alkane/alkene peaks (the pyrolysis product of an aliphatic macropolymer) ranging from C-8 to C-33, as well as lignin products and prist-1-enes and prist-2-enes. Polysaccharide and protein moieties were not detected but some samples provide the first reliable demonstration of cutin in fossil leaves. The beetles also yield an aliphatic signature and chitin and protein are absent. No resistant aliphatic macropolymer is present in the extant analogues of several of our samples including conifer needles, oak leaves and beetles. Thus the macromolecular composition of the fossils must be the result of diagenesis. It is clear that short chain aliphatic compounds, with or without other constituents, condense into a macromolecule of cross-linked n-alkyl units with carbon chain lengths up to at least C-33. This mechanism has been referred to as the *in-situ polymerisation model*. The striking similarity between pyrolysates of plant and arthropod fossils and kerogens (the dominant sedimentary organic matter) suggests that *in-situ polymerisation* is important in kerogen formation.

***A new archaeopteridalean progymnosperm from Venezuela**

Susan Hammond

Dept. of Earth Sciences, Cardiff University, PO Box 914, Park Place, Cardiff CF10 3YE, Wales, UK <hammonds2@cf.ac.uk>

Coalified compressions of new archaeopteridaleans were collected from the lowermost Upper Devonian Campo Chico Formation, Sierra de Perijá, Venezuela. The spectacularly preserved specimens made up of branching axes and leaves initially appear two-dimensional like extant fern fronds, but are probably leafy branches of an early tree. *Archaeopteris* itself was originally classified as a fern based on its planated fronds, and only recently has its three-dimensional nature been documented. Morphologically this has put the genus much closer to *Svalbardia*, another archaeopteridalean, which has always been known to have spirally arranged axes but has more deeply dissected leaves than *Archaeopteris*. This study has demonstrated a three-dimensional structure of the new archaeopteridaleans and leaf morphology more or less intermediate between *Svalbardia* and *Archaeopteris*. Clearly the morphology of the Venezuelan plant is similar to that of both *Archaeopteris* and *Svalbardia* indicating its archaeopteridalean nature. The fertile parts closely resemble *A. fissilis/S. polymorpha*, vegetative leaves share



characteristics with *A. sphenofillifolia* and *A. macilenta*, and there is an indication of leaf dimorphism as seen on *A. roemeriana*. It is anticipated that further morphological comparisons, especially with archaeopteridaleans, will lead to a better understanding of the Venezuelan plant's affinities and its place in evolution.

***Responses of paratropical vegetation over different time scales to climate changes in the Palaeogene**

Guy Harrington

Department of Paleobiology, Smithsonian Institution, P. O. Box 37012, Natural History Building MRC 121, Washington, DC 200013, USA

<harrington@nmnh.si.edu>

Understanding the response of vegetation to climate changes on time scales from 10⁶ – 10⁴ years is central to many hypotheses on speciation and predictions on future vegetation change. This is especially the case in greenhouse climates that Quaternary vegetation reconstructions are poorly equipped to model. Pollen and spore data from >240 samples are presented here from the eastern US Gulf Coast (palaeo-latitude c. 32° N) that span an interval of c. 3 my and are centred on the Palaeocene–Eocene boundary (54.93 ma). The vegetation type is paratropical throughout and the climate (MAT c. 27°C) was probably comparable to parts of the present-day Amazon basin. The sampling resolution varies considerably but a section near the Palaeocene–Eocene boundary is sampled every 4-8 ky and spans c. 250 ky. Changes in vegetation reveal a probable eccentricity cycle, that is statistically significant through power spectral analysis, but chord analyses show the actual change in vegetation is slight and noted only by a change in abundance of myricaceous pollen. Overall, chord analyses demonstrate that vegetation composition is affected far more strongly over 10⁵ – 10⁶ years by secular climate change such as warming throughout the late Palaeocene, additional warming across the Palaeocene–Eocene thermal maximum (PETM) and cooling in the early Eocene.

***Cornulites serpularius—pursuing a Palaeozoic enigma**

Liam Herringshaw

Lapworth Museum of Geology, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK <LGH865@bham.ac.uk>

The Much Wenlock Limestone Formation (Silurian) of the English Midlands and Welsh Borderlands has yielded more than 650 species of exquisitely preserved fossils. The vast majority can be placed in extant phyla, but a number of problematica remain. One of the most abundant and distinctive, yet least understood, is *Cornulites serpularius* Schlotheim, 1820. *C. serpularius* is a calcareous, annulated, tube-dwelling organism, and the type species of a group that has received various systematic assignments, the most persistent being with the polychaete annelids. However, its characteristics have never been satisfactorily described, such that the diagnosis of other tubular, calcareous fossils as cornulitids is cast into doubt. A comprehensive reassessment of *C. serpularius* has been carried out, revealing shell structures that have not previously been described. These features enable comparison with other purported cornulitids and provide new insights into the biological affinities and functional morphology of both *C. serpularius* and the group as a whole.

***Mid Cretaceous fossil forests from Alexander Island, Antarctica**

Jodie Howe

Department of Earth Sciences, University of Leeds, Leeds LS2 9JT and British Antarctic Survey

Spectacular fossil forests are preserved in mid Cretaceous rocks on Alexander Island, Antarctic Peninsula. Fossil trees and shrubs are preserved within fossil soils in their original positions of growth, within a sequence of river channel sands and floodplain sands and silts. Statistical analysis of the fossil plant data reveals that certain types of plants always occurred together. Three plant assemblages were identified: i) a conifer/fern assemblage with mature conifers of mainly araucarian type and an understory of *Sphenopteris* ferns, ii) a mixed conifer, fern and cycad assemblage with araucarian conifers and *Ginkgo* trees, iii) a disturbance flora of liverworts, *Taeniopteris* shrubs, ferns and angiosperms. These plant assemblages were also statistically coupled to specific fluvial environments. Areas near river channels that were frequently flooded by silt-bearing flood waters were colonised by a flora of pioneer species and early colonisers, such as angiosperms, liverworts and ferns, plants that became established quickly and reproduced rapidly. Areas further from the river channels were colonised by more mature vegetation of conifers that were flooded only intermittently so that the large trees were not disturbed.

Bone invasion: Microbial focal destruction in Late Miocene mammal bone

George Iliopoulos

Department of Geology, University of Leicester, Leicester LE1 7RH, UK <gi6@le.ac.uk>

The taphonomic investigation of Upper Miocene (MN 11-12) fossil mammal bones from Kerassia (Euboea Island, Greece) was undertaken on material from seven different sites near Kerassia, where at least two fossiliferous horizons occur. Polished thin sections of fossil bone and teeth from both horizons of Kerassia and, for comparison, eight other Late Miocene Greek localities were studied under the SEM (using backscatter imaging) and analysed using a microprobe. All Kerassia bones and teeth (in dentine and cement) showed extensive microbial focal destruction (MFD). It can be seen as zones of damaged bone, around the perimeter of the bones, around the marrow cavity and as randomly scattered foci. The MFD foci in three dimensions are ellipsoid nodules with their long axes parallel to the long axis of the bone. The rims of these nodules are permineralised. Microprobe analyses show that the apatite in the rims is enriched in calcium phosphate relative to the whole bone and calcium phosphate is depleted in the foci. The internal structure of the foci is manifest as a series of parallel microtunnels. The diameter of these microtunnels is between 150-400 nm, indicating that the invading microorganisms were bacteria. Bone material from the other Late Miocene Greek localities revealed the same or similar extensive bacterial damage. Therefore, during the Late Miocene a temperate to warm and relatively moist climate in the North-Eastern Mediterranean can be inferred.

***How to make dinosaur tracks: interpreting dinosaur footprint formation and preservation using laboratory controlled simulations**

Simon Jackson

Department of Geography, University Of Sheffield, The Dainton Building, Brookhill, Sheffield, S3 7HF, UK <glp00sjj@shef.ac.uk>

The laboratory simulation of dinosaur footprints has the potential to yield significant information on their formation and preservation. Such studies are particularly useful as the variables involved in the trackmaking episode can be selectively investigated, with a rigorous degree of control not entirely possible in experimental animal studies. The three-dimensional study of the tracks reveals important insight into the interaction between the dinosaur foot and the substrate at the time of track formation. Vertical sections taken through simulated footprints, preserved in layered sediments, reveal a variety of both brittle and ductile deformation structures. The style and degree of this deformation is fundamentally determined by the shape of the foot, the kinematics of the trackmaker and the nature of the sediment into which the foot penetrates. The analysis of this deformation of the sediment leads to a greater understanding of dinosaur foot morphology, dinosaur gait and the environments they once lived in.

The evolutionary diversification of Palaeozoic echinoids

Charlotte Jeffery

Department of Geology & Geophysics, University of Edinburgh, Grant Institute, West Mains Road, Edinburgh EH9 3JW, UK <charlotte.jeffery@glg.ed.ac.uk>

Compared to their post-Palaeozoic counterparts, the palaeobiology and evolutionary history of Palaeozoic echinoids are poorly understood. In part this is due to their non-rigid tests which dissociate rapidly on death and their resultant poor fossil record. However, under favourable conditions, Palaeozoic echinoids may be preserved complete with external appendages and feeding apparatus, and where more robust Mesozoic and Cainozoic echinoid tests can be transported after death, complete specimens of Palaeozoic echinoids are found only in the environment in which they lived. This means that although there are comparatively few specimens available, the ones that do exist commonly preserve large suites of characters and provide information about palaeoenvironment. Here I present a new, cladistically derived phylogeny for the Palaeozoic echinoids and combine this with a functional morphological approach to investigate the relationship between evolutionary diversification, ecosystem utilization and palaeoenvironment of this important but poorly characterised group.

Holocene reef structure and growth at Mavra Litharia, southern coast of Gulf of Corinth, Greece: a simple reef with a complex message

Steve Kershaw¹ and Li Guo²

¹ Geohazards and Environmental Catastrophes Research Group (GECRG), Department of Geography & Earth Sciences, Brunel University, Uxbridge UB8 3PH, UK <stephen.kershaw@brunel.ac.uk>

² CASP, Department of Earth Sciences, University of Cambridge, Cambridge CB3 0DH, UK <lg203@cam.ac.uk>

A Holocene reef at Mavra Litharia on the southern coast of the central part of the Gulf of Corinth, Greece, is constructed of a coral-algal frame, bound by laminated micritic carbonate crusts of possible microbial origin. The reef reveals a two-stage history:

- a) growth of reef, without detectable ecological zonation, followed by uplift into subaerial conditions, where a cave system developed throughout the upper part of the reef. The cave system was partly filled with clastic debris washed from nearby hills of uplifted footwall blocks
- b) resubmergence and colonisation of eroded surfaces by barnacles, serpulid worms and rock-boring bivalves, followed by uplift to its present setting, where much of the reef has been removed by erosion.

The relative sea-level changes represented by the history of the reef took place under a regime of presumed continuously rising global sea level in the Gulf during the Holocene; global SL rose rapidly in the early part of the Holocene up to the mid-Holocene quasi-stillstand (c.8-6.5 ka), then more gradually up to modern times. Thus the reef's history demonstrates an apparent interplay between SL rise and tectonic vertical movement against the backdrop of stepwise footwall uplift along the southern margin of the Gulf of Corinth.

The evolution of swimming among ammonoids

Christian Klug¹ and Dieter Korn²

¹ Staatliches Museum für Naturkunde, Am Rosenstein 1, 70191 Stuttgart, Germany <klug.smns@naturkundemuseum-bw.de>

² Humboldt-Universität zu Berlin, Museum für Naturkunde, Institute of Palaeontology, 10099 Berlin, Germany <dieter.korn@uni-tuebingen.de>

Ammonoid conch geometry is the key to their mode of life, because of their poorly known soft parts. Among the conch parameters, the whorl expansion is especially significant, representing a proxy for the apertural orientation in planispiral ammonoids which grew approximately isometric. Apparently, the origin of ammonoids lies within the Bactritidae which usually had orthoconic conchs and thus downward oriented apertures. Their horizontal movements were probably slow. In more derived Bactritidae with curved conchs, the aperture reached an oblique downward orientation (*Cyrtobactrites*: 20-30°). During the early Emsian, the curvature increased during phylogeny and simultaneously, the orientation of the aperture moved from oblique upward to horizontal (*Metabactrites Erbenoceras Mimosphinctes Mimagoniatites*: 40-70°). The late Emsian Latanarcestidae gave rise to four important Middle Devonian ammonoid families

(Agoniatitaceae, Anarcestaceae, Pharcicerataceae, Tornocerataceae). Throughout phylogeny of these clades, transformations of conch geometry and orientation happened. Many apomorphic forms of these clades had similar whorl expansion rates as adults, the same almost horizontal orientation of the aperture (70-80°), smooth slender conchs, and a narrow umbilicus. These features indicate moderate to good horizontal swimming abilities, a selective advantage with respect to the search for prey, mating partners, or spawning sites.

New perspectives in palaeoscolecidans

Oliver Lehnert and Petr Kraft

Charles University Prague, Institute of Geology and Palaeontology, Albertov 6, 128 43, Prague 2, Czech Republic
<lehnert@natur.cuni.cz> <kraft@natur.cuni.cz>

Palaeoscolecidans are an extinct class of vermiform organisms with a prominent annulation ranging from the Lower Cambrian to the Silurian. The outer cuticle of their segments possesses microelements mineralized by calcium phosphate. Such sclerites have been mainly isolated from carbonates. There is extensive unpublished material especially in conodont collections, at least from Laurentia. Preliminary data show a stratigraphic value of some morphotypes. Therefore, after detailed taxonomic revision, palaeoscolecidans may represent potential index fossils.

Future comparison of the microelements with larger fragments of palaeoscolecidans or whole body fossils, mainly recovered from fine-grained siliciclastics, is necessary, not least to avoid producing many parataxa. The study of material from different palaeocontinents might be of significant value for the solutions of biostratigraphical and palaeobiogeographical questions. Some taxa may be good tools to correlate from tropical realms (e.g. Laurentia) over temperate areas to cold regions such as peri-Gondwana.

Hydrothermal vent and cold seep molluscs: view from the fossil record

Crispin T.S. Little¹ and Kathleen A. Campbell²

¹ School of Earth Sciences, University of Leeds, Leeds LS2 9JT, UK
<c.little@earth.leeds.ac.uk>

² Department of Geology, University of Auckland, Private Bag 92019, Auckland, New Zealand <ka.campbell@auckland.ac.nz>

Molluscs first appeared in vent and seep environments early in the Palaeozoic. A few Palaeozoic vent and seep assemblages are dominated by bivalves, but others contain no molluscs, or are outnumbered numerically by brachiopods. Some of these Palaeozoic vent and seep molluscs belong to extinct groups, common in contemporaneous non-vent and non-seep fossil assemblages. Preservation factors do not allow chemosymbiotic lifestyles to be established with any certainty for these ancient taxa. The record is better in the Mesozoic and Cenozoic, especially for seeps. Towards the later Mesozoic, brachiopods become increasingly rare in vent and seep communities, and bivalves and gastropods become the dominant shelly taxa. The Mesozoic marks the first appearance in vents and seeps of a group of chemosymbiotic bivalves (mytilids, lucinids, and solemyids) which are important constituents of modern chemosynthetic

communities, but also have Palaeozoic, non-vent, non-seep origins. The first provannid gastropods and vesicomid bivalves appear in late Jurassic and early Cretaceous seeps, respectively. These two families are today endemic in chemosynthetic environments and have many chemosymbiotic species. Many modern vent and seep molluscs, particularly the smaller gastropods, have yet to be identified in the fossil record. In summary, Phanerozoic vent and seep deposits contain a rich and growing record of fossil molluscs. These data can be used to test phylogenetic hypotheses generated by molecular data from living chemosymbiotic molluscs.

***Application of high-resolution computed tomography in palaeontology: analysis of a Middle Devonian labyrinthodont tooth from New York State, USA**

Vicky MacEwan

Department of Earth Sciences, University of Manchester, Oxford Road, Manchester M13 9PL, UK <vmacewan@fs1.ge.man.ac.uk>

An unidentified labyrinthodont tooth was discovered as an isolated specimen from the Middle Devonian Panther Mountain Formation in Central New York State, USA. Studies on the internal structure of labyrinthodont teeth have traditionally relied on mechanical sectioning, resulting in at least partial destruction of the specimen. High-resolution x-ray computed tomography is a non-invasive three-dimensional imaging technique, which provides a non-destructive alternative to sectioning and serial grinding. By passing x-rays through the sample the variation of x-ray attenuation can be measured. This corresponds closely to contrasting densities within the specimen. These data are mapped as a series of two-dimensional slices, which are assembled into a three-dimensional stack with a resolution of about ten microns. The labyrinthodont tooth was scanned at the high-resolution x-ray computed tomography unit at the University of Texas, USA. Although badly degraded, marginal dentine is preserved and internal folds are present in both horizontal and vertical planes. The tooth has an open pulp cavity with the suggestion of bone extending between the folds, characters more typical of labyrinthodont tetrapod than labyrinthodont fish teeth. Further fossil discoveries from the area may help to demonstrate that this tooth represents the earliest known example of a tetrapod.

Use of Morphometrics to Identify Character States

Norman MacLeod

Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK <N.MacLeod@nhm.ac.uk>

Much of the classic cladistic literature has opposed the idea of using morphometric methods to identify characters and their associated states. Several authors have suggested that morphometric methods are limited in this context because they produce continuous size-shape variables that must be rendered discrete by arbitrary means in order to be coded appropriately. Others have raised questions about the conformance of morphometric variables to the concept of homology. These issues may be addressed successfully in the context of a morphometric investigation by remembering that (1) the focus of any such investigation is to

locate and document discontinuities in the distribution of shapes across organic forms, and (2) good systematic practice requires that variation in unified characters be considered in isolation from other such characters. If these principles are kept in mind when designing an analysis, a morphometric approach can yield substantial advantages. Moreover, use of morphometrics approaches to model the theoretical space around multivariate shape ordinations provides systematists with new tools designed to explore this space. Such explorations can improve character-state definitions as well as facilitating the discovery of new character states. These approaches are illustrated with examples drawn from invertebrate palaeontology, palaeobotany and morphological simulation studies.

The palaeoclimatic significance of the Devonian-Carboniferous boundary

J.E.A. Marshall¹, T.R. Astin², F. Evans³ and J. Almond⁴

¹ School of Ocean and Earth Science, University of Southampton, Southampton Oceanography Centre, European Way, Southampton SO14 3ZH, UK <jeam@soc.soton.ac.uk>

² Postgraduate Research Institute for Sedimentology, University of Reading, P.O. Box 227, Whiteknights, Reading RG6 6AB, UK

³ c/o Department of Earth Sciences, SFU, Burnaby V5A 1S6, Canada

⁴ Natura Viva cc, P.O. Box 12410 Mill Street, Cape Town 8010, South Africa

A number of Late Devonian global events have been recognised. These are characterized by significant faunal and microfloral turnover. One such event is the Hangenberg which occurs at the D-C boundary. In East Greenland the D-C boundary occurs within the 3m thick Obrutschew Bjerg Formation. This formation represents a short interval when the basin was occupied by a huge anoxic lake. During lake development the terrestrial flora initially diversifies. However the main part of the lake cycle shows the same pattern of microfloral extinctions and impoverishment as widely reported in marginal marine sediments.

There has been much recent discussion of Late Devonian glacial diamictites. We interpret these as representing episodes of glacial collapse. Such collapses occur at the climatic maximum and are accompanied by a significant strengthening of the monsoon. This caused the short-lived 'greening' of large parts of the modern Sahara Desert and the flooding event in the African lakes. The Obrutschew Bjerg Formation is seen as analogous. Clearly this interpretation relies on the precise identification of the D-C boundary in high latitude glacial diamictite bearing sections. Such sections have been investigated at outcrop in both South Africa and Bolivia.

**The morphology of hyolithids and its functional implications**Mónica Martí Mus¹ and Jan Bergström²¹ Área de Paleontología, Facultad de Ciencias, Universidad de Extremadura, Avda. de Elvas s/n (Edificio antiguo rectorado), E-06071 Badajoz, Spain <martimus@univ.es>² Department of Palaeozoology, Swedish Museum of Natural History, P.O. Box 50007, SE-104 05 Stockholm, Sweden <jan.bergstrom@nrm.se>

Hyolithids were armoured with a four-pieced scleritome that easily fell apart after death. It consisted of a conch, an operculum and a pair of conspicuous but fragile spines called helens. While the anatomical relation between conch and operculum is straightforward, the precise position and orientation of helens has proven problematic, rendering the scleritome a puzzling “model kit”. Numerous muscle scars on conch and operculum indicate that the latter provided the animal with solid surfaces for muscle attachment as well as with a protective cover. The function of helens has on the other hand remained as intriguing as their structure and form. Study of exceptionally preserved specimens has shed light on these problematic aspects of hyolithid morphology.

Helens were solid and had a shell microstructure consisting of concentric lamellae. They curved ventrally and were partially internal, extending outside the conch with the dorsal edge tilted forwards. Their internal portion did not lean against the operculum as previously believed but held free on the aperture plane. Hyolithids possessed a complex, non-seriated musculature likely involved in the articulation of the scleritome. Helens were probably mobile and could have contributed both to locomotion and stabilization.

***The influence of substrate consistency on footprint morphology: field experiments with an emu**

Jesper Milàn and Richard G. Bromley

Geological Institute, University of Copenhagen, Oestervoldgade 10, DK-1350 Copenhagen K, Denmark <nj240474@geo.geol.ku.dk>

In order to demonstrate the influence of substrate consistency on vertebrate track morphology, field experiments were conducted by encouraging an emu to walk through prepared areas of sand and mud of different thickness and with different water content. Tracks sat in dry substrates either collapsed immediately after removal of the foot as in the case of sand, or failed to leave an impression at all as in mud. Damp sand and mud produced tracks preserving a high quality of details. With increasing water content, several variations of semi-collapsed and collapsed tracks were produced as well as related phenomena such as material ejected during withdrawal of the foot. Substrates of semi-liquid consistencies caused the track walls to flow together destroying the shape immediately after the foot was lifted. Horizontal sections through tracks sat in soft cement show that even though a track seems to have collapsed at the surface, the shape of the track is clearly recognizable at deeper levels. Lateral variation in substrate properties, such as water content, can cause tracks deriving from one individual to show highly different morphologies; this bears strong implications for the interpretation of fossil tracks and trackways.

***A Global Overview of the *lundgreni* (Wenlock, Silurian) Graptoloid Extinction Event**

Lucy Muir

University of Edinburgh, Grant Institute of Geology, West Mains Road, Edinburgh EH9 3JW, UK <lucy.muir@glg.ed.ac.uk>

The extinction event at the end of the *lundgreni* biozone was one of the most severe to affect graptoloids during the Silurian. I have assembled a database from the literature of graptoloid occurrences before and after the *lundgreni* event, recording species occurrences at the zonal level. The data were used to test the hypotheses that victims of the event were geographically restricted and that life history strategy (whether a species is K- or r-selected) determines extinction probability. Ecological theory predicts that K-selected species are less likely to survive extinction events than r-selected species. K-selected species are large, long-lived and have few offspring, most of which survive; r-selected species are small, short-lived and have many offspring, few of which survive. Geographical distribution does not appear to affect extinction likelihood. The limited data available on life history strategies indicate that K-selected species are more vulnerable to extinction than r-selected ones.

Microplankton associations and biofacies: testing Silurian palaeoenvironmental models

Gary L. Mullins, Richard J. Aldridge and David J. Siveter

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

<glm2@leicester.ac.uk> <ra12@leicester.ac.uk> <djs@leicester.ac.uk>

Cluster and correspondence analyses of the temporal distribution of the acritarchs and prasinophyte algae through the lower part of the type Ludlow Series (Silurian) have defined recurrent associations of microplankton species and biofacies. This has enabled fine scale environmental fluctuations to be recognized. A recurrent association of endemic taxa are abundant throughout the section. These taxa are considered to be the most environmentally tolerant species. Also recognized are recurrent associations of taxa that generally coincide with the formations defined in the lower part of the Ludlow Series. Further, a recurrent association of species that are most abundant at a level where other taxa are rare suggests that some microplankton adapted to periods of environmental stress. The distribution of microplankton through the sequence support aspects of the sea level model and Jeppsson's oceanic model of environmental change.



The cranial morphology and systematics of the enigmatic basal ornithischian *Heterodontosaurus tucki* Crompton and Charig, 1962

David B. Norman, Alfred W. Crompton and Alan J. Charig
Sedgwick Museum, Department of Earth Sciences, Downing Street,
Cambridge, CB2 3EQ, UK <dn102@esc.cam.ac.uk>

The discovery of a nearly complete skull of an ornithischian dinosaur exhibiting a mammal-like heterodont dentition in the Early Jurassic of South Africa was unexpected. It led to a rapid reappraisal of a number of specimens previously identified as mammal-like reptiles from similarly aged localities (*Geranosaurus* and *Lycorhinus*). Preliminary description of this skull in 1962 was not followed by a more detailed account of its anatomy. Subsequently, a well-preserved, articulated skeleton attributed to this species was recovered. The postcranial skeleton was described in 1980, but the skull remained undescribed.

The cranial anatomy of *Heterodontosaurus* is described in detail on the basis of the holotype and referred skulls. The skull exhibits an unusual degree of anatomical specialisation in such an early dinosaur; this is particularly so when compared with approximately contemporary taxa such as the basal ornithischian *Lesothosaurus* and the early armoured taxon *Scelidosaurus*. Systematic analyses that include basal ornithischian dinosaurs have adopted a fairly consistent topology with respect to the placement of *Heterodontosaurus* (and closely related heterodontosaurids) as the most basal members of the clade Ornithopoda. Study of the cranial anatomy (combined with the known postcranial material) of this taxon has provided an opportunity to reassess its systematic position within Ornithischia.

A revised high-resolution ammonite time scale for the Lower Jurassic of Great Britain

Kevin N. Page
Department of Geological Sciences, University of Plymouth, Drake Circus,
Plymouth PL4 8AA, UK <KevinP@bello-page.fsnet.co.uk>

Ammonites remain as the most important correlative tools for Jurassic marine sequences, and form the backbone of a standard Jurassic chronostratigraphic time scale, the Lower Jurassic part of this scheme being established for Britain by W.T. Dean, D.T. Donovan and M.K. Howarth in 1961. A considerable volume of work has subsequently been carried out across Europe (including in France, Germany and Britain) which has facilitated a very significant increase in resolution of this time scale through the recognition of biohorizons or horizons (= "zonules") at sub-subchronozonal level—thereby creating a high-resolution time scale with an averaged resolution of less than 120,000 years. Surprisingly, however, awareness of advances in this field seems limited in the UK, and Dean *et al.*'s now somewhat dated scheme is still widely used. The aim of this presentation, therefore, is to review the current "state of the art" for Lower Jurassic ammonite-based stratigraphy and introduce to a wider audience the potential inherent for other palaeontological and geological studies of the high-resolution time scale now available (Hettangian – 24 biohorizons in 3 chronozones; Sinemurian – 78 biohorizons in 6 chronozones; Plienbachian – 36 horizons in 5 chronozones; Toarcian – 40 biohorizons/horizons in 8 chronozones).



Phylogenetic Congruence Between Hard and Soft Part Data Sets: How Taphonomy Affects Ostracod Phylogenies

Lisa E. Park
Department of Geology, University of Akron, Akron, OH 44325-4101, USA
<lepark@uakron.edu>

Taphonomic bias against soft tissue preservation is widely considered to be a barrier to understanding evolutionary relationships and diversification patterns in the fossil record. A morphologically based phylogenetic analysis of a clade of lacustrine podocopid ostracods from Lakes Tanganyika and Malawi was done using hard and soft characters (PAUP, v. 4.0). Eliminating all hard part characters in subsequent analyses caused the collapse of many branches to polytomies and significantly decreased the agreement of the hard part trees. Analyses excluding all soft part characters increased the number of most parsimonious trees and decreased the resolution of the trees by creating many unresolved polytomies, but produced similar islands of stability as the original combined analysis.

This study verifies that the loss of either hard or soft part characters reduces phylogenetic resolution. It also demonstrates that more resolution was lost by omitting soft versus hard part characters, suggesting that soft part preservational bias in the ostracod fossil record may have an appreciable effect (loss of ~20%) on diversity approximations. The hard part only tree may be less resolved because those features are likely to be ecophenotypic and therefore more plastic, which is consistent with previous studies on ecologically promoted variation in ostracod carapaces.

*Halkieriids in Middle Cambrian phosphatic limestones from Australia

Susannah M. Porter
Center for Astrobiology, Institute of Geophysics and Planetary Physics,
3845 Slichter Hall, UCLA, Los Angeles, CA 90095-1567, USA

Halkieriids are part of a distinctive Early Cambrian fauna preserved mostly as phosphatic and secondarily phosphatized skeletal elements. The distinctiveness of this fauna is ascribed, in part, to its preferential elimination during end-Early Cambrian mass extinction event. Newly discovered halkieriids in phosphatic limestones of the Middle Cambrian Monastery Creek Formation, Georgina Basin, Australia, now indicate that the group not only survived this extinction, but was at least locally abundant thereafter. Most of the Georgina halkieriid sclerites can be accommodated within a single species *Australohalkieria superstes* gen. et sp. nov., described and partly reconstructed here. Remaining sclerites represent two additional, rare halkieriid species. The Monastery Creek Formation provides a valuable window on Middle Cambrian life, because it provides information that is distinct from but complementary to other, similarly-aged windows, and because it represents a taphonomic window similar to those that preserve Early Cambrian small shelly problematica. A decline during the Cambrian in conditions necessary for the early diagenetic phosphatization of shallow shelf and platform limestones may have effectively closed this window, biasing apparent patterns of diversity change. Certainly, the Monastery Creek halkieriids indicate that this clade was not a short-lived biological 'experiment' but a successful and long-ranging component of Cambrian communities.

***Microfaunas across the Bathonian-Callovian boundary**

K.J. Riddington

Lapworth Museum of Geology, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK <KJR887@bham.ac.uk>

The Cornbrash Formation (Upper Bathonian-Lower Callovian, Middle Jurassic) forms a thin, persistent outcrop from the Yorkshire coast to Dorset. Its abundant and well-preserved macrofauna, especially the Brachiopoda and Bivalvia, have been well documented since the 19th century. A faunal turnover has been reported at the boundary between the Lower and Upper Cornbrash (Bathonian-Callovian boundary) and it is here that Raup and Sepkoski (1984, 1986) placed one of the missing peaks in their periodic extinction theory. However, on closer examination, few brachiopod or bivalve species actually become extinct at this horizon, merely diminish in abundance.

An independent test of the hypothesis is offered by the microfauna of the Cornbrash Formation, which is more poorly known. Foraminifera genera present include *Citharina*, *Dentalina*, *Fronidularia*, *Lenticulina* and *Haplophragmoides*; as with the macrofauna, specimens are abundant and generally well-preserved. Basov and Kuznetsova (2000) recorded the highest foraminiferal extinction rates in the Jurassic at the Bathonian-Callovian boundary. However, the NW European record suggests that there is no obvious change in the microfauna at the boundary that cannot be explained by local and mesoscale parameters.

Body building in *Halkieria* and comparisons with chitons and other possible stem-group molluscs

Bruce Runnegar

Dept. of Earth and Space Sciences, Institute of Geophysics and Planetary Physics, and Molecular Biology Institute, Univ. California, Los Angeles, CA 90095-1567, USA <runnegar@ucla.edu>

Models of articulated skeletons (scleritomes) of *Halkieria evangelista* Conway Morris & Peel from the Cambrian of Greenland are used to reconstruct the growth of halkieriids. As in chitons (polyplacophorans), growth occurred inboard from the edge of the body along narrow zones that connect the lateral growing edges of the anterior and posterior shells. Also, new rows of cultrate sclerites were added near the body margins as growth proceeded. These similarities with polyplacophorans are reinforced by the presence of relict sclerites within the shell plates (valves) of the Cambrian chiton *Matthevia*. *Matthevia* valves resemble the fused-sclerite shells of the Early Cambrian fossil *Maikhanella* (Bengtson, *Lethaia* 25, 401, 1992) and may also serve as morphological intermediates between the tissue-filled sclerites of the halkieriids and sensory esthetes embedded in the outer layer of the valves of living chitons.

If this assessment of the growth of *Halkieria evangelista* is correct, its affinities lie closer to the Mollusca than to the Annelida or Brachiopoda (Conway Morris and Peel, *Phil. Trans.* B 347, 305, 1995). However, exclusion of halkieriids from the molluscan crown group (all descendants of the last common ancestor of living molluscs) depends upon the placement of the class Aplousobranchia. If aplousobranchians are secondarily simplified, perhaps by progenesis (Scheltema, *Biol. Bull.* 184, 57, 1993), halkieriids may belong to the molluscan stem group. Alternatively, if aplousobranchians

talks

are primitively vermiform and spiculate, halkieriids may be members of the molluscan crown group. In any case, other mollusc-like organisms such as hyoliths may be used to explore features of early development in stem group molluscs. Pooling all information from living and extinct taxa provides a paradigm for body building in primitive lophotrochozoans.

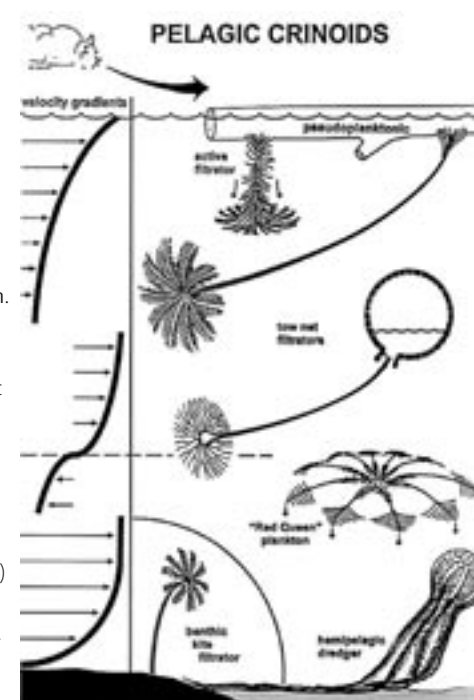
Constructional Morphology of Pelagic Crinoids

Adolf Seilacher¹ and Rolf B. Hauff²

¹ Geolog. Institut, Tübingen and Geology Department, Yale University

² Urwelt-Museum, Holzmaden

While all modern crinoids are benthic filter feeders, some fossil forms from low-oxygen Lagerstätten were probably pelagic. Most pseudoplanktonic forms were attached to driftwood (*Seirocrinus*; *Traumatocrinus*); they had long fast-growing, rope-like stems and enlarged, permanently splayed filter fans, as required by a tow-net function. The short and heavily cirrated stem of *Pentacrinus briareus*, however, suggest active filtration. If the buoyant lobolith acted as a swim bladder, *Scyphocrinites* could use its tow-net in the velocity gradient near a boundary layer. Paradigms are different for stemless forms, whether they floated passively over the bottom (*Uintacrinus*) or filtrated actively in the water column (Roveacrinids and *Saccocoma*). Our theoretical models characterize peaks in the adaptive landscape and can be checked against taphonomic, morphological, and evolutionary evidence.



talks

Ancient weavers on the silk road: Jurassic spiders from China

Paul Selden¹ and Dong Ren²

¹ Department of Earth Sciences, University of Manchester, Manchester M13 9PL, UK

² Dong Ren, Capital Normal University, Beijing 100037, P. R. China

Among the feathered dinosaurs, salamanders and abundant insects, a collection of more than 60 new specimens of spiders from the Upper Jurassic Yixian Formation and the Middle



Jurassic Jiulongshan Formation of north-east China has been amassed and is described briefly here. Until now, only two spiders were known from the Jurassic period worldwide; thus the new collection represents an enormous addition in the fossil record of these rarely preserved animals. The spiders are preserved in lacustrine deposits, and were apparently knocked into the water by volcanic ash falls. Their preservation is exquisite, allowing fine morphological details to be observed. Many of the new specimens belong to the extant orb-weaver family Uloboridae and superfamily Araneoidea. These are already known from the Mesozoic. There are also rare members of the ground-dwelling fauna. Because of the rarity of Mesozoic spiders, the new finds shed no light on stratigraphic problems of the Jehol biota.

Palaeobiology of Carboniferous microcrinoids

George Sevastopulo

Department of Geology, Trinity College, Dublin 2, Ireland <gsvstpul@tcd.ie>

Most Carboniferous microcrinoids (crinoids with adult thecae less than 2mm high) belong either to the disparid family Allagecrinidae or to the cladid family Codiocrinidae. They inhabited environments ranging from relatively deep, low energy basin floor, through higher energy, open shelf, to shallow water, inner shelf. Allagecrinid crowns were probably raised higher above the substrate than those of codiocrinids of comparable thecal size; the theca of one codiocrinid was cemented directly to the substrate. Allagecrinids were suspension feeders that used the arms to capture minute particles that entered the theca through slits between the opened orals. Many codiocrinids were either armless or had less than five arms. They probably fed using podia that were exposed when the orals were pushed open. Both types of microcrinoids may also have utilised dissolved organic matter as a nutrient source. There is tenuous evidence that allagecrinids had a single internal gonad. The small node on the CD oral was a hydropore not a gonopore: gametes were shed by opening of the orals. Larvae of such small crinoids might have been expected to be planktotrophic but the presence of brooding structures in one allagecrinid suggests that some, at least, were lecithotrophic.

*Microevolution of the charophyte genus *Harrisichara* across the Eocene-Oligocene transition in the Isle of Wight, Southern England

Nick P. Sille^{1,2}, Michal Kucera¹, Margaret E. Collinson¹ and Jerry J. Hooker²

¹Department of Geology, Royal Holloway, University of London, Egham, Surrey, TW20 OEX <n.sille@gl.rhul.ac.uk>

²Department of Palaeontology, Natural History Museum, Cromwell Road, London, SW7 5BD

The Eocene-Oligocene transitional strata in the Isle of Wight offer a unique opportunity to study how the terrestrial realm responded to the global cooling event that occurred at this time. Three diverse biotic elements [charophyte gyrogonites, *Stratiotes* seeds and rodent teeth] are being investigated for microevolutionary change. Results will be used to assess how terrestrial biotas responded to Eocene-Oligocene cooling and to attempt to erect an integrated biostratigraphic framework. Charophytes are currently used in the European correlation charts



for the Palaeogene and therefore have a known biostratigraphic value in correlating across the terrestrial basins of Northern Europe. Studies currently being carried out (using image analysis and morphometrics) aim to show how microevolutionary change can be used to refine the biozonation and increase resolution of the zones.

Microevolutionary results will be presented from a study of *Harrisichara* through a number of levels within the Solent Group in Southern England. Up to 150 specimens from each level have been picked and various measurements made using image analysis software. Principle component analyses have been carried out using six defined independent variables including eigenshape values, length/width ratio and intertubercle ornament density.

*The Early Cambrian *Mickwitzia* from Greenland and Nevada and the origin of the brachiopods

Christian Skovsted¹, Lars E. Holmer¹ and Alwyn Williams²

¹Department of Earth Sciences, Uppsala University, Norbyvägen 22, Uppsala, SE-752 36, Sweden <christian.skovsted@geo.uu.se> <lars.holmer@pal.uu.se>

²Palaeobiology Unit, University of Glasgow, 8 Lilybank Gardens, Glasgow, G12 8QQ, UK <alwyn@dcs.gla.ac.uk>

The affinities of the Early Cambrian bivalve *Mickwitzia* Schmidt, 1888 have been discussed for more than a century. Conventionally included in the paterinid brachiopods, it has alternatively been excluded from the phylum Brachiopoda or placed in its stem-group. Etched material of *M. cf. occidens* Walcott, 1908 from the Early Cambrian of Greenland and Nevada demonstrates that *Mickwitzia* shares a number of characters with linguliform brachiopods: a lingulid-like juvenile shell with trails of nick-points reflecting the movement of marginal setae; a lingulid-like pseudointerarea with a pedicle groove in juvenile and early mature ventral valves; an organophosphatic shell with a columnar lamination homologous with that characterizing acrotretides. The shell, however, is also pervaded by striated apatitic tubes indistinguishable from those permeating the sclerites of the problematic *Micrina* Laurie, 1986. The tubes are presumed to have contained setae and are absent in all crown group brachiopods. These features suggests that *Mickwitzia* is a stem group brachiopod.

Origins of teeth amongst jawed stem group gnathostomes

Moya Meredith Smith¹ and Zerina Johanson²

¹Craniofacial Development, Dental Institute KCL, Guy's Campus, London Bridge, SE1 9RT, UK <Moya.smith@kcl.ac.uk>

²Earth Sciences, Australian Museum, 6 College Street, Sydney 2010, Australia

Placoderms as the sister group of crown group gnathostomes represent the most primitive forms with jaws, but the consensus view is that teeth, homologous with those of chondrichthyans, acanthodians and osteichthyans, are absent. Lack of structural evidence for both regular dentine and patterned successional teeth in placoderms is the basis for this opinion. Thus the co-evolution of teeth with jaws and their origin is questioned and instead teeth, those developed from tooth specific tissues (dental lamina) are proposed as a synapomorphy of all except placoderms.



Placoderms have statodont dentitions, those not replaced but adapted to wear by hard tissue growth. However, amongst arthrodires, alongside worn cutting edges there are ordered rows of new conical structures providing dental tissues during growth. Sectioned cones show regular dentine, formed around a pulp chamber, and a tissue different from semidentine of the dermal tubercles. Together with sequential unitary addition, comparable with tooth addition in gnathostome jaws, these demonstrate teeth in derived placoderms. The origin of teeth late in placoderm phylogeny suggests that this evolution occurred independently at least twice within jawed gnathostomes. These observations challenge the consensus view of the origins of teeth and propose the presence of a dental lamina in certain placoderms.

Composition, depositional setting and palaeoecology of *Siphonodendron* biostromes in the late Viséan of SE Ireland

Ian D. Somerville and P. Cózar

Department of Geology, University College Dublin, Belfield, Dublin 4, Ireland
<ian.somerville@ucd.ie> and <pedro.cozar@ucd.ie>

Siphonodendron biostromes are recorded from well-bedded dark grey limestones of Brigantian (late Viséan) age in counties Carlow and Kilkenny (SE Ireland). They occur in the Clogrenan Formation, which is exposed in several working quarries within the region. The limestones form part of a widespread shallow water shelf sequence in which periodic subaerial exposure is recognised by palaeokarsts and palaeosols. Two coral biostromes in the middle of the formation can be correlated between quarries 5 km apart and a third biostrome is developed higher in the formation. All of the biostromes are dominated by *Siphonodendron* colonies and are usually tabular with pronounced peripheral growth strategies. The dimensions of fasciculate colonies are typically 15-20 cm high and 50-90 cm in width, but some colonies can reach 4.5 m in width. The corallites in many colonies have the same upper growth level. Associated rugose corals in the biostromes are *Diphyphyllum*, *Lonsdaleia* and the cerioids *Lithostrotion* and *Actinocyathus*, together with the tabulate *Syringopora*, but all form accessory roles in constructions. The youngest biostrome is the most diverse with 13 genera and 15 species. Gigantoproductid brachiopods are an important related element, commonly forming concentrations of *in situ* shells below or above the *Siphonodendron* colonies. Comparisons are made with other upper Viséan *Siphonodendron* biostromes in NW Ireland, northern England and SW Spain.

Waptia fieldensis, a possible crustacean from the Middle Cambrian Burgess Shale of British Columbia, Canada

Rod S. Taylor¹ and Desmond H. Collins²

¹Department of Earth Sciences, University of Cambridge, Cambridge
CB2 3EQ, UK <rstaylor@mac.com>

²Department of Palaeobiology, Royal Ontario Museum, 100 Queen's Park,
Toronto, Ontario M5S 2C6, Canada <desc@rom.on.ca>

Examination of approximately 1,300 specimens of *Waptia fieldensis* has led to an improved understanding of the biology of this animal. *W. fieldensis* possesses a bivalved carapace that



covers the cephalon and most of the thorax. The cephalon possesses up to five segments plus a complex array of feeding appendages, made up of three to five limbs. One pair of elongate antennae is present, as are a pair of short lobed structures positionally equivalent to the second antennae of Crustacea. The anterior thorax possesses four somites and has segmented, stenopodous-like limbs, while the posterior thorax demonstrates six gill-like limbs. The abdomen is limbless and is made up of five segments plus a telson and bilobed tailfan.

The somite and limb patterns demonstrated by *W. fieldensis* closely resemble those of many modern Eumalacostracan groups, suggesting Walcott's original placement of *Waptia* within the Crustacea may have been correct. The presence of what may be second antennae further supports a crustacean relationship for *Waptia*. The recent description of *Ercaia miniscula*, a crustacean from the Early Cambrian Chengjiang biota of China, further supports the notion that Crustacea may also have existed in the Middle Cambrian Burgess Shale.

*Trackways meet trackmakers: the composition of early tetrapod communities

Lauren Tucker

Lapworth Museum of Geology, University of Birmingham, Edgbaston,
Birmingham B15 2TT, UK <LXT758@bham.ac.uk>

A Late Carboniferous (Westphalian D; Moscovian) footprint fauna from Alveley, southern Shropshire, UK, is a significant example of an early, marginal-terrestrial tetrapod community. As the only vertebrate ichno-assemblage of its age in Europe, it presents a valuable insight into the interval between the appearance of tetrapods in the Devonian and the amniote dominated faunas of the Early Permian. Ichnodiversity has been determined with the aid of numerical, multivariate methods, and morphological variation within the assemblage has been studied, providing a comprehensive review of the ichnofauna. However, in order to produce a full palaeoecological interpretation, enabling comparison with skeletal assemblages, an accurate method of determining trackmaker identity using selected trackway features is required. Synapomorphy-based character analysis has been combined with phenetic and coincidence correlation techniques to examine trackmaker identities in detail. This is the first such study that has been undertaken on Late Palaeozoic ichnofaunas, ultimately aiming to chart the evolution of terrestrial tetrapod communities through the Late Carboniferous and Early Permian.

Significance of a recently discovered, exceptionally diverse, Early Triassic marine assemblage from Oman

Richard J. Twitchett

Department of Earth Sciences, University of Bristol, Queen's Road, Bristol
BS8 1RJ, UK <r.j.twitchett@bris.ac.uk>

An exceptionally diverse Early Triassic fauna has been discovered in the Wadi Wasit region of the Central Oman mountains. The fauna is Griesbachian in age (on the basis of abundant conodonts and ammonoids), and was deposited in a well-oxygenated, storm-winnowed seamount off the Arabian platform margin. The earliest Griesbachian assemblage (*parvus* Zone) is a low diversity, opportunistic fauna dominated by the bivalves *Promyalina* and *Claraia* (typical of the aftermath

of the end-Permian extinction event). The mid-upper Griesbachian sediments (*isarcica* and *carinata* Zones) contain an incredibly diverse and partially silicified benthic fauna of bivalves (dominated by large *Claraia*), ten gastropod taxa (including large *Naticopsis*), the articulate brachiopod *Crurithyris*, a new and locally abundant rhynchonellid, a new, undescribed crinoid, fragmentary echinoids and ostracods. This fauna is more diverse and ecologically complex than “typical” mid-late Griesbachian age faunas, described from oxygen-restricted settings worldwide. This supports the hypothesis that the apparent delay in recovery after the end-Permian extinction can be attributed to widespread and prolonged benthic oxygen restriction. However, if the anoxic event also caused the extinction, then Permian holdovers would be expected in this fauna. None are found, casting serious doubts on the hypothesis that oceanic anoxia was an important kill mechanism.

Cambrian food chains: new perspectives

Jean Vannier¹, Chen Junyuan², Zhu Maoyan³ and Huang Diying^{1,2}

¹ Université Claude Bernard Lyon 1, UFR Sciences de la Terre, UMR 5125 PEPS, Paléoenvironnements & Paléobiosphère, Bâtiment Géode, 2, rue Raphaël Dubois 69622 Villeurbanne, France <jean.vannier@univ-lyon1.fr>

² Nanjing Institute of Geology and Palaeontology, Academia Sinica (NIGPAS), Nanjing 210008 and Early Life Research Centre, 18 Wenmiao St., Chengjiang 652500, Yunnan, China <chenjunyuan@163.net>

³ Nanjing Institute of Geology and Palaeontology, Academia Sinica (NIGPAS), Nanjing 210008, China <myzhu@nigpas.ac.cn>

Fossil evidence from exceptional biotas attests to the existence of diverse marine ecosystems in the Cambrian, but still very little is known of their functioning (e.g. primary production, food sources, feeding strategies, prey/predator relationships). A set of new information obtained from the Maotianshan Shale (Early Cambrian) and the Kaili (early Middle Cambrian) Lagerstätten from South China offers new perspectives for the reconstruction of Cambrian food chains. This includes:

- Arthropod gut contents with identifiable skeletal remains (eodiscoid and possibly bradoriid arthropods)
- Preserved digestive systems and feeding organs
- Possible coproliths and isolated gut contents with recognisable elements such as carapaces of bivalved arthropods (e.g. bradoriids, waptiids), hyolith shells and fragments of trilobite exoskeletons

In the Early Cambrian, predators were present in endobenthic (e.g. priapulid worms), epibenthic (several arthropod groups) and midwater niches (e.g. anomalocaridids, medusoid-like eldoniids, ctenophores). Proliferous organisms living at the interface layer between water and sediment (e.g. vagile bradoriid arthropods and larvae; poorly motile epibenthic hyoliths) and in the lower part of the water column (e.g. demersal phyllocarid-like arthropods such as waptiids) most probably constituted the major food source for the macrophagous predators.

*Calcareous nannofossil assemblages during the Messinian Salinity Crisis: evidence from the Polemi Basin, Cyprus

Bridget S. Wade¹ and Paul R. Bown²

¹ Department of Geology and Geophysics, University of Edinburgh, Grant Institute, West Mains Road, Edinburgh, EH9 3JW <bwade@glg.ed.ac.uk>

² Department of Geological Sciences, University College London, Gower Street, London, WC1E 6BT <p.bown@ucl.ac.uk>

Nannofossil assemblages within the Messinian units from the Polemi Basin, Cyprus, provide a unique picture of environmental changes associated with the Messinian Salinity Crisis. Results indicated that the intercalated marls, chalks and clays between the Messinian gypsum units were autochthonous and deposited in a marine environment. The large variations were found in nannofossil assemblages, suggesting a highly fluctuating environment. *Reticulofenestra minuta*, *Dictyococcites antarcticus*, *Helicosphaera carteri* and *Umbilicosphaera jafari* are suggested to be r-mode opportunists, adapted to a eutrophic, unstable environment and capable of establishing massive blooms; *Sphenolithus abies* occupied more stable environments. *R. minuta* is indicated to be able to tolerate variations in salinity. Fluctuations in nutrient levels have been interpreted to be the primary factor controlling the alterations in nannofossil assemblages. The calcareous nannoplankton results were integrated with those of the siliceous diatoms and used to formulate a model of the palaeoenvironment, indicating that the Polemi Basin was a semi-enclosed, neritic to littoral environment, subject to repeated influxes of marine and fresh water.

Early ontogenetic development of blastoids

Johnny A. Waters¹ and Sara A. Marcus²

¹ Department of Geosciences, State University of West Georgia, Carrollton, GA 30118, USA

² Department of Geology, University of Kansas, Lawrence, KS 66047, USA

Postembryonic ontogeny of blastoids follows a multistage developmental path similar to modern comatulid crinoids, such as *Antedon*. In *Antedon*, the prejuvenile stage lasts about four months, and includes: 1) the doliolarial stage, which lasts two to three days; 2) the cystidian stage, which lasts about a week; and 3) the pentacrinoid stage, which lasts about fifteen weeks. Specimens that would be classified as the cystidian stage in the comatulid life cycle were the subject of pioneering studies of the early ontogeny of blastoids. In addition, *Passalocrinus*, originally described as a microcrinoid, has been determined to be a juvenile blastoid. The presence of oral plates places *Passalocrinus* in the cystidian stage of development. It has been hypothesized that *Passalocrinus* developed into typical adult blastoid morphology by resorption of the oral plates and development of ambulacral tracts and lancets. Specimens of juvenile blastoids from Lower Carboniferous black shales from Xinxu, Guangxi Province, Peoples Republic of China demonstrate an intermediate stage between the cystidian stage (*Passalocrinus*) and adult blastoid morphology. Basal and radial plates are well developed, although deltoids and orals are lacking. Initial basal and radial plates are characterized by microperforate stereom and are surrounded by 44 to 50 distinct growth lines. The oral surface lacks well-developed ambulacra,

but has food grooves in each ray leading to three sets of terminal brachiolar(?) attachment pits. Based on this material, we conclude that blastoids had multi-staged ontogenetic development similar to that seen in modern comatulid crinoids.

Tantalizing fragments of the earliest land plants

Charles H. Wellman

Department of Animal and Plant Sciences, University of Sheffield, Alfred Denny Building, Western Bank, Sheffield S10 2TN, UK
<c.wellman@sheffield.ac.uk>

There is a huge disparity between the first appearance of microfossil and megafossil evidence for the earliest land plants. The earliest evidence for land plants is dispersed spores that first appear in the Llanvirn (Mid Ordovician). It is not until the Wenlock (Late Silurian), some 40 million years later, that the earliest undisputed land plant megafossils occur. It is generally considered that the early spore producers were non-vascular land plants (bryophytes). These almost certainly lacked recalcitrant parts and thus had very low fossilization potential (spores excepted). It is not until much later that vascular plants (tracheophytes) evolved. These probably possessed recalcitrant (e.g. lignified) parts and thus had much greater fossilization potential. The first appearance of early land plant megafossils possibly coincides with the appearance of tracheophytes. Because of the absence of megafossils, little is known of the earliest bryophytic land plants. Recently, however, top sieving during routine palynological processing of Caradoc (Ordovician) deposits from Oman has produced relatively large fragments of these plants. These consist of spore masses and fragments of sporangia. These fossils confirm that the early dispersed spore record does indeed represent the earliest land plants, and provide the first tantalizing evidence for the nature of the producers.

*Conodonts, cladistics and the fossil record

Linda M. Wickström

Lapworth Museum of Geology, University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK <lmw034@bham.ac.uk>

Most phylogenetic hypotheses of conodonts have been reconstructed on the basis of the stratigraphic distribution of taxa. Cladistic analysis, based on morphological data alone, includes no *a priori* assumptions about stratigraphic ordering. The resulting phylogeny can therefore be utilized in further applications based on evolutionary data, such as assessment of the fossil record and biogeography.

The conodont fossil record putatively represents one of the best archives of an extinct lineage. It has been appreciated for its richness and is widely used in local and global biozonation schemes throughout the Palaeozoic and Triassic. Despite the extensive use of the conodont fossil record in biostratigraphy, its quality has never been critically assessed. In this study, the fossil record of the Silurian conodont genus *Kockelella* has been investigated. Two independent methodologies have been used, the fit of a cladistic hypothesis to stratigraphic data and the calculation of confidence intervals. Both approaches indicate incompleteness in the fossil record of conodonts.

The resulting phylogeny of *Kockelella* has also provided the basis for a study in which palaeobiogeography and phylogeny have been combined. The results constitute a powerful tool in the understanding of evolutionary patterns and processes within the genus.

The end-Permian mass extinction: sudden or gradual?

Paul B. Wignall

School of Earth Sciences, University of Leeds, Leeds LS2 9JT, UK
<wignall@earth.leeds.ac.uk>

The speed with which the late Permian mass extinction happened has long been a subject of debate. Nearly 50 years ago Schindewolf challenged the prevailing consensus of a protracted extinction spread over many million years. Using evidence from the Salt Range of Pakistan he suggested that the extinction was instantaneous and may have been caused by a supernova. Perhaps because of his non-trendy, extra-terrestrial extinction mechanism, Schindewolf's ideas gained few adherents at the time. However, over the past few years "Schindewolfian rapidity"—to coin a phrase—has begun to gain respectability. Based on detailed studies of marine boundary sections, particularly those at Meishan in China and the Dolomites of Italy, several workers propose that the end-Permian mass extinction was very rapid and perhaps even instantaneous. However, distinguishing between a rapid and an instantaneous extinction event is not easy and neither the Chinese nor the Italian sections are ideal for resolving this problem. The Meishan section is ultra-condensed (sedimentation rates < 1 m/myr) and in the Dolomite sections the extinction level corresponds to a change to dolomitised, peritidal oolites—hardly ideal facies to determine last appearance data. The global synchronicity of the end-Permian extinction has also yet to be fully determined, but recent work on boundary sections in southern Tibet suggest a considerable diachroneity. This region lay at high southern palaeolatitudes and it records a considerably delayed extinction crisis, perhaps as much as one million years after the crisis occurred in lower palaeolatitudes. Therefore instantaneous kill mechanisms are not applicable to this particular mass extinction.

Calamari catastrophe

Philip Wilby¹, John Hudson², Roy Clements² and Neville Hollingworth³

¹ British Geological Survey, Keyworth, Nottingham NG12 5GG

² Dept. of Geology, University of Leicester, Leicester LE1 7RH

³ Natural Environment Research Council, Swindon, Wiltshire SN2 1EU

A new exposure in the Oxford Clay Formation of southern England, equivalent to the famous and now inaccessible lagerstätte at Christian Malford, Wiltshire, has yielded numerous coleoid cephalopods with phosphatized soft-tissues. Most of the coleoids from the new locality, and some from the old one, are preserved in closely associated "pairs." Individuals within each "pair" are mutually aligned and may be either of a single species and of a similar size, or of two different species. It is proposed that the coleoids formed large schools that were killed *en masse*, together with other elements of the associated fauna, in one or more catastrophic mass mortality events that affected a significant area. During the event(s), many coleoids preyed upon

moribund fish and other coleoids before becoming overcome themselves. Phosphatization of their soft-tissues was facilitated by the large number of associated decaying carcasses which had the effect of augmented levels of dissolved phosphorus in the sediment.

Walking with Millipedes: Kinematics of Locomotion in *Polyxenus* and Implications for Reconstructing the Functional Morphology of the Palaeozoic Millipede *Arthropleura*

Heather M. Wilson

Department of Entomology, 4112 Plant Sciences Building, University of Maryland, College Park, MD 20742, USA <wilsonhm@wam.umd.edu>

The kinematics of walking in the penicillate millipede *Polyxenus anacapensis* were analyzed using high speed video and digitization software and compared to that of representative chilognath millipedes. The parameters measured included speed, stepping frequency, stride length, angle of appendage swing, period, ratio of protraction to retraction, and phase lag. When *Polyxenus* locomotes at relatively low speeds contralateral legs step synchronously and footfalls plot in a continuous series. In contrast, when *Polyxenus* locomotes at relatively high speeds contralateral legs step alternately and footfalls plot in discrete clusters. This difference in trackway morphology is due largely to an increase in stride length generated through a stretching of the body at faster speeds. Chilognath millipedes locomote with contralateral legs stepping synchronously at all speeds and their skeletomuscular anatomy does not allow for significant elongation of the trunk. The trunk ring architecture is similar in Polyxenida and the extinct giant Palaeozoic millipede *Arthropleura*. Large *Diplichnites* trace fossils attributable to *Arthropleura* are well known from North America and Europe. *Arthropleura* produced two distinct types of trackways: those consisting of a continuous series of footfalls and those with footfalls grouped into crescentic clusters. Given the morphological similarities between *Polyxenus* and *Arthropleura*, it seems reasonable to hypothesize that *Arthropleura* also utilized distinct gaits at different speeds.

The origin of metazoan reefs: Neoproterozoic of the Nama Group, Namibia

Rachel Wood,^{1,3} John P. Grotzinger² and J.A.D. Dickson³

¹ Schlumberger Cambridge Research, High Cross, Madingley Road, Cambridge CB2 0EL, UK

² Department of Earth, Atmospheric and Planetary Sciences, Massachusetts Institute of Technology, Cambridge, Massachusetts 02139, USA

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

Skeletal metazoans are first found within long-established microbial reef communities in the late Neoproterozoic, coincident with the Ediacara biota (~550 Myr BP). This fauna includes large, modular, metazoans with biologically controlled biomineralization, appearing some 15 million years earlier than previously documented. This begs the questions, were any innovations necessary for metazoans to become part of reef communities? And what were the origins of their various ecological roles?

Three genera of reef-associated metazoans are now known from the Nama Group of northern Namibia, *Cloudina*, *Namacalathus* and *Namapoikia*. All showed gregarious behaviour, but occupied notably different ecological niches within thrombolite-stromatolite-dominated reefs. The problematicum *Cloudina* appears to have been a generalist, occupying soft-sediment as well as hard-substrate reef settings, whereas the similarly problematic *Namacalathus* had a specialist stalk-like holdfast structure. Both these genera were solitary and weakly biomineralised. By contrast, modular *Namapoikia*, which reached up to 1m in diameter, had the ability to encrust, and has been found in a notably unusual niche: attached to the vertical walls of syndimentary reef fissure systems. *Namapoikia* shows a complex and robust skeleton, and probably represents a cnidarian or poriferan. These few occurrences suggest that both generalists and specialists were present within the earliest metazoan communities, but that they occupied a diverse range of ecological niches.

Reserve: *Solenopora* is not an alga

Robert Riding

Earth Sciences Department, Cardiff University, Cardiff CF10 3YE, UK
<riding@cardiff.ac.uk>

For over one hundred years the Ordovician fossil *Solenopora* Dybowski has been widely considered to be a calcified red alga. The type species, *Solenopora spongioides*, consists of tubes with longitudinally flexuous walls, lobate-petaloid cross-sections 30-175 μm across with septal projections, and only sporadic cross-partitions. This internal micromorphology is not characteristic of calcified red algae, but is consistent with the original interpretation of *Solenopora* as a chaetetid, and with subsequent recognition of chaetetids as sponges. *Solenopora* is widely misidentified in Silurian and younger rocks. Removal of *Solenopora* from the algae underscores the need comprehensively to reassess the palaeoecological and phylogenetic significance of numerous disparate Ordovician-Miocene fossils currently classed as solenoporaceans.

Poster presentations

Poster presentations will be in the Department practical labs on the second floor, in conjunction with morning coffee (10:30–11:00), lunch (1:00–2:00) and afternoon tea (3:30–4:00); they will be attended during the morning coffee break and lunch. Half of the posters will be presented on each day, arranged alphabetically according to author: Anemone to Märss/Miller on Monday, Moore to Zuykov/Fritsch on Tuesday.

Abstracts for poster presentations

Paleocene and Eocene mammal bearing deposits from the Great Divide Basin, Southwestern Wyoming

Robert L. Anemone

Department of Anthropology, Western Michigan University, Kalamazoo, MI 49008, USA <anemone@wmich.edu>

The Great Divide Basin is an internal drainage basin surrounded by two diverging branches of the Continental Divide in Sweetwater County, Wyoming, USA. It forms the eastern part of the Greater Green River Basin, an area of extensive deposition of early Tertiary sediments that has yielded some of the best known mammalian faunas from the early Eocene of the American West. Following preliminary investigations by USGS and Smithsonian Institution field parties in the late 1950s and early 1960s, we began systematic investigations into the palaeontological resources of the Great Divide Basin in 1994.

Eight field seasons of palaeontological and geological investigations in early Tertiary sediments of the Great Divide Basin have yielded approximately 7,000 catalogued mammalian specimens from more than 50 localities spanning the Palaeocene-Eocene boundary. This time interval includes the latest Palaeocene thermal maximum (LPTM), a period of rapid global warming coinciding with the first appearances of many mammalian taxa in North America, Europe, and Asia. In this poster, I review the fauna from several different sets of localities ranging in time from the middle Clarkforkian to the late Wasatchian. Special attention is paid to the biostratigraphic and stratigraphic relationships of these localities and their faunas.

Yochelcionellids from Northern Greenland

Christian J. Atkins and John S. Peel

Department of Earth Sciences, Uppsala University, Norbyvägen 22, SE-752 36 Uppsala, Sweden <christian.atkins@geo.uu.se>

Yochelcionella are small cap-shaped molluscs, of Cambrian age, easily identifiable by a prominent snorkel on the sub-apical wall. Globally, twenty-three species, including seven in open nomenclature, have been reported. To this four new species are added from the Lower

Cambrian of Peary Land North Greenland: *Y. greenlandica* sp. n., and *Y. americana* Runnegar and Pojeta, 1980, from the Aftenstjernesø Formation, *Y. paralleldalensis* sp. n., from the Paralleldal and Henson Gletscher Formations from the Brñlund Fjord Group, *Y. gracilis* sp. n., and *Y. sp. n.*. The palaeogeographical range of *Y. americana* is extended. Palaeogeographic maps are included to illustrate the dispersal of species during the Cambrian.

The ichnofossil record across the Triassic/Jurassic Boundary

Colin Barras

Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol BS8 1JR, UK <colin@barras.ws>

The effects of the end Triassic mass extinction on the marine trace fossil record has been examined in England and Austria. Locally in England, there is heavy bioturbation immediately prior to the Late Rhaetian extinction horizon, with *Diplocraterion*, *Arenicolites*, and *Rhizocorallium* recorded. There is a short interval of unbioturbated sediments above the extinction horizon, with thoroughly bioturbated sediments reappearing before the boundary between the Rhaetian and the *planorbis* zone of the lower Hettangian. However, the ichnotaxon *Rhizocorallium* does not re-appear until the upper *planorbis* zone, while *Diplocraterion* and *Arenicolites* do not re-appear until the upper *angulata* zone. *Diplocraterion*, on its re-appearance, is significantly smaller than its pre-event counterparts.

The Rhaetian sediments of Austria are thoroughly bioturbated where examined some 60 metres below the Rhaetian/Hettangian boundary, with *Rhizocorallium*, *Diplocraterion*, and *Zoophycos* recorded. Immediately below the boundary itself, however, these ichnotaxa are absent. Above the boundary, laminated sediments are common throughout the Hettangian, and the ichnotaxa found in the Rhaetian are not recorded in either the Hettangian or early Sinemurian. The extinction event in Austria thus apparently began at an earlier stage than in England, and the recovery interval of the pre-event fauna is evidently longer.

The Paleo/Mesoproterozoic Stirling Biota

Stefan Bengtson¹, Birger Rasmussen², Ian R. Fletcher² and Neal J. McNaughton²

¹ Department of Palaeozoology, Swedish Museum of Natural History, Box 50007, SE-104 05 Stockholm, Sweden <stefan.bengtson@nrm.se>

² Centre for Global Metallogeny, University of Western Australia, Crawley, 6009, Australia <brasmuss@geol.uwa.edu.au> <ifletche@geol.uwa.edu.au> <nmcnaugh@geol.uwa.edu.au>

The Stirling Biota in Western Australia is between 2.0 and 1.2 Ga old and is represented by trace fossils and discoidal fossils in low-grade metamorphic sandstones. The discoidal fossils have previously been interpreted as Ediacaran, but are of uncertain nature. The associated trace fossils nevertheless indicate the presence of animal-like organisms. The traces are preserved in convex hyporelief on the sole of a thick bed of fine-grained sandstone. They consist of fine ridges, about 0.5–1.0 mm wide and high, forming parallel-sided pairs, 1.5–2.5 mm wide and

up to more than 2 cm long. The ridge-pairs may be straight, but usually curve more or less irregularly. A recurring morphology is characterized by the ridges at one end coming together in a U-shape and at the other end flaring to about 3.5 mm width before terminating. There is no evidence of deeper penetration into the underlying sediment. The ridges are interpreted as natural moulds of mucus-reinforced sediment strings formed by the surface movements of a vermiform organism. The organism had well-developed mucus-producing capacity and probably a hydrostatic skeleton to allow it to change shape. Whereas in today's biota this would be a description of an animal, it is possible that the traces were made by extinct multicellular or syncytial organisms outside the crown-group metazoans. Whichever type of organism made the traces, the Stirling biota offers a glimpse of a Mesoproterozoic or even Palaeoproterozoic biosphere which was more complex than the singularly microbial–algal world that is usually assumed.

Two exceptionally-preserved Ordovician sponge faunas from Mid Wales

Joseph P. Botting

Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ, UK <joseph00@esc.cam.ac.uk>

The Palaeozoic sponges of Avalonia have been barely studied for over a century, and it is normally assumed that fossils are so rare and non-diverse as to be of little importance. This poster introduces two Middle Ordovician faunas from disparate palaeoenvironments of central Wales, that contradict this view. The Llandegley Rocks site (middle Llanvirn: *murchisoni* Biozone) contains at least 15 species of spicular and aspicular demosponges, hexactinellids and a heteractinid from very shallow, coarse siliciclastics, preserved as silicified external moulds. In two specimens, silicification was sufficiently rapid to preserve parts of the proteinaceous skeleton. A root-tuft like sponge, *Pyritonema*, dominates the fauna, but is shown to be a monaxonid hexactinellid derived from lyssakids. The Llanfawr Quarries locality (basal Caradoc: *gracilis* Biozone) preserves about 15 species (dominantly reticulosisid hexactinellids, and a hazeliid demosponge) in black mudstones. The fauna occurs at several horizons, representing different communities, and includes *Asthenospongia* Rigby, King and Gunther, and a strongly spinose relative, a species of *Cyathophycus*, a variety of early reticulosisans including some with dermal specialisation, and two new demosponges.

A new stem tetrapod from the mid-Carboniferous of Northern Ireland

J.A. Clack¹ and P.E. Ahlberg²

¹ University Museum of Zoology, Cambridge, Downing St., Cambridge CB2 3EJ, UK

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

We report on the first Carboniferous tetrapod specimen discovered in Northern Ireland, and one of the most primitive tetrapods known from the UK. The specimen consists of a partial left jaw ramus showing sufficient features to diagnose it as a new taxon. The specimen was discovered

in 1843 by Portlock, described as a rhizodont fish and housed with the British Geological Survey. However, this specimen belongs to an undoubted early tetrapod. The precise locality is uncertain, but it derives from near Londonderry, possibly Maghera. Palynological evidence is equivocal, ranging from late Viséan through early Westphalian, but samples of other specimens from Maghera are Tournaisian (CM zone), which would make it one of the earliest tetrapods known. The specimen extends the geographical range of known Early Carboniferous tetrapods, which have now been found much further westwards in the British Isles than previously reported, and suggests the possibility of further discoveries in this region.

A preliminary analysis of lower jaw characters places the new taxon in the neighbourhood of “cf. *Tulerpeton*” (late Famennian jaw material from Andreyevka, Russia) and *Whatcheeria*, above all other Devonian tetrapods, and below *Crassigyrinus*, *Greererpeton*, *Megaloccephalus* and an anthracosaur-temnospondyl clade. It may belong to an early and wide-ranging post-Devonian tetrapod radiation.

Tracking Dinosaurs in Scotland

Neil D.L. Clark

Hunterian Museum, University of Glasgow, Glasgow G12 8QQ, UK <Nclark@museum.gla.ac.uk>

The first *in situ* dinosaurs from Scotland were discovered at the top of the Duntulum Formation (Bathonian, Jurassic) near to Staffin in northeastern Skye at the beginning of this year. Fifteen individual tridactyl footprints were recorded of which two pairs appear to be partial trackways. The footprints are preserved as natural casts on a mud-cracked calcareous sandstone surface. The individual track sizes range from about 30cm to over 50cm in length with narrow to broad digits suggestive of having been made by a medium to large bipedal dinosaur. These are also the youngest record of dinosaurs in Scotland and the largest!

Middle Cambrian cambroclavids from the Cantabrian Mountains (northern Spain): new clues for systematic re-appraisals

Sébastien Clausen and J. Javier Álvaro

UMR-LP3 CNRS, USTL, SN5, 59655 Villeneuve d'Ascq, France

<Sebastien.Clausen@ed.univ-lille1.fr > <Jose-Javier.Alvaro@univ-lille1.fr>

Recent etching of glauconitic bioclastic limestones (Beleño facies) from the first Middle Cambrian biozone (*Acadoparadoxides mureoensis*) of the Láncara Formation (Esla nappe, Cantabrian Mountains) has yielded key cambroclavids to test the phylogenetic relationships of these sclerites, commonly reported from the Lower Cambrian. Two species are distinguished: *Parazhijinites guizhovensis* and *Wushichites* n.sp. Although Bengston *et al.* (1990) reported the genus *Wushichites* as a junior synonym of *Cambroclavus*, and Conway Morris *et al.* (1997) considered *W. polyedrus* as a junior synonym of *W. minutus* (the type species), the new Cantabrian species (the first finding of this taxon outside China) allows us to re-erect formally the genus, in which a second species is now recognized.

A new approach to interpreting palynological data from the Late Carboniferous tropical coal forests

C.J. Cleal¹ and T.Kh. Dimitrova²

¹Department of Biodiversity and Systematic Biology, National Museums & Galleries of Wales, Cardiff CF10 3NP, UK

²Geological Institute, Bulgarian Academy of Sciences, Acad. G. Bonchev Street, Block 24, 1113 Sofia, Bulgaria

Using the dispersed palynology of the Late Carboniferous (Pennsylvanian) tropical coal forests for vegetational analysis has traditionally been difficult because we did not know which plants produced many types of pollen and spore. A.H.V. Smith identified distinctive palynological associations at different levels within coal seams, but it was difficult to relate this to vegetation change in any detail. However, this situation has changed through recent studies on *in situ* spores and pollen, and we can now start reinterpreting the dispersed palynological data. Evidence from South Wales, the Forest of Dean, the Dobrudzha Coalfield (Bulgaria) and the Sydney Coalfield (Cape Breton) suggests a progressive expansion of the lycophyte-dominated wetlands during the late Westphalian D, resulting in a distinct *Lycospora*-spike at the Westphalian-Stephanian boundary. Traditionally, work on the dispersed palynology of these deposits has been mainly on the coals, but our evidence suggests that the palynology of the clastic deposits gives the best evidence for the overall composition of the forests.

Questioning the tetrapod diversity of a Jurassic island, Glamorganshire

I.J. Corfe and L.K. Säilä

Flat 7, 37 Royal York Crescent, Clifton, Bristol BS8 4JU, UK

<ic1962@bris.ac.uk> <ls1607@bris.ac.uk>

Non-mammalian tetrapod remains from a new Early Jurassic fissure fill in Pant quarry, South Wales, indicate a more diverse fauna than previously described. A small region of Glamorgan, named St. Brides Island, remained above water throughout Hettangian times, before being submerged early in the Sinemurian. The average St. Brides *Hirmeriella* faunal associations, named after the widespread conifer fossil *Hirmeriella muensteri*, consists of only three tetrapod genera, whereas the new Pant 4 fissure has revealed many more. In addition to the usual one lepidosaur (*Gephyrosaurus bridensis*) and two mammalian genera (*Morganucodon* and *Kuehneotherium*), remains of sphenodontians, tritylodontids, archosaurs, and other mammals have been discovered. Concentrating on non-mammalian components (Pam Gill, another Bristol postgraduate, is examining the mammalian finds), the previous identification of three new sphenodontid and up to three new tritylodont species from the fissure is analysed. Material from the new fissure, excavated in 1973 and 1978, is described. Dating of the fauna is complicated by the depositional nature of fissure fills and taphonomic processes undergone by the bones before burial. Predator accumulation, reworking of remains, and geographically close fissures not being contemporaneous may account for the high diversity of the Pant-4 tetrapod fauna.

Significance of calcareous algae for the recognition of the Brigantian Stage (late Viséan) in Ireland and Great Britain

Pedro Cózar and Ian D. Somerville

Department of Geology, University College Dublin, Belfield, Dublin 4, Ireland

<pedro.cozar@ucd.ie> <ian.somerville@ucd.ie>

Brigantian rocks in deep water facies in Britain have been traditionally dated with goniatites and conodonts, whereas in shallow water carbonate facies, rugose corals have been used for zonation, but these fossils have palaeoecological constraints. Foraminifera are one of the best microfaunal groups for biostratigraphic studies in shallow water facies and their utility is widely demonstrated in European Carboniferous basins. In Ireland and Britain, however, many studies have shown the limitations of using foraminifera for the Asbian-Namurian interval, because the typical European markers do not occur at the base of the different stages, or they are extremely rare, or not even recorded. On the other hand, calcareous algae have been generally ignored for biostratigraphic studies, because of mostly long-ranging taxa. The recent but progressive improvement in the knowledge of this microfloral group shows their use as biostratigraphic markers. Detailed investigations of sequences in upper Viséan rocks in Ireland suggest a distinct relay of algal genera throughout the Asbian, early Brigantian and late Brigantian. Similar assemblages of algae are recognised in northern England and Scotland. Some of the genera used for characterising biozones are: *Koninckopora*, *Kamaenella*, *Ungdarella*, *Coelosporrella*, *Windsoporella*, *Fourstonella*, and *Calcifolium*. Comparison of Irish and British algal assemblages allows us to propose a reliable zonal scheme for shallow water facies in the late Viséan, as an alternative to the classical foraminiferal schemes.

Testing the phylogenetic relationships of 'complex' conodonts

Rosie Dhanda

Lapworth Museum of Geology, University of Birmingham, Edgbaston,

Birmingham B15 2TT, UK <RXD803@bham.ac.uk>

Evidence from the ultrastructure and soft tissues of conodonts establishes that they are vertebrates, but phylogenetic relationships within the clade remain poorly understood. The main reason for this is that most phylogenetic hypotheses have relied on two basic assumptions: the conodont fossil record is complete, and that P elements alone are sufficient for phylogenetic reconstruction. This has led to the creation of phylogenetic hypotheses through the correlation of stratigraphic occurrences. The two major classification schemes constructed to date by Sweet (1988) and Dzik (1991), show major discrepancies with respect to the division of the three orders of complex conodonts, raising the issue of one (if not both) of the schemes being inaccurate.

The central premise of this work is to elucidate the inter-relationships of prioniodontid, prioniodinid and ozarkodinid conodonts using all of the constituents of the apparatus in a cladistic analysis, thus eschewing stratigraphic data. Initial results indicate that the prioniodontids are a plesiomorphic paraphyletic group and that prioniodinids and ozarkodinids form monophyletic clades—this concurs generally with the hypothesis of relationships developed by Sweet and Donoghue (2001). The study will be extended to clarify basal relationships and those within the two more derived clades.



Sub-fossil beetles from the Gortian interglacial site at Derrynadivva, Co. Mayo, Ireland: a palaeoenvironmental study and its stratigraphical implications

Alexander Thomas Dixon

Dept. Earth Sciences, University of Cambridge, Cambridge CB2 3EQ, UK

Subfossil beetle remains from a sequence of silts and peats at Derrynadivva, Co. Mayo, Ireland provide the first known beetle assemblage of Gortian age. Although the age of the Gortian is not generally agreed upon, sites are characterised by their palaeobotanical record which suggests correlation with British interglacials showing Hoxnian-type vegetational development. Previous studies of Gortian sites record a flora without analogue today, including highly Atlantic species presently distributed in Ireland and northern Iberia but not Britain, as well as thermophilous species from southern and eastern Europe/western Asia.

The beetles as proxy indicators provide detailed information on the local palaeoenvironment and climate, indicating that at Derrynadivva, summer temperatures were slightly warmer and winter temperatures slightly colder than those of Ireland today although the climate was nevertheless oceanic. This would suggest a climate without modern analogue in Atlantic Europe. This climatic information also has a stratigraphical value because different interglacials show different patterns of climatic development. Of the two British interglacials showing Hoxnian-type vegetational development (OIS 9 and 11), Beetles from British OIS 9 sites indicate temperatures significantly higher than those at Derrynadivva which, if they can be extrapolated to Ireland, would suggest that Derrynadivva was not the OIS 9 interglacial, although the Gortian may conflate sites of more than one age.

Morphology, proposed life habits and phylogeny of “*Lithiotis*” facies bivalves

Nicole M. Fraser and David J. Bottjer

Department of Earth Sciences, University of Southern California, Los Angeles CA 90089-0740, USA

Following extensive Late Triassic coral-constructed reefs and the aftermath of the Triassic-Jurassic mass extinction, Early Jurassic buildups are rare and constructed primarily by bivalves. The Pliensbachian exhibits a radiation of aberrant pteriod bivalves, the “*Lithiotis*” facies bivalves, which include: *Lithiotis problematica*, *Cochlearites loppianus*, *Gervilleioperna* sp., *Mytiloperna* sp. and *Lithioperna scutata*. These large bivalves with bizarre morphologies are ubiquitous in tropical, nearshore deposits.

Over 500 specimens of “*Lithiotis*” facies bivalves were collected from study sites (Western North America, Morocco and Italy) or observed in museum collections. Morphology, microstructure and phenotypic variability were examined for each of the “*Lithiotis*” facies bivalves. “*Lithiotis*” bivalves’ life habits were assessed by field observations of various morphotypes and orientation of *in situ* specimens. The reef-building bivalves, *Lithiotis* and *Cochlearites*, have upright, stick-shaped growth forms. The other “*Lithiotis*” facies bivalves, *Lithioperna*, *Mytiloperna* and *Gervilleioperna* lived in lagoonal facies and exhibit a variety of morphotypes. All five “*Lithiotis*” facies bivalves share microstructures and ligament arrangements common to the pteriod families Isognomidae and



the Bakevellidae. *Mytiloperna*, *Gervilleioperna* and *Lithioperna* have a broad-tooth plate and byssal attachment, characteristics of the Bakevellidae. However, *Lithiotis* and *Cochlearites* lack these traits. A phylogenetic analysis proposes that “*Lithiotis*” facies bivalves are a paraphyletic group.

Miocene cold seep communities from the Caribbean region

Fiona Gill¹, Crispin T.S. Little¹, and Ian C. Harding²

¹ School of Earth Science, University of Leeds, Leeds LS2 9JT, UK

² School of Ocean & Earth Science, University of Southampton, Southampton Oceanography Centre, European Way, Southampton SO14 3ZH, UK

Miocene aged cold seep communities have been discovered in the Caribbean islands of Barbados, Trinidad and the Caribbean coast of Venezuela. These communities contain fossil representatives of taxonomic groups characteristic of modern and other Cenozoic cold seeps, including tube worms, nuculanid, vesicomid, mytilid, lucinid, thyasirid and solemyid bivalves, and provannid gastropods, as well as other taxa not known from modern seep sites (e.g. the deep-sea gastropod *Abyssochrysos*). The vast majority of these fossils are presently undescribed. Work over the next few years will involve thorough taxonomic and palaeoecological analysis of the Caribbean Miocene seep fossils, with the aim of investigating the origin of the cold seep communities in the Gulf of Mexico and Caribbean/western Atlantic region, and whether cold seep faunas of the Pacific and Caribbean/western Atlantic were linked and shared species prior to the raising of the Isthmus of Panama.

An exceptionally preserved biota from Upper Silurian submarine channel deposits, Welsh Borderland

David Gladwell

Dept. of Geology, University of Leicester, Leicester LE1 7RH, UK
<djg15@leicester.ac.uk>

An exceptionally preserved biota of Upper Silurian (Ludlow Series) age is found in Lower Leintwardine Formation Channel fill deposits around Leintwardine in the Central Welsh Borderland. There are six submarine channels in total, although only four outcrop and yield fossil faunas. The deposits are of special importance as they represent a rare example of exceptional preservation in organisms of Silurian age; they also provide a unique palaeoenvironmental setting. The fauna is diverse, containing common representatives of Silurian biotas (such as brachiopods and trilobites), along with more unusual forms such as ophiuroid and asteroid seastars, eurypterids, xiphosurids and phyllocarids. The degree of invertebrate disarticulation varies throughout the fauna; the echinoderms are mostly complete, whilst the majority of the arthropod material is made up of disarticulated components. Specimens are predominately preserved as hard-parts, although occasional soft-body preservation is encountered in the form of rare “worm” fossils. In addition to the dominant invertebrate fauna, relatively rare disarticulated components of heterostracan fish are found; the sole taxon found, *Archaegonaspis ludensis* (Salter, 1859) is the earliest known British species of its Order. The most fossiliferous channel is that at Church Hill, which has yielded 80% of the total fauna so far studied.

An Assemblage of the Carboniferous trilobite *Paladin mucronatus* (M'Coy, 1844)

John Hampton

Department of Geology and Geophysics, University of Edinburgh, Edinburgh EH9 3JW, UK <john.hampton@glg.ed.ac.uk>

The trilobite *Paladin mucronatus* (M'Coy, 1844) has been frequently noted in marine Brigantian and Pendleian strata spanning the Lower and Upper Carboniferous boundary in northern Britain and corresponding deposits elsewhere in Europe. A pygidium, clearly assignable to the species, from Northumberland was figured as early as 1837, but despite many subsequent records few detailed studies of the trilobite have been made and as yet no ontogeny for it produced. A rich assemblage of *P. mucronatus* fragments, from an exposure of Lower Carboniferous Brigantian Yoredale facies marine shales at Carpley Green, near Bainbridge, Wensleydale, is illustrated, and the problems of constructing an ontogeny from incomplete poorly preserved trilobite material briefly discussed.

Reconstructing polar forest-climate dynamics from fossil wood and computer models

Melise Harland¹, Jane Francis¹, David Beerling², Colin Osborne², and Stuart Brentnall²

¹Department of Earth Sciences, University of Leeds, Leeds LS2 9JT, UK

²Department Animal and Plant Sciences, University of Sheffield, UK

Climate models used to simulate past climates have commonly prescribed the polar regions as ice-covered. However, for most of the geological past, high-latitude regions were covered by dark dense forests. These forests would have significantly modified both the polar and global climate due to their low albedo and their effect on the land-surface heat budget and hydrological cycle.

Fossil wood is abundant in many high-latitude sedimentary sequences, representing the remains of forest vegetation that once thrived in polar regions in past greenhouse climates. These forests are being studied to determine their geographical distribution, their botanical composition and their techniques for survival in the unusual polar light regime. Their leaf life span (evergreen versus deciduousness) may have been a critical adaptation for their survival and an important contribution to the local carbon cycle. Reconstructions of palaeovegetation maps and forest growth dynamics will be used to constrain simulations from vegetation and GCM palaeoclimate models for Cretaceous and Tertiary times.

An unusual deep-water fauna from the Silurian rocks of the west of Ireland

David A.T. Harper¹, Stephen K. Donovan² and Ann Laursen¹

¹Geological Museum, University of Copenhagen, Øster Voldgade 5-7, DK-1350 Copenhagen, Denmark <dharper@savik.geomus.ku.dk>, <ann@savik.geomus.ku.dk>

²Department of Palaeontology, Nationaal Natuurhistorisch Museum – Naturalis, Postbus 9517, 2300 RA Leiden, The Netherlands <Donovan@naturalis.nnm.nl>

Abundant and diverse shelly faunas have been known for over a century from the Upper Llandovery Finny School beds (upper Telychian) on the Kilbride Peninsula, western Ireland. Only recently have the stratigraphical relationships between many of these faunal assemblages been clarified. Mass mortality horizons, dominated by a range of tabulate corals, are associated with volcanoclastics and occasional bentonites in the upper part of the Finny School beds. Overlying these beds is an unusual assemblage dominated by abundant, long stems of a new species of the crinoid *Segmentocolumnus* (col.); taphonomic study suggests some postmortem reworking of the fauna by weak, low-velocity currents. The remainder of the assemblage includes a relatively diverse assemblage of brachiopods dominated by *Atrypa*, *Clorinda*, *Dolerorthis* and *Lingulella* together with matlike tabulate corals. Rarer components of the fauna include bryozoans, trilobites and dendroid graptolites. A deep-water setting is confirmed in the overlying red mudstones of the Tonalee Formation by the presence of a marginal-*Clorinda* type assemblage, dominated by *Dicoelosia*. No comparable assemblages have been reported elsewhere from the Midland Valley of Scotland and its Irish counterparts. The biota may have represented a response to a peculiar, deep-water environment periodically charged with the distal flows of volcanoclastic surges.

Late Neogene dinoflagellates and sequence stratigraphy of the Southern North Sea Basin

Martin J. Head¹ and Stephen Louwye²

¹Department of Geography, University of Cambridge, Downing Place, Cambridge CB2 3EN, UK <mh300@cam.ac.uk>

²Palaeontology Research Unit, University of Ghent, Krijgslaan 281/S8, B-9000 Ghent, Belgium <stephen.louwye@rug.ac.be>

The correlation of Upper Cenozoic marine deposits across the southern North Sea basin has been fraught with difficulties. However, dinoflagellate cysts and marine acritarchs are shown to be useful for the correlation and environmental reconstruction of these deposits, owing to their wide salinity tolerance, high taxonomic diversity (more than 100 taxa), and good preservational potential. In eastern England only the Pliocene and lower Pleistocene are represented substantially by marine deposits, and even here the record is highly incomplete. Dinoflagellates help constrain the age of these deposits. In northern Belgium, Neogene marine deposits represent the southeastern margin of the southern North Sea Basin. These deposits are also discontinuous, but include the lower, middle and upper Miocene as well as lower and

upper Pliocene. The Miocene and lower Pliocene dinoflagellate assemblages are particularly diverse and well preserved, and facilitate correlation across the North Atlantic and as far as the US Atlantic coastal plain and shelf. The Pliocene assemblages can be correlated with those of eastern England and into the North Atlantic.

We present a biostratigraphic synthesis for the southern North Sea Basin and attempt to reconcile the stratigraphy of this region with the sequence chronostratigraphic framework of Hardenbol *et al.* (1998).

Angiospermid pollen from the Middle Triassic: Morphology, biostratigraphy and possible affinity

P.A. Hochuli¹ and S. Feist-Burkhardt²

¹ Paläontologisches Institut und Museum, Universität Zürich, Karl Schmid Str. 4, CH-8006 Zürich, Switzerland <peter.hochuli@erdw.ethz.ch>

² Palaeontology Department, The Natural History Museum, Cromwell Road, London SW7 5BD, UK <s.feist-burkhardt@nhm.ac.uk>

Middle Triassic sediments of the Barents Sea area contain a variety of dispersed colpate, and operculate pollen grains of angiospermid morphology. Seven different pollen types can be differentiated, all from the same stratigraphic interval (Ladinian to Anisian). Due to their consistent occurrence some of them have been used as stratigraphic markers under the designation of *Retisulcites* sp. 1, 2 (Hochuli *et al.* 1989) and *Retisulcites* sp. A (Vigran *et al.* 1998). All the described forms are characterised by well-developed semitectate reticulate sexines, which are connected by columellar structures to thin nexines (footlayer and endexine). Due to the pollen's very small size, their microscopical analysis is near the limit of optical resolution. So, in addition to high-resolution transmitted light microscopy, Confocal Laser Scanning Microscopy (CLSM) has been used for morphological analysis of the very delicate wall and surface structures. In CLSM the specimens were imaged in very thin, only ca. 360 nm thick, optical sections using fluorescence mode (excitation 568 nm, detection 590 nm LP). The optical sections were subsequently re-composed to generate extended focus images and 3D computer models. Pollen grains of comparable morphologies are common in sediments of Early Cretaceous age (Aptian / Albian). For the Middle Triassic all these pollen types are new; some of them show resemblance to the forms described by Cornet (1989) from the Carnian of the Richmond Basin (VA, USA). In the Barents Sea area the consistent occurrence of these angiospermid pollen shows that the producing (mother) plants were widely distributed and their diversity suggests that several species were involved. Among modern angiosperms reticulate, monocolpate pollen are generally associated with magnoliid affinity, however, it cannot be excluded that these pollen represent a so far unknown group of gymnosperms which produced pollen of angiospermid morphologies.

The ancestry of priapulid body plan

Huang Diying^{1,2}, Jean Vannier² and Chen Junyuan¹

¹ Nanjing Institute of Geology and Palaeontology, Academia Sinica (NIGPAS), Nanjing 210008, China <huangdiying@sina.com> <chenjunyuan@163.net>

² Université Claude Bernard Lyon 1, UFR Sciences de la Terre, UMR 5125 PEPS, Paléoenvironnements & Paléobiosphère, Bâtiment Géode, 2, rue Raphaël Dubois 69622 Villeurbanne, France <jean.vannier@univ-lyon1.fr>

The priapulid worms form a small ecdysozoan phylum with only 17 species living in present-day marine environments. Fossil evidence indicates that they were important elements of the endobenthic communities in the Early and Middle Cambrian but the evolutionary relationships of modern priapulid lineage to their Cambrian ancestors have so far never been resolved. Current studies of priapulids in the Early Cambrian Maotianshan Shale (SW China) bring new information on the ancestry of the priapulid body plan.

1. Early Cambrian priapulids are diverse with at least four different lineages (Acosmiidae, Corynetidae-Anningidae, Selkirkiidae and Palaeoscolecida) all characterised by distinctive features of their body plan
2. Some key-features of the body plan of modern priapulids such as the pentagonal arrangement of circum-oral teeth and the caudal appendage are recognised in the Early Cambrian priapulid *Anningia*
3. A new (extinct) body plan of particular evolutionary significance is represented by the Corynetidae-Anningidae (smooth contracted introvert)
4. *Acosmia* and *Xiaoheiqingella* may represent the ancestral body plan (swollen introvert bearing scalds, caudal appendage) from which modern Priapulidae derived.

Palaeoecological zonation in crinoids from marginal marine environments in the Bathonian of Central and Southern England

Aaron W. Hunter

Research School of Earth Sciences, Birkbeck and University College London, Gower Street, London WC1E 6BT, UK <aw.hunter@geology.bbk.ac.uk>

New research into the palaeoecology of echinoderms has demonstrated a lack of understanding of their environmental palaeoecology. This is in part due to taxonomy being based on exceptionally preserved whole specimens and not single ossicles whose affinity is problematic, in addition to the general absence of studies of echinoderms from facies lacking entire tests. Thus it has become necessary to consider fragmentary remains in defining a more representative palaeoecology. Bulk sampling (10 to 40 kg) of the Bathonian sediments of England, where marine environments ranging from open shelf to lagoon are represented, has revealed members of echinoderm groups inhabiting a full range of environments/salinity conditions. Extensive work on exceptionally preserved Middle Jurassic crinoids from Northern Switzerland and the British Liassic has enabled identification of crinoid columnals from the English Bathonian to generic level, thus allowing the community structure of the crinoids to be exemplified within

clearly defined ecosystems delineated by facies and degree of marine connection. Results indicate distinct crinoid communities based on the presence and absence of generic indicators. Examples include smaller forms, e.g. *Chariocrinus* and *Balanocrinus* inhabiting fully marine conditions, while larger *Millericrinus* and *Ailsacrinus* have been found inhabiting the carbonate shelf. *Pentacrinites* appears to inhabit the oolite shoal. *Isocrinus* on the other hand, is found to predominate in lagoons, but only up to a marked ecological cut off point, defined by low salinity/low oxygen conditions.

Ontogenetic variation in the frog ilium and its impact on classification

Marc E.H. Jones, Susan E. Evans, and Brian Ruth

Department of Anatomy and Developmental Biology, University College London, Gower Street, London WC1E 6BT, UK <marc.jones@ucl.ac.uk>

Anurans are a successful group of vertebrates comprising around 4,000 extant species. Their fossil record extends back to the Early Jurassic. Most fossils are preserved in one of three ways: impressions, articulated skeletons, and disarticulated 3-D elements from microvertebrate localities. In the latter case, new taxa are often diagnosed and described on the basis of ilia. Common diagnostic features include: the shape and size of the acetabulum, superior iliac tuberosity, and dorsal crest, and the prominence of the partes ascendens and descendens. However sample size is often small and we need to ascertain whether any observed variation is phylogenetically significant or due to individual differences (e.g. ontogeny, sexual dimorphism). In order to evaluate the importance of ontogeny on iliac form, we examined growth series for two anuran species, *Bufo punctatus* (Bufonidae) and *Hyla regillia* (Hylidae). Most of the commonly used diagnostic features did not change substantially. However, in *B. punctatus*, the shape of the dorsal tubercle and the relative height of the acetabulum varied to some degree, while in *H. regillia* changes were more subtle and involved the prominence of crests and depressions. In addition, the angle of the iliac shaft altered with maturity in both taxa.

A spinosaurid furcula and its phylogentic implications

Christine Lipkin¹ and Paul C. Sereno²

¹Department of Earth Sciences, University of Bristol, Bristol BS8 1RJ, UK

²Department of Organismal Biology and Anatomy, University of Chicago, Chicago, IL 60637, USA

Furculae (fused clavicles) have been identified in several groups of theropod dinosaurs, including allosaurids, tyrannosaurids, oviraptorids, therizinosaurids, dromaeosaurids, troodontids, and herein the spinosaurids. A recently discovered skeleton of the African spinosaurid *Suchomimus tenerensis* confirms the presence of an ossified furcula and suggests that this fused bone characterized the earliest tetanurans. Indeed, the very recent report of furculae in coelophysoids (*Syntarsus*, *Segisaurus*) that are Early Jurassic age suggest a Triassic origin among basal neotheropods. The condition in neotheropod outgroups is uncertain for herrerasaurids, but an ossified furcula is not present in the basal theropod *Eoraptor*. Preservational bias has played a dramatic role in questioning the near universal presence of this fused bone in neotheropods.

The flattened, V-shaped bone has a width of approximately 31 cm and has a short, tongue-shaped hypocleideum approximately 2 cm in length. An elliptical scar about 8 cm in length is present at the distal end of each epicleideal ramus for attachment to the anterior margin of the coracoid and acromion. The intrafurcular angle is 111 degrees. The furcula closely resembles that of *Allosaurus*.

Sereno *et al.* (1998) initially described *S. tenerensis* from a partial skeleton from the Lower Cretaceous (Aptian), Elrhaz Formation, Gadoufaoua, Niger, Africa. In 2000, a nearly complete postcranial skeleton was recovered that included a furcula. Prior to this find and the recent report of coelophysoid furculae, the most primitive tetanuran furcula was that of *Allosaurus*.

Age and palaeoenvironments of a shallow marine Pliocene sequence in northern Belgium revealed by dinoflagellate cyst stratigraphy

Stephen Louwey¹, Martin J. Head² and Stijn De Schepper²

¹Palaeontology Research Unit, Ghent University, Krijgslaan 281/S8, B-9000 Ghent, Belgium <stephen.louwey@rug.ac.be>

²Department of Geography, University of Cambridge, Downing Place, Cambridge CB2 3EN, UK <mh300@cam.ac.uk>

The subsurface Pliocene of northern Belgium was deposited in a shallow marine environment at the southern margin of the North Sea Basin. Basal gravel lags and characteristic lithologies permitted a robust lithostratigraphic subdivision in the 1970s, but correlation with the sequence chronostratigraphic framework of Hardenbol *et al.* (1998) remained incomplete owing to imprecise biostratigraphic control. The effects of deposition under a varying sea level regime in a marginal marine environment are clearly observed in the Pliocene by distinct and rapid facies variations. Well-preserved dinocyst assemblages were recovered from a Pliocene deposit in two temporary exposures in Antwerp harbour. These assemblages reflect age, depositional environment, and climatic events.

The dinocyst assemblages from the Kattendijk Sands point to deposition under warm-temperate conditions in open waters during early Pliocene times. A correlation of the lower boundary with sequence boundary Me2 is proposed. Cooling associated with the overlying Luchtbal Sands persists into the base of the transgressive Oorderen Sands, after which mild conditions were reestablished. An uppermost clayey unit here identified as the Kruisschans Sands announces a shallowing of the depositional environment. Dinoflagellate evidence indicates that the Kruisschans Sands predate northern hemisphere glaciation at 2.6 Ma.



Silurian thelodonts from the Welsh Borderland and co-occurrence with conodonts

Tiiu Märss¹ and C. Giles Miller²

¹Institute of Geology, Tallinn Technical University, Estonia Avenue 7, Tallinn 10143, Estonia <marss@gi.ee>

²Department of Palaeontology, Natural History Museum, Cromwell Road, London SW7 5BD, UK <G.Miller@nhm.ac.uk>

New data on thelodonts from the Middle Llandovery-lowermost Lochkovian of the Welsh Borderland are presented as well as the distribution of co-occurring conodonts. Thelodonts are rare in the Llandovery and Wenlock Series. Like the Wenlock, the basal part of the Ludlow Series is mostly barren of thelodonts but small numbers of the important species *Paralogania martinsoni* and *Thelodus laevis* are present with long ranging conodont species of *Ozarkodina* and *Panderodus*. In the uppermost part of the Upper Bringewood Formation, *Paralogania kaarmisensis* and *Phlebolepis elegans* have been recovered together with the zonal conodont *Polygnathoides siluricus* (P.C.J. Donoghue and R.E. Elliott *pers. comm.*). The Whitcliffe Formation, uppermost Ludfordian, provides the most diverse and well-preserved material.

Frequent *Thelodus parvidens* and *Thelodus trilobatus* occur in association with the rarer zonal conodonts *Ozarkodina snajdri*, *Ozarkodina crispera* and *Ozarkodina remscheidensis eosteinhornensis*. At the base of the Pridoli Series there is a change to a thelodont fauna dominated by *Paralogania ludlowiensis*, which first appears at this level, in association with *Nethertonodus prodigialis*. Higher in the Pridoli Series, a succession of thelodont faunas including *Katoporodus timanicus*, *Goniporus alatus*, *Paralogania kummerowi* ssp. 1, *P. kummerowi* ssp. 2 and *Loganellia unispinata* can be traced before the incoming of the lowermost Devonian taxon *Turinia pagei* along with *Nikolivia toombsi*. Similarities in thelodont faunas between the Welsh Borderland and the Baltic are presented, showing new correlations in the lower part of the Ludlow Series and uppermost Pridoli Series, where zonal conodont species are extremely rare or absent in Britain.

Quantitative vertebrate palaeocommunity analysis – A realistic goal?

Jason R. Moore

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

The application of modern statistical techniques to palaeoecology allows quantification of what has previously been a very scenario-driven branch of palaeontology. Given these techniques, which aspects and to what degree can vertebrate palaeocommunities be accurately reconstructed, if at all? Many recent analyses use simple species lists to describe palaeocommunities. More useful than this is an appreciation of the abundances of those organisms present, as not only does it reflect ecological dominance but also illustrates finer scale variability in ecosystem composition. Several conditions must be met by the analysed community in order for there to be any chance of relative abundance being preserved; the community must have been stable for a significant period of geological time (>100 ka),



taphonomic and taxonomic biases must have been constant or predictably varying and fossils must be present from a wide range of facies. Accurate community analysis also requires a change in sampling protocol as many vertebrate fossil deposits represent catastrophic events which should not be included in abundance analyses. I attempt to model this using a C++ program written for the purpose, incorporating the effects of sampling as well as the effects of biases on the final community composition in order to demonstrate whether it is possible to make any reconstruction of relative abundance in vertebrate palaeocommunities.

New synziphosurines from the Lower Silurian of Wisconsin

Rachel Moore

Department of Earth Sciences, University of Bristol, Bristol BS8 1RJ, U.K <rachel.moore@bristol.ac.uk>

Synziphosurines are a primitive group of paraphyletic Xiphosura (Chelicerata), with a reliable fossil record from the Mid Silurian to the Late Devonian. New synziphosurines, represented by approximately ten specimens, attributable to at least two new taxa, are described from the Llandovery Waukesha Konservat-Lagerstätte of Wisconsin, U.S.A. They form part of an unusual assemblage including trilobites, phyllocarids, ostracods, thylacocephalans and a myriapod, which lacks shelly faunas typical of regional carbonate deposits. The new synziphosurine material preserves their prosomal appendages, which are extremely rare amongst this group, only previously described from *Weinbergina optzi*, from the Devonian Hünsruck Slate. This material therefore extends the known fossil record of synziphosurines back to the Lower Silurian and provides additional morphological characters which are important in elucidating the complex evolutionary history of primitive Chelicerata.

Late Wenlock Graptolites from near Orange, New South Wales

Lucy Muir

University of Edinburgh, Grant Institute of Geology, West Mains Road, Edinburgh EH9 3JW, UK <lucy.muir@glg.ed.ac.uk>

Assemblages of graptolites from sections at One Tree Hill and Wallace Creek are described. The Wallace Creek specimens come from the *lundgreni* zone. A possible faecal pellet made up of individuals of *Monograptus testis* (Barrande 1850) was found at one locality. Most of the One Tree Hill specimens come from the *praedeubeli-deubeli* zone, the zone succeeding the *lundgreni-testis* zone. The fauna includes several species of retiolitid, *Colonograptus ludensis* (Murchison 1839) and *Monograptus insperatus* Koren' 1992. This is the first record of *Monograptus insperatus* from New South Wales and the second outside central Asia. This has implications for graptoloid biogeography after the *lundgreni* event, implying a faunal connection between central Asia and Australia at this time.

A Lower Carboniferous sipunculan from the Granton Shrimp Bed, Edinburgh

Lucy Muir¹ and Joseph Botting²

¹ University of Edinburgh, Grant Institute of Geology, West Mains Road, Edinburgh EH9 3JW, UK <lucy.muir@glg.ed.ac.uk>

² Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ, UK <joseph00@esc.cam.ac.uk>

The Granton Shrimp Bed is a Konservat-Lagerstätte, with a restricted biota including abundant arthropods, and rare polychaete worms, nautiloids, conodont animals and problematica. Here we describe a specimen of a sipunculan from this locality. Sipunculans (Phylum Sipuncula) are sedentary marine worms with a partly evertible trunk, believed to represent an early coelomate grade, probably with a close relationship to the annelids. They are unmineralised and extremely rare in the fossil record; poorly preserved specimens would also be difficult to recognise, since they possess few distinguishing features. Identification in this case relies largely on the arrangement of transverse and longitudinal wrinkling of the cuticle, reflecting the distinctive underlying musculature. The present specimen shows close similarity to *Lecthaylus gregarius* Weller, 1925, from the Silurian of Illinois, and is referred to that genus. This is the first known fossil sipunculan from the Carboniferous, or from the UK.

A new dipnoan fish from the Middle Devonian of Scotland and its importance to the evolution of the dipnoans

M.J. Newman¹ and J.L. den Blaauwen²

¹ 72 Bremner Way, Kemnay AB51 5FW, UK <ichthyman@newman.freeseerve.co.uk>

² Swammerdam Institute for Life Sciences, Plantage Muidergracht 12, 1018TV, Amsterdam, The Netherlands <jdblaauw@science.uva.nl>

In the last century Ramsey Traquair (1914) described specimens of the Devonian lungfish *Pentlandia macroptera* as existing in the area of Baligill, Sutherland, Scotland. Later Miles and Westoll (1963) could not find the specimens referred to by Traquair and put the Baligill deposits at the Eifelian horizon, well below the Givetian where all specimens of *P. macroptera* have previously been found. New specimens with a superficial resemblance to *P. macroptera* have been discovered by the authors from Baligill and elsewhere. Also, specimens probably used by Traquair in his identification of *P. macroptera* have been found housed in the National Museums of Scotland which belong to the new species. The new species, *Balipinnalatus saxoni*, shows primitive characteristics of the skull but also advanced characteristics of the post cranial body. This is important to the recognised textbook evolution of the dipnoans.

The Middle Oxfordian ammonite faunas of Upware, Cambridgeshire, eastern England—a remarkable bridge between Boreal and Tethyan realms

Kevin N. Page¹ and John K. Wright²

¹ Department of Geological Sciences, University of Plymouth, Drake Circus, Plymouth PL4 8AA, UK <KevinP@bello-page.fsnet.co.uk>

² Department of Geology, Royal Holloway College, University of London, Egham, Surrey TW20 0EX, UK <j.wright@gl.rhul.ac.uk>

Substantial new exposures of Middle Oxfordian limestones and marls at Upware, Cambridgeshire (eastern England), have yielded an unusually diverse ammonite fauna, including Boreal Cardoceratidae and Tethyan Perisphinctinae, often in almost equal proportions. The sequence of species of *Cardioceras* demonstrates a gradual change in the proportion of morphospecies present with time through the uppermost Densiplicatum (fauna I) and into the Tenuiserratum chronozones (faunas II-IV). Perisphinctidae show more radical changes, however, from regularly ribbed *Arisphinctes* (with “*Otosphinctes*” microconchs; faunas I-II) to strongly variocostate *Perisphinctes* sensu stricto (with *Dichotomosphinctes* microconchs; faunas III-IV). This change corresponds to the Submediterranean Plicatilis-Transversarium chronozone boundary—for the first time the position of this change, which can be recognised over much of Europe, can be established within a Boreal cardioceratid zonal scheme, and lies *within* the Tenuiserratum Subchronozone (Tenuiserratum Chronozone). Occasional records of the Tethyan Aspidoceratinae and Ochotoceratinae provide useful additional comparisons with the faunas of southern areas. As the sequence of faunas at Upware has great potential to link Submediterranean and Boreal province successions precisely, a sequence of biohorizons is proposed: aff. *pickeringius* (I), aff. *maximus-sopotense* (II), *antecedens* (III), *parandieri-tenuiserratum* (IV).

The Upware locality will be visited by the Association during the conference field excursion.

Quaternary Land Snails from Tenerife; Clues to the Palaeoclimate?

Claire Pannell

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

Tenerife, situated approximately 150 km off the west coast of Africa, is the largest island in the Canarian archipelago and originated by hotspot volcanism over a slow-moving oceanic plate. Pumice fall deposits, ash layers and ignimbrites preserve a record of some of the eruptions. The Bandas del Sur formation, the most well researched sequence, occurs in the south east of the island and Argon/Argon dating of sanidine crystals from the pumice fall deposits has produced dates for six of the eruptions dated back approximately 600,000 years. Pumice fall deposits contain a record of organisms within and on the soil surface at the time of the eruptions and commonly contain land snail shells. Dating of the deposits provides a stratigraphic constraint for the snails that can be superimposed on the marine oxygen isotope curve to infer the temperatures at the time. Land snail shells are composed of calcium carbonate that has a carbon and oxygen isotope composition determined by diet, atmospheric CO₂ and precipitation. Future stable isotope studies of the snail shell carbonate will enhance the marine core data by suggesting the palaeo-vegetation, precipitation and temperatures. This poster aims to link the various data to reconstruct the Quaternary palaeoclimate.



The morphology and phylogenetic position of the enigmatic, extinct arachnid order Phalangiotarbida

Jessica R. Pollitt

Department of Biology and Biochemistry, University of Bath, Bath BA2 7AY, England, UK <jessicapollitt@hotmail.com>

Phalangiotarbids are an order of extinct, enigmatic arachnids that have been found only in the Early Devonian of Germany and the Coal Measures of North America and Europe. They are characterized by a single median ocular tubercle bearing six eye lenses, a broad prosoma-opisthosoma junction, six abbreviated anterior tergites, four larger posterior opisthosomal tergites and a dorsal anal operculum. This study of the abundant *Phalangiotarbus subovalis* material from the Upper Carboniferous of Writhlington, Somerset, UK, reveals new information about the morphology of the apotele (i.e. the distal podomere of the walking legs), the fifth sternite, the opisthosomal segmentation, and confirms the anal operculum as a dorsal feature.

Their phylogenetic affinities are obscure. They have been claimed to have close affinities with Opiliones, Acari, Pedipalpi and Amblypygi. A new comprehensive cladistic analysis, based on sixty-four characters of thirteen terminal arachnid taxa (plus a hypothetical outgroup), resolves Phalangiotarbida as sister-group to Palpigradi + Tetrapulmonata. A 'fossil-friendly' approach, whereby those characters that could only be coded in extant taxa are excluded from the analysis, produces a strict consensus tree that shows Phalangiotarbida placed in an unresolved clade with Ricinulei, Acari, Palpigradi, Araneae and Trigonotarbida, and basal to the other tetrapulmonata taxa. The topologies recovered from both approaches are, thus, broadly congruent.

The Lilliput Effect in the aftermath of the end-Permian extinction event

Nathan Price-Lloyd and Richard J. Twitchett

Department of Earth Sciences, University of Bristol, Queen's Road, Bristol BS8 1RJ, UK <r.j.twitchett@bris.ac.uk>

Fossil organisms in the immediate aftermath of extinction events are much smaller than in the pre-extinction fauna (the Lilliput effect). The cause(s) of this phenomenon remain unknown. Is it due to a disappearance of large taxa, the appearance of many small (opportunistic?) taxa, or a general dwarfism affecting the whole fauna?

We present the first quantitative study of within-lineage size decrease, and subsequent increase, through the Permian-Triassic (P-Tr) extinction and recovery interval. Four unrelated taxa were studied from P-Tr sections of Europe. *Bellerophon* and *Lingula* both pass through the P-Tr event. The mean size of Late Permian *Bellerophon* and *Lingula* is 17 mm and 5 mm respectively. Both taxa are much smaller in the Early Griesbachian (*parvus* Zone): mean lengths 5 and 3 mm respectively. A return to pre-event size took place in the later Griesbachian (*carinata* Zone). The bivalves *Unionites* and *Claraia* are also very small in the Early Griesbachian (4 and 7 mm respectively), before also increasing in size in the *carinata* Zone (18 and 24 mm). All differences are statistically significant. Size decrease is clearly temporary, and affects all taxa equally, suggesting a phenotypic response to environmental change such as a period of reduced food supply.



Natural assemblages of *Idioproniodus* (Conodonta, Vertebrata) and the first accurate three-dimensional skeletal model of a prioniodinid conodont

Mark A. Purnell¹ and Peter H. von Bitter²

¹Department of Geology, University of Leicester, Leicester LE1 7RH, UK <map2@le.ac.uk>

²Department of Palaeobiology, Royal Ontario Museum, and Department of Geology, University of Toronto, Toronto, Ontario M5S 2C6, Canada <peterv@rom.on.ca>

Without natural assemblages preserving articulated skeletons, our understanding of conodonts would be radically different. Hypotheses of multielement composition, apparatus architecture, element homology, phylogenetic relationship, and taxonomic assignment all ultimately rest on data derived from natural assemblages.

Conodonts assigned to the Family Prioniodinida, especially those from the Late Palaeozoic, provide clear examples of the difficulties in dealing with groups of conodonts for which natural assemblages are unknown. In this context, species of *Idioproniodus* are important as they may constitute the stem lineage from which many late Palaeozoic and Triassic prioniodinids evolved. But there is no agreement concerning the homologies of the elements in the apparatus, and as a result analysis of the evolutionary relationships of *Idioproniodus* is problematic, to say the least. We have discovered two specimens that preserve articulated remains of *Idioproniodus* and from these we have produced a 3D model of the apparatus. The model confirms that the architecture of prioniodinid conodonts was essentially the same as that of the better known ozarkodinid conodonts, but highlights a number of differences and difficulties, particularly concerning the orientation of digyrate elements in S and P positions. Notwithstanding these difficulties, knowledge of the 3D architecture of *Idioproniodus* and direct evidence for topological homology of the elements will provide a more secure framework for reconstruction and phylogenetic analysis of problematic Late Palaeozoic prioniodinids.

Devonian ichthyoliths from northern Spain (Asturias) and northern Italy (Carnic Alps): a Gondwana–Euramerica connection

Carine Randon

CNRS-UPRESA 8014 Sciences de la Terre, Université des Sciences et Technologies de Lille, 59655 Villeneuve d'Ascq cedex FRANCE <Carine.Randon@ed.univ-lille1.fr>

During the Devonian, southern Europe occupied a privileged situation for the study of relationships between Euramerica and Gondwana because of its location between both continents. Vertebrate microremains have been poorly studied in this region. Gnathostome ichthyoliths from the Devonian of northern Spain (Asturias) and northern Italy (Carnic Alps) are described; they complement data from other Spanish regions and give a first idea of the Italian fauna. 49 placoderms, chondrichthyans, acanthodians, actinopterygians and sarcopterygians taxa are described morphologically. Emsian acanthodians predominate in the Spanish fauna whereas Famennian chondrichthyans predominate in the Italian fauna. The stratigraphical

distribution of studied taxa is established for both regions. The palaeobiogeographical distribution of these vertebrate faunas is located within the intertropical zone and affinities are shown for Gondwana as well as for Euramerica. The Carnic Alps late Famennian assemblage seems to be equivalent to the *Phoebodus* biofacies (*sensu* Ginter), but it differs from it by the occurrence of *Siamodus*, which suggests a new definition of late Famennian chondrichthyan biofacies.

Lower Palaeogene microfossil biostratigraphy of the Davis Strait, offshore West Greenland

Jan Audun Rasmussen and Emma Sheldon
 Geological Survey of Denmark & Greenland, Dept. of Stratigraphy, Øster Voldgade 10, DK-1350 Copenhagen, Denmark <jar@geus.dk>

Microfossils from the Palaeocene and Early Eocene succession from the Davis Strait, offshore West Greenland have been investigated. The study concentrated especially on foraminiferids but diatoms, radiolarians and other fossil groups were also analysed. In general, the five boreholes contained fairly well preserved and diverse faunas and floras, but the diversity and density varied significantly both laterally and stratigraphically. The studied interval was subdivided into three foraminiferid biostratigraphic intervals, in ascending stratigraphic order, the *Stensioeina beccariiformis*, *Praeglobobulimina ovata* and *Pseudohastigerina wilcoxensis* intervals, and five biostratigraphic intervals based on additional microfossil groups (the *Thalassiosiropsis wittiana*, *Fenestrella antiqua-Coscinodiscus morsianus*, Ostracod, *Aulacodiscus hirtus* and *Cenodiscus-Cenosphaera* intervals). In most cases, it was possible to correlate the biostratigraphic intervals with the existing zonations of the Labrador Sea.

Carbonate depositional environments and their influence on exceptional preservation in the Much Wenlock Limestone Formation of Dudley, England

David C. Ray
 School of Earth Sciences, The University of Birmingham, Edgbaston, Birmingham B15 2TT, UK <daveray01@yahoo.com>

The Much Wenlock Limestone Formation (Silurian), exposed near the town of Dudley, England, contains one of the richest known Silurian carbonate faunas. Over 600 species representing nearly 30 taxonomic groups are known from the Dudley inliers, and for many species, Dudley represents the type locality. The exceptional preservation and diversity of the fossil biota, in particular pelmatozoan echinoderms and trilobites, has been the object of scientific inquiry since the late seventeenth century. Yet in spite of much scientific interest relatively little is known as to their precise stratigraphic distribution and faunal/sedimentological associations.

This study is based upon comparisons between outcrop and museum collections and has identified a number of stratigraphic discriminators that allow the identification of the intervals from which much of the Dudley material originated. Exceptional preservation appears to be restricted to those sediments deposited between SWB and FWWB and has been further enhanced during periods of transgression. Thus the identification of the horizons from which the Dudley

collections originated allows fresh insights into the palaeoecology and taphonomy of the Much Wenlock Limestone Formation.

Taphonomy of larger benthic foraminifera and its relevance for the interpretation of the fossil record

Willem Renema
 Nationaal Natuurhistorisch Museum, PO Box 9517, 2300 RA Leiden, The Netherlands <renema@naturalis.nl>

Larger foraminifera occur on carbonate platforms and reefs. The stratigraphy of this type of environment is largely based on the occurrence of larger foraminifera, because of their relatively rapid evolution. Less attention has been paid to the ecological importance of benthic foraminifera though. In this study I compared the distribution of living benthic foraminifera shelf with the distribution of empty tests. The study was performed on the Spermonde Shelf (SW Sulawesi). Species living on the reefs are poorly represented in the fossil record, whereas species living on the reef base and further from the reefs are better preserved. The latter group turned out to be also the best group to represent environmental parameters.

Jurassic dinosaur tracks and communities from the Cleveland Basin, Yorkshire: the story nine years on

Mike Romano and Martin A. Whyte
 Department of Geography, University of Sheffield, Dainton Building, Brookhill, Sheffield S3 7HF, UK
 <m.romano@sheffield.ac.uk> <m.a.whyte@sheffield.ac.uk>

Work carried out by the authors since 'Pal. Ass. 1993' has led us to believe that dinosaur tracks characterize the non-marine Middle Jurassic sequences exposed along the 55 km stretch of coast between Filey and Staithes, Yorkshire. Nearly 30 different track morphotypes have now been recognized. These may be readily categorized into three major groups; (a) large tracks made by habitual quadrupeds, (b) tridactyl tracks made by habitual bipeds, and (c) tracks consisting of essentially parallel digit imprints, resulting from a swimming behaviour. The validity of these morphotypes will be discussed in terms of whether they are distinct ichnotaxa; or if they may represent preservational variants, ontogenetic growth series or sexual dimorphs. Our present conclusions indicate that the track morphotypes possibly represent at least 15 ichnotaxa. These ichnotaxa in turn were probably made by some 10 species of dinosaur. Although it is not possible at present to postulate distinct dinosaur communities throughout the Middle Jurassic of Yorkshire, we are in a position to present a 'combined' community that inhabited the coastal plain complex of the Cleveland Basin.

All done without the use of bones!

**Fine-scale variants of the Haptophyte alga *Calcidiscus leptoporus*: 'Cryptic' species or ecophenomorphs?**Blair A. Steel^{1,2}, Markus Geisen², Patrick S. Quinn³, Ian Probert⁴ and Jeremy R. Young²¹Department of Geological Sciences, University College London, Gower Street, London WC1E 6BT, UK <b.steel@gl.rhul.ac.uk>²Department of Palaeontology, The Natural History Museum, Cromwell Road, London, SW7 5BD, UK³Geological Institute, Eidgenössische Technische Hochschule Zürich, CH-8092 Zürich, Switzerland⁴Laboratoire de Biologie et Biotechnologies Marines, Université de Caen Basse Normandie, Esplanade de la Paix, 14032 Caen, France

The cosmopolitan coccolithophorid *Calcidiscus leptoporus* has long been thought to exemplify the phenomenon of fine-scale speciation (an evolutionary mechanism giving rise to groups of weakly divergent morphotypes, traditionally bracketed as single species, which can in fact be separated on the basis of consistently expressed recondite morphological differences). However, the validation of such a model is contingent on the successful discrimination of 'true' genetic variation from background ecophenotypic morphological responses. This study has utilised cultured strains of *C. leptoporus*, grown across a range of temperatures (13-23°C) and subsequently analysed using semi-automated morphometrics, as a means of evaluating the relative importance of environmentally mediated plasticity and genetically controlled morphological variation. The two strains analysed grouped consistently (although with some overlap) into disparate regions of a two-dimensional morphospace field (defined by two independent measurements of distal shield diameter), one around a mean of 6.09µm (corresponding to the 'Intermediate' morphotype of Knappertsbusch *et al.* 1997), the other with a mean of 8.64µm (equivalent to their 'Large' morphotype). Although a weak ecophenotypic overprint may be present, expressed morphology is largely unaffected by temperature. A series of spontaneous heterococcolith-holococcolith phase-changes in monoclonal populations confers increased confidence that *C. leptoporus* 'Intermediate' is exclusively associated with the holococcolith *Crystallolithus rigidus*, further reinforcing interpretation of morphological variation within the *C. leptoporus* concept as a result of evolutionary processes.

Neglected Girvan molluscs muscle in on Ordovician biodiversity patterns

Sarah E. Stewart

Division of Earth Sciences, University of Glasgow, Glasgow G12 8QQ, UK <sarahste@earthsci.gla.ac.uk>

The Ordovician successions of the Girvan district, SW Scotland are well suited for the study of regional scale changes in the whole fauna during the global diversification event. They represent a wide range of shelf and upper slope environments on the Midland Valley Terrane, close to the Laurentian margin. Some groups, including brachiopods and trilobites, are well documented but others, including, rare and problematic taxa, have long been neglected. Detailed sampling



and examination of museum collections suggest that these groups are more abundant and diverse than the literature indicates. Their analysis is therefore important if changes in overall biodiversity and palaeoecology are to be understood.

The molluscs are amongst these neglected groups. Recent sampling has revealed bivalves from the uppermost Llanvirn–lower Caradoc in both nearshore and offshore facies. These may be amongst the earliest bivalves to reach the Laurentian margin, following their early Ordovician diversification in Gondwana. They occur with greater diversity, abundance and variety of mode of life in the upper Caradoc and Ashgill faunas. Cephalopods, polyplacophorans, 'monoplacophorans', rostroconchs and gastropods are present throughout the succession, with gastropods in particular being ubiquitous across the entire spectrum of environments, although some genera are more restricted in habitat type.

Depositional depth estimation and the bathymetric distributions of modern populations of some common Neogene Bryozoa from New ZealandPaul D. Taylor¹, Dennis P. Gordon² and Peter B. Batson³¹Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD²National Institute of Water & Atmospheric Research, P. O. Box 14-901, Kilbirnie, Wellington, New Zealand³Department of Marine Science, University of Otago, 304 Castle St., Dunedin, New Zealand

Estimates of depositional depth are routinely sought by geologists. Fossils of extant species provide one method of inferring palaeodepth using depth ranges of present-day populations. This method has not been adequately tested for bryozoans because of the paucity of comprehensive data on the depth ranges of modern species. Bryozoans are among the most abundant benthic animals living on the continental shelf around New Zealand. Here we test their utility in palaeodepth estimation by recording the bathymetric distributions of four distinctive endemic species—*Cinctipora elegans*, *Attinopora zealandica*, *Diaperoecia purpurascens* and *Celleporaria emancipata*—all of which are commonly found in the Neogene of New Zealand. A survey of the extensive collections of the New Zealand Oceanographic Institute, comprising more than 9,000 benthic stations, revealed very wide bathymetric ranges: 17-914 m for *C. elegans*, 35-1156 m for *A. zealandica*, 0-1156 m for *D. purpurascens*, and 68-690 m for *C. emancipata*. There is little scope therefore for applying these four bryozoan species in palaeodepth estimation. More general problems in using azooxanthellate benthic animals to infer depositional depth are highlighted.



The first Silurian chasmataspid (Chelicerata: Chasmataspidida) from Lesmahagow, Scotland, and phylogenetic implications for eurypterids

O. Erik Tetlie and Simon J. Braddy

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

<o.e.tetlie@bristol.ac.uk> <s.j.braddy@bristol.ac.uk>

A new chasmataspid (Chelicerata: Chasmataspidida) is described from the Early Silurian (Late Llandovery–Early Wenlock) of Lesmahagow, Scotland. It is distinguished from related forms by the low tapering ratio of the postabdomen and a heart-shaped metastoma. It is the first Silurian chasmataspid to be described from the fossil record and bridges some of the morphological gap between the Ordovician Chasmataspididae and the Devonian Diploaspidae, and supports a monophyletic Chasmataspidida. Ventral prosomal and opisthosomal structures are described, revealing pediform prosomal appendages, a very eurypterid-like heart-shaped metastoma, a genital appendage and a three-segmented genital operculum. Chasmataspids are regarded as a primitive sister group to the eurypterids; the three-segmented genital operculum of *Dolichopterus*, and *Stylonurina* are considered plesiomorphic within Eurypterida, while the two-segmented genital operculum, with deltoid plates, of Eurypterina is considered apomorphic.

Biodiversity and climate change in Antarctic Palaeogene floras

Anne-Marie Tosolini¹, Jane Francis¹ and David Cantrill²

¹ Department of Earth Sciences, University of Leeds, Leeds LS2 9JT, UK

² British Antarctic Survey (now Swedish Museum of Natural History)

The Cenozoic was a critical period in Earth's climatic history, during which greenhouse climates of the early Palaeogene switched to the icehouse climates of today. However, as yet we know little about terrestrial environments and vegetation response at high latitudes during this time.

Some of the best preserved plant fossils of Palaeocene to Eocene age in the Southern Hemisphere were collected from Seymour Island, Antarctic Peninsula. Thirty six angiosperm leaf types have been identified, along with pteridophytes (ferns), and podocarp and araucarian conifers. Plants with affinities to living families typical of cool-warm temperate (e.g. Nothofagaceae, Proteaceae) and sub-tropical (e.g. Lauraceae, Sterculiaceae) vegetation dominate the assemblage. Quantitative analysis of these angiosperm leaves provides a mean annual temperature of $13.5 \pm 0.7^\circ\text{C}$ for the late Palaeocene. This warm climate was able to sustain large forests, even at such high latitudes. Younger Eocene floras show decreasing diversity and increased dominance by *Nothofagus* trees as a response to cooler, more seasonal climates (mean annual temperature 10.8°C).



A chitinozoan study in the type area of the Ashgill Series, Cumbria, UK: preliminary results

Thijs Vandenbroucke¹, Barrie Rickards² and Jacques Verniers¹

¹ Research Unit Palaeontology, Ghent University, Krijgslaan 281 / S 8, 9000 Ghent, Belgium

<Thijs.vandenbroucke@rug.ac.be> <Jacques.verniers@rug.ac.be>

² Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ, UK <rbr1000@esc.cam.ac.uk>

In a recent study, Rickards (in press) has shown that the Rawtheyan Stage of the type Ashgill Series, Howgill Fells, Cautley District, is of *linearis* graptolite Biozone age, implying that the base of the Ashgill, in graptolitic terms, begins at least two graptolite zones earlier than previously supposed. A dozen samples, taken from the graptolite slabs, all originating from Ingham's (1966) zone five, six and seven within the Rawtheyan part of the Cautley Mudstone Formation, are investigated for their chitinozoan content. They yield diverse assemblages of moderately well preserved chitinozoans, including index species described before in other places on the Avalonia and Baltica palaeocontinents (e.g. *Lagenochitina baltica* and *Conochitina rugata*) as well as new species. Based on these preliminary but encouraging results, sixty more samples have been collected this summer from the upper Onnian to the lower Silurian strata from the Westerdale, Taythes and Murthwaite Inliers. They are currently being investigated, in order to produce a consistent chitinozoan biozonation in this stratigraphically important area, tied to the revised graptolite data.

Ingham, J.K. 1966. The Ordovician Rocks in the Cautley and Dent Districts of Westmoreland and Yorkshire. *Proceedings of the Yorkshire Geological Society*, **35**, 455-504.

Rickards, R.B. In press. The graptolitic age of the Type Ashgill Series (Ordovician), Cumbria, U.K. *Proceedings of the Yorkshire Geological Society*.

The extinction of *Morozovella* and calibration of some Middle and Late Eocene planktonic foraminifera bioevents to an astronomical time-scale

Bridget S. Wade

Department of Geology and Geophysics, University of Edinburgh, Grant Institute, West Mains Road, Edinburgh EH9 3JW <bwade@glg.ed.ac.uk>

New and existing planktonic foraminiferal biostratigraphic events of the late middle Eocene have been examined with a sampling resolution of ~3 kyr. These have been calibrated to an astronomical time-scale to define accurately the timing of key biostratigraphic events, particularly the extinction of *Morozovella spinulosa*, which is a distinct biomarker for late middle Eocene sediments. The final large acarininids (*Acarinina praetopilensis*) terminate 8 kyr prior to the extinction of *Morozovella spinulosa* and dwarfed acarininids continue in the smaller size fractions (<125 µm) until 36.43 Ma.

High-resolution stable isotopic analyses ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$) have been conducted on planktonic foraminifera from the western North Atlantic, to reconstruct sea surface temperatures and the structure of the thermocline around this major biotic turnover. Whilst the extinction of

Morozovella spp. and *Acarinina praetopilensis* occur during a long-term cooling trend, there is no major palaeoceanographic event associated with the extinction that can be deduced from stable isotopic analyses alone. It is concluded that the extinction of *Morozovella* spp. and the decline in the acarininid lineage was probably related to nutrification of surface waters and / or symbiont elimination.

A new gastropod fauna from the Early Triassic of Oman

James R. Wheeley¹ and Richard J. Twitchett²

¹ Department of Earth Sciences, Cardiff University, PO Box 914, Cardiff CF10 3YE, UK <jameswheeley@hotmail.com>

² Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queens Road, Bristol BS1 1RJ, UK <R.J.Twitchett@bristol.ac.uk>

The Griesbachian (Lower Triassic) Al Jil Formation of Oman has yielded a new, rich and partially silicified gastropod fauna. These gastropods form part of a larger shallow marine assemblage, which is the only silicified Griesbachian assemblage known to date. A large proportion (69%) of Permian-Triassic gastropods are Lazarus taxa in the Griesbachian, which Erwin (1996) attributed to the absence of silicified faunas at this time. The discovery of the Oman assemblage allows us to test Erwin's hypothesis: does it contain any of the missing Lazarus taxa as predicted by the silicification hypothesis?

Ten gastropod genera are present in the fauna: *Ananias*, *Bellerophon*, *Chartronella*, *Coelostylina*, *Naticopsis*, *Omphaloptychia*, *Soleniscus*, *Strobeus*, *Worthenia*, and *Zygopleura*. It is the most diverse Griesbachian gastropod assemblage known. Two of these (*Ananias* and *Soleniscus*) were previously unknown as fossils in the Griesbachian (i.e. they represent some of the missing Lazarus taxa). Thus, while some Lazarus taxa are present, as predicted, the majority of the assemblage is composed of "typical" Griesbachian forms. There are several possible reasons for this. Our analysis raises to fifteen the total number of Griesbachian gastropod genera that are represented by actual fossils. Twenty-seven Lazarus genera remain to be found in this interval.

Stromatolite morphology controlled by flow regime: an abiogenic model

Lucy Wilson¹ and Martin Brasier²

¹ Department of Earth Sciences, University of Cambridge, Cambridge CB2 3EQ, UK

² Department of Earth Sciences, University of Oxford, Oxford OX1 3PR, UK

The nature of stromatolite morphogenesis is one of the current challenges to Archaeal palaeobiology. The debate is fundamental to our understanding of the evolution of early life since stromatolites at present provide the oldest evidence for life on Earth. The question is whether stromatolites inherently require a biological community in order to form, or if they can be generated by physical and chemical processes alone. If it can be shown that the existence of stromatolites does not oblige the existence of life then a serious review of our current stance on early life is in order. The issue also has great implications for the search for the evidence of life on Mars.

New experimental techniques, using spray paint as a suitable analogue to the sedimentary environment, have been applied to the problem in order to enhance our understanding of the generation of stromatolite morphologies. Stromatolitic fabrics were successfully produced and found to occur in zones linked to different flow regimes. A new model incorporating the effects of flow regime and viscosity governed by the Mullins-Sekerka Instability is proposed and, although it does not exclude the interaction of microbial organisms in the construction of stromatolite morphologies, it discards the necessity for a biological input therefore placing doubt on the biological nature of many ancient stromatolites, and calls into question our understanding of early life on Earth.

Radiolarians and conodonts from radiolarites in NW-Thailand; witnesses of a 140 my (at least) oceanic realm

Nutthawut Wonganan, Carine Randon and Martial Caridroit
 CNRS-UPRESA 8014 Sciences de la Terre, Université des Sciences et Technologies de Lille, 59655 Villeneuve d'Ascq cedex FRANCE
 <Martial.Caridroit@univ-lille1.fr>

Radiolarians and conodonts remains have been found from several radiolarite sections in NW-Thailand for which Devonian to Triassic ages are proposed. These new datings allow the establishment of a new stratigraphical scheme and indicate that the geological structure is made of a series of large nappes, similar to those observed in an alpine type orogeny. The position of the suture zone between the Shan-Thai and the Indochina continental blocks is discussed. This suture zone is considered to be the continuation of the Changning-Menglian zones in China. Moreover, these radiolarites are the witness of an oceanic realm which must have been largely open in the Early Devonian and cannot have been closed before the Late Triassic. The size and development speed of this part of the Palaeotethys are tackled. This work shows that the study of radiolarites is an important tool for understanding palaeogeography.

Mid-Coniacian Chalk in the Berkshire Downs: a biostratigraphical problem resolved and a sedimentological enigma recognised

M.A. Woods, D.T. Aldiss and I.P. Wilkinson
 British Geological Survey, Keyworth, Nottingham NG12 5GG, UK
 <MAW@bgs.ac.uk> <DTA@bgs.ac.uk> <IPW@bgs.ac.uk>

Lack of preserved macrofossils has long hampered biostratigraphical interpretation of the Mid-Coniacian Upper Chalk succession in the Berkshire Downs. With the recent advent of a more refined lithostratigraphical classification for the Chalk Group, this problem appeared to be resolvable by means of geophysical interpretation. In Sussex, the Mid-Coniacian equates with the Lewes Nodular Chalk / Seaford Chalk boundary, which is coincident with the *M. cortestudinarium* / *M. coranguinum* Zonal boundary, and is also indicated by a marker-bed named Shoreham Marl 2, traceable on geophysical logs.

Integration of new macro- and micropalaeontological data with lithological and geophysical observations demonstrates that, in the Berkshire Downs, the top of the *M. cortestudinarium* Zone

is in soft, non-nodular chalk, above the geophysical signature previously assumed to represent Shoreham Marl 2. This non-nodular chalk facies has been mapped as Seaford Chalk Formation, but it is coeval with the top of the Lewes Nodular Chalk Formation in the Sussex Basin. As the Berkshire Downs region was a shallow marine shelf during Late Turonian to Mid-Coniacian times, nodular chalk would be expected to be better developed here compared to the Sussex Basin. This was the case in the Late Turonian, but, enigmatically, not in the Mid-Coniacian.

The brachiopod genus *Platystrophia*: return to their original concept

Michael A. Zuykov¹ and Edith Fritsch²

¹ Department of Paleontology, St. Petersburg State University, 29, 16 Liniya, 199178 St. Petersburg, Russia <zuykov@riand.spb.su>

² Natural Sciences Collections, The Museum of Berlin, Germany

Platystrophia was established as a genus by King (1850) with *Terebratulites biforatus* Schlotheim (1820) as the type species. The brief original description of *T. biforatus* was based on a single specimen which was not illustrated and was lost by the twentieth century. The type area was determined as south of France. Thus the species name *T. biforatus* can be applied to spirifer-looking taxon from the Palaeozoic or Mesozoic of France, where however there is no indication of the occurrence of *Platystrophia* (*sensu* King). Taxonomic confusion accompanying the name of *T. biforatus* was initiated by Buch (1837), who supposed Baltic “origin” for this species. Consequently, the genus *Platystrophia* is still valid but represents *nomen dubium*. However, the present accepted concept of *Platystrophia* embraces a number of species forming a distinct morphological group. Thus the generic name *Platystrophia* could be saved, but only for the Baltoscandian taxa, as it was proposed originally by King. In particular the type species of the genus can be replaced by *Platystrophia costata* (Pander, 1830) from the late Arenig of St. Petersburg region. The majority of the Late Ordovician North American (Laurentian) species presently referred to *Platystrophia* must be referred to a separate genus because of significant morphological differences from the Baltoscandian taxa.



Overseas Representatives

- Argentina: DR M.O. MANCERNIDO, Division Paleozoologia invertebrados, Facultad de Ciencias Naturales y Museo, Paseo del Bosque, 1900 La Plata.
- Australia: DR K.J. McNAMARA, Western Australian Museum, Francis Street, Perth, Western Australia 6000.
- Canada: PROF RK PICKERILL, Dept of Geology, University of New Brunswick, Fredericton, New Brunswick, Canada E3B 5A3.
- China: DR CHANG MEE-MANN, Institute of Vertebrate Palaeontology and Palaeoanthropology, Academia Sinica, P.O. Box 643, Beijing.
DR RONG JIA-YU, Nanjing Institute of Geology and Palaeontology, Chi-Ming-Ssu, Nanjing.
- France: DR J VANNIER, Centre des Sciences de la Terre, Universite Claude Bernard Lyon 1, 43 Blvd du 11 Novembre 1918, 69622 Villeurbanne, France.
- Germany: PROFESSOR F.T. FÜRSICH, Institut für Paläontologie, Universität, D8700 Würzburg, Pliecherwall 1.
- Iberia: PROFESSOR F. ALVAREZ, Departamento de Geologia, Universidad de Oviedo, C/Jésus Arias de Velasco, s/n. 33005 Oviedo, Spain.
- Japan: DR I. HAYAMI, University Museum, University of Tokyo, Hongo 7-3-1, Tokyo.
- New Zealand: DR R.A. COOPER, New Zealand Geological Survey, P.O. 30368, Lower Hutt.
- Scandinavia: DR R. BROMLEY, Geological Institute, Oster Voldgade 10, 1350 Copenhagen K, Denmark.
- USA: PROFESSOR A.J. ROWELL, Department of Geology, University of Kansas, Lawrence, Kansas 66044.
PROFESSOR N.M. SAVAGE, Department of Geology, University of Oregon, Eugene, Oregon 97403.
PROFESSOR M.A. WILSON, Department of Geology, College of Wooster, Wooster, Ohio 44961.

TAXONOMIC/NOMENCLATURAL DISCLAIMER

This publication is not deemed to be valid for taxonomic/nomenclatural purposes [see Article 8.2 of the International Code of Zoological Nomenclature (4th Edition, 1999)].