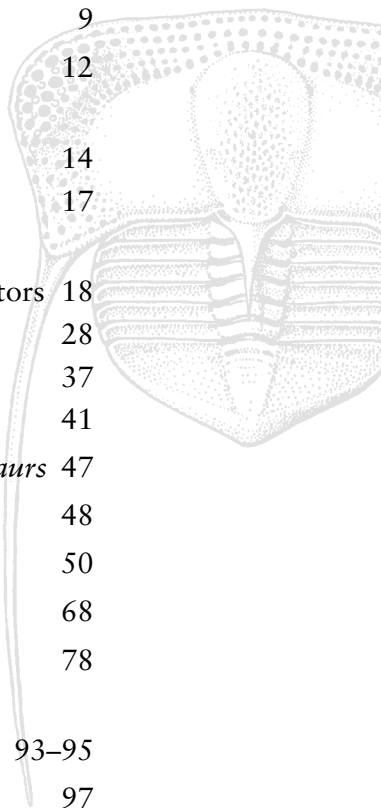


# The Palaeontology Newsletter

55

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Reminder: The deadline for copy for Issue no 56 is 25th June 2004

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

## Association Business

### Awards and Prizes 2003

A number of awards were made at the 47th Annual Meeting of the Association, which was held on 14–17th December 2003, at the Department of Geology, University of Leicester, UK.

#### *President's Award*

The President's Award went to Maria McNamara (University College Dublin) for her presentation *Exceptional preservation of amphibians from the Miocene of NE Spain*.

The President also made special mention of the talk by Bjarte Hannisdal (University of Chicago) entitled *Inferring evolutionary patterns from the fossil record using Bayesian inversion: an application to synthetic stratophenetic data*.

#### *Council Poster Award*

This year there were two recipients of the Council Poster Award: James Wheeley (Cardiff University) for his poster with Lesley Cherns and Paul Wright on *Missing molluscs: captured in the Carboniferous!*, and to Jennifer England (University of Glasgow) for her poster with Maggie Cusack and Martin Lee on *Protein control over calcium carbonate biomineralisation*.

The President also made special mention of Joseph Botting (University of Cambridge) for his poster with Nick Butterfield on Heteractinid and hexactinellid sponges, Frederica Menon (University of Manchester) for her paper with David Penney, Paul Selden and David Martill on a centipede from the Cretaceous of Brazil, and Lucy Wilson (University of Cambridge) for her poster with Paul Ratcliffe on the preservation of a Lower Cambrian hyolith gut.

#### *2003 Hodson Fund*

The 2003 Hodson Fund, awarded for a notable early contribution to the science by a palaeontologist under the age of 35, was this year awarded to Dr Charlotte Jeffery of the University of Liverpool, UK.

Charlotte's PhD, supervised by Andrew Smith, was undertaken jointly at the Natural History Museum and Imperial College, London. She explored echinoid evolution across the Cretaceous-Tertiary boundary. There were 307 species in 72 genera before her analysis, and 129 species in 51 genera afterwards. Charlotte showed that only 35% of heart urchin genera became extinct (half the number suggested by previous studies). This led to publications in *Nature*, *Geology* and *Paleobiology*, and a major volume of *Special Papers in Palaeontology*.

Having completed her PhD in 1997 she moved to the University of Oregon Institute of Marine Biology, as a NSF funded postdoctoral fellow. There she investigated the evolution of larval developmental patterns in temnopleurid echinoids from the Tertiary to the present day, and considered their phylogeny using morphological and molecular data. She has published papers in *Evolution* and in *Molecular Biology and Evolution*.

In 2000 she returned to the UK on a NERC personal research fellowship first in the Department of Geology and Geophysics at the University of Edinburgh, and then in Liverpool. She has been investigating patterns of diversification in the earliest echinoids from Palaeozoic strata, which are rare and poorly resolved in phylogenetic terms.

In 2002 she was appointed to her present position as lecturer of Palaeontology in the Department of Earth and Ocean Sciences at the University of Liverpool.

### Nominations now being sought

#### *Hodson Fund*

Conferred on a palaeontologist who is under the age of 35 and who has made a notable early contribution to the science. Nominated by at least two members of the Association, the application must be supported by an appropriate academic case. Closing date for nominations is **1st September 2004**. Nominations will be considered and a decision made at the October meeting of Council. The award will comprise a fund of £1,000, presented at the Annual Meeting.

#### *Mary Anning Award*

The award is open to all those who are not professionally employed within palaeontology but who have made an outstanding contribution to the subject. Such contributions may range from the compilation of fossil collections, and their care and conservation, to published studies in recognised journals. Nominations should comprise a short statement (up to one page of A4) outlining the candidate's principal achievements. Members putting forward candidates should also be prepared, if requested, to write an illustrated profile in support of their nominee. The deadline for nominations is **1st September 2004**. The award comprises a cash prize plus a framed scroll, and is usually presented at the Annual meeting.

**Nominations for these Awards should be submitted to the Association Secretary, Howard Armstrong <secretary@palass.org>.**

## Important notice for authors intending to submit papers for publication in—

### PALAEONTOLOGY SPECIAL PAPERS IN PALAEONTOLOGY FIELD GUIDES TO FOSSILS FOLD-OUT FOSSILS

The 'Notes for authors' have recently been updated and expanded. Authors should pay close attention to all of the requirements, and act on them accordingly, before submitting their papers for publication in any of these series.

Three changes of particular importance are:

1. From Volume 47, Part 4 (2004) onwards, proofs of papers for *Palaeontology* will be dispatched to authors electronically as Acrobat PDF files. Instructions on procedure, and Offprint Order and Copyright Assignment forms, will be e-mailed with them.
2. Next year the page size of *Palaeontology* and *Special Papers in Palaeontology* will be increased to **sub-A4 (210 × 276 mm) with a print area of 170 × 230 mm in a double-column layout, the width of each column being 82 mm. Authors should prepare their tables, text-figures and plates to suit this new format.**
3. The Appendix of the 'Notes' now refers authors to a Blackwell Publishing website on digital illustration standards.

## New arrangements for access to online version of *Palaeontology*

In future, the electronic version of *Palaeontology* will be hosted by the Blackwell *Synergy* site, rather than by Ingenta (as hitherto). All individual members (Ordinary Members, Retired Members, Student Members) will receive this service free, as at present, but they will have to register with *Synergy*. To do this, please follow the instructions on the next page. After you have successfully registered as a user on Blackwell *Synergy* you will then need to activate your journal access. To do this you will need to use your Last Name and Membership ID number, which will be recognised automatically by matching against the name and number that we have supplied to Blackwell on your behalf. This is the same as those on the database which we use for communication with you.

### Please take careful note of the following:

**Membership ID Number:** This is a four digit number, preceded by an upper case M (you will need to enter both the M and the number, without a space between them). Examples: M2010, M0018, M1814, M0846. This number will henceforth appear on the address labels of publications that we send to you. Please make a note of it, because it may take some time for us to send you reminders if you forget it. Please do not contact Blackwell if you do not know your Membership Number.

**Last Name:** To communicate with you, we use the initials of forenames, followed by the Last Name. These appear on the address labels of the Newsletter and of parts of *Palaeontology*. This information was initially supplied by yourselves; we may not have all your initials and there may even be some spelling mistakes that have arisen from legibility problems. Please enter your last name as it appears on the labels. If (as in a few cases) we use forenames rather than initials on the address labels, then your Last Name is the final name to appear on the first line.

### How to Register with Synergy:

#### Step One: Register or Log In:

**Either: If you have never used Blackwell Synergy, please register as a user:**

1. Go to <<http://www.blackwell-synergy.com/>>.
2. Select 'Register' from the tabs at the top of the screen.
3. Complete the registration page, noting your username and password for later.
4. Your name will now appear at the top of the page and you can proceed to Step Two of these instructions below.

**Or: If you already have a Blackwell Synergy Account, please log in:**

1. Log in at <<http://www.blackwell-synergy.com/>> with your username and password.
2. Your name will now appear at the top of the page and you can proceed to Step Two:

#### Step Two: Activating your journal access:

1. Once successfully logged in, select 'My Synergy' from the tabs at the top of the screen.
2. In the Offer Code box, enter the Offer Code **PalAss** and click 'Continue'.
3. In the Last Name box, enter your last name exactly as it appears on your address labels.
4. In the Member ID box, enter the number exactly as it appears on your address labels including the M at the beginning.
5. Click 'Continue'.
6. Your subscriptions will now be listed on the Journals tab. You can access your journal from here or directly from the *Synergy* homepage.

Next time you wish to view the journals simply log in and select *Palaeontology* from the list. If you have any technical queries or problems with registration, please use the help links on the website or E-Mail <[OnlineMembership@Blackwellpublishing.com](mailto:OnlineMembership@Blackwellpublishing.com)> rather than contacting the Association, who have no technical advice to offer.



## *PalAss vs. Paxman: a date for your diaries*

Late last year, Granada Television invited the Palaeontological Association to enter a team for the 2004 series of *University Challenge: The Professionals*. Seeing it as an opportunity to raise further the profile of PalAss, the offer was accepted, and Tim Palmer given the responsibility of forming a quartet. Almost without possibility of appeal, Tim was also made team captain, and using selection criteria as obscure and mysterious as the builders of the Pyramids, Richard Fortey, Norm MacLeod and I were chosen as his underlings. Our first task was to convene in London for an interview with the show's producers.

Along with other wannabe contestants from the British Library and the Royal Society of Literature, we were led up to a room on the 18th floor of the LWT building and interrogated over why we wanted to be on the show. 'Because you asked us to apply,' was Tim's perfectly logical response, although this appeared to baffle the panel somewhat. Clearly they weren't used to honest, non-sycophantic answers. Our punishment was to be put through an exam, with 40 questions on topics as diverse as Italian sausages, lichen, and the cartoon super-hero Bananaman. I didn't come out of it filled with optimism and, when the date on which we'd be told whether we'd made it onto the televised rounds came and went, resigned myself to the disappointment of failure. Our pitiful knowledge of Mediterranean meats had let us down.

But then Tim sent an e-mail informing us *we were on*. Granada had obviously decided that University Challenge needed palaeontologists. We weren't so daft after all. Then they told us we had to spend a day wandering round in the field, being filmed doing whatever it was they thought palaeontologists did, and it seemed maybe we were. Especially when this was coupled with the prospect of an evening being grilled by Jeremy Paxman in front of a studio audience.

The show is due to be broadcast on BBC2 some time in July or August, but if you can't wait until then to find out what happened, there will be a full and incriminating report in the next edition of the Newsletter. Unless of course we get thrashed, in which case you'll hear nothing from us ever again.

**Liam Herringshaw**  
<lgh865@hotmail.com>

## *IGCP Project No. 469 – Variscan terrestrial Biotas and Palaeoenvironments*

This project is investigating changes in tropical wetland habitats during the late Westphalian and early Stephanian Epochs, focusing particularly on the Variscan and Appalachian Forelands and adjacent Mountains, and the Eastern and Western Interior Coalfields of North America. The aim is to document the decline and eventual virtual extinction of these tropical habitats, which had resulted from uplift and drainage of the wetlands following Variscan tectonic activity. The collapse of this habitat removed a major carbon sink and is thus likely to have had a global environmental impact.

The project will integrate four principal data-sets from across the Variscan area:

1. *Sedimentology*. This will focus particularly on changes in drainage patterns and the distribution of climatically sensitive deposits (coals, red-beds, etc). Subsidence patterns in the different basins will also be investigated.
2. *Coal petrology*. Coal petrology will be used to characterize hydrological types of ancient mires and consequently to interpret possible controls (climatic or tectonic).
3. *Floras*. Macrofloral changes will be examined to determine chronological and geographical changes in the clastic substrate vegetation. Palynology of the coals will be studied to identify changes in the back swamp (peat forming) communities. Palynology of the clastic deposits will be used to identify overall changes in the wetland vegetation.
4. *Faunas*. The distribution of terrestrial invertebrate and (where available) vertebrate faunas will be investigated to determine changing biogeographical patterns.

The project will operate around a series of meetings to be held in various centres across the study area. The inaugural meeting was held in August 2003 in Utrecht, as part of the International Congress on Carboniferous and Permian Stratigraphy. The next meeting will be in April 2004, in Sofia. Other planned meetings are in Bucharest (2005) and Prague (2006). A Newsletter is also available (copies from the Project Administrator – <helen.fraser@nmgw.ac.uk>).

There are four Regional Coordinators of the project:

- North America – Prof. Erwin Zодrow <erwin\_zodrow@ucsb.ns.ca>
- Western Europe – Prof. Barry Thomas <bat@aber.ac.uk>
- Central Europe – Dr Stanislav Oplustil <oplustil@mail.natur.cuni.cz>
- Eastern Europe – Prof. Yanaki Tenchov <tadi@geology.bas.bg>

The overall project leader is Dr Christopher Cleal <chris.cleal@nmgw.ac.uk>. Anyone interested in participating in the project should contact the relevant Regional Coordinator.

### **Dr Christopher Cleal**

*Department of Biodiversity & Systematic Biology, National Museums & Galleries of Wales, Cathays Park, Cardiff CF10 3NP, UK*

## *Santana fish go back to Brazil*

Replica casts of two historically and scientifically important fossil fish from the Lower Cretaceous Santana Formation were recently presented to the government department overseeing palaeontological research in Ceará, northeast Brazil, by John Nudds (University of Manchester) and David Martill (University of Portsmouth). The original specimens had been collected in 1838 by Glaswegian botanist George Gardner, and were used by Agassiz as syntypes for his species *Vinctifer comptoni* and *Notelops brama*. Following a lead from Dr Jane Washington-Evans these specimens were re-discovered last year by John Nudds in the collections of Manchester University Museum, where they had been "lost" for over 150 years.

The photograph (by Bob Loveridge) shows John Nudds and Dave Martill presenting the specimens to Dr Artur Andrade (centre), Head of the DNPM, in the Museum of the Centro de Pesquisas Paleontológicas do Chapada do Araripe, Crato, Brazil. The casts had been expertly prepared by Lorraine Cornish and her team in the London Natural History Museum's Conservation Department.

The British team was in Brazil in January 2004 continuing its collaborative work with Dr Paulo Brito (UERJ) on the palaeontology of the Crato and Santana formations. Should anyone wish to visit the Chapada do Araripe to see these remarkable fossil Konservat Lagerstätte first hand they should contact Dr Artur Andrade at <[dnpmcpca@netcariri.com.br](mailto:dnpmcpca@netcariri.com.br)>.



# Progressive Palaeontology 2004

CARDIFF

9th and 10th June 2004

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

Progressive Palaeontology is a conference for postgraduate research students who wish to present their results at any stage of their research.

All aspects of palaeontology welcome.

One day of oral and poster presentations.

Free fieldtrip to the Glamorgan Heritage Coast.

Exciting social events including a reception at the National Museum and Gallery, Cardiff.

Convenors: James Wheeley, Susannah Moore, Susan Hammond and Christian Baars.

For further information please visit

<<http://www.earth.cardiff.ac.uk/news/conferences.shtml>>

Or contact James <[WheeleyJR@cardiff.ac.uk](mailto:WheeleyJR@cardiff.ac.uk)> or

Susannah <[MooreS@cardiff.ac.uk](mailto:MooreS@cardiff.ac.uk)>

School of Earth, Ocean and Planetary Sciences

Cardiff University

Main Building

Park Place

Cardiff

CF10 3YE

## ASSOCIATION MEETINGS



### 48th Annual Meeting of the Palaeontological Association

Lille, France 17 – 20 December 2004

The 48th Annual Meeting of the Palaeontological Association will be held in the Congress Centre of the Université des Sciences et Technologies de Lille (USTL), on its campus at Villeneuve d'Ascq.

The opening session with a seminar on Palaeobiogeography will be held on Friday afternoon, 17th December, in the lecture hall of the Beaux Arts Museum in the centre of Lille, followed by the Annual Address. In the evening the Icebreaker Party will be held in the Natural History Museum of Lille, in the heart of the *Capitale Européenne de la Culture 2004* <<http://www.lille2004.fr/>>.

The technical sessions will consist of two full days of talks in the main lecture hall of the Congress Centre at Villeneuve d'Ascq on Saturday 18th and Sunday 19th December, with poster sessions in an adjoining lecture hall. Technical sessions are open to all aspects of palaeontology. No parallel sessions are organised, and all talks will be scheduled for 15 minutes with a further five minutes for discussion. It is thus possible that some proposed oral contributions will have to be rescheduled as posters.

On Monday 20th December, one or two geological excursions will be organised. Further information will be available soon.

After Copenhagen in 2001, the PalAss meets again outside Britain in the city of Lille <<http://www.mairie-lille.fr/>>, which can be reached easily from London by Eurostar <<http://www.eurostar.com/>> in less than two hours. Tickets at reduced prices are available if you book some weeks in advance. Lille can also be reached easily from Paris and its airport Charles de Gaulle (about 1 hour) and from Brussels (about 40 minutes) by TGV high speed trains.

The events of Friday 17th December will take place in the centre of Lille. The technical sessions on Saturday and Sunday are scheduled to take place on the campus of the University at Villeneuve d'Ascq, which can easily be reached by the underground 'Metro' in about 15 minutes from the city centre.

Accommodation will be organised in IBIS hotels around the Congress Centre at Villeneuve d'Ascq and in the city centre. Prices should be around £25 for B&B in double (twin bed) rooms and around £45 in single rooms. Accommodation for students and participants from Central and Eastern Europe is available at a reduced rate of about £20 for B&B in a hotel near the Congress Centre. Participants are free to book alternative accommodation at a wide range of prices. Please note that the strict deadline for reservation of accommodation through the organisers is 10th September. After this date, accommodation must be arranged by the participants themselves. Please note that rooms are likely to be fully booked out fairly early, because of Lille being the Cultural Capital of Europe in 2004 and because of the Christmas markets.

...continued overleaf

Intending contributors should forward an abstract, preferably by e-mail, of not more than 200 words to the local secretary <[Lille2004@palass.org](mailto:Lille2004@palass.org)> before 10th September. The format of abstracts should follow the style adopted in previous years, which you can find in the Association's Newsletter and also on the Association's website <[www.palass.org](http://www.palass.org)>. Please also indicate if your abstract is for an oral or a poster presentation. If too many proposals for oral presentations arrive, those presenters who have not spoken in previous year(s) will be given priority. Presenters under the age of 30 on 18th December who are members of the Association and wish to be considered for the President's awards for best talk or best poster should inform the local secretary when submitting their abstracts.

Special group meetings before or after the meeting may also be arranged.

Completed booking forms together with full payment should reach the local secretary before **10th September**.

**The deadline for submission of abstracts of 200 words or less is 10th September.**

Further, continuously updated, information will be available from the Association's website <[www.palass.org](http://www.palass.org)>.

**Thomas Servais (chair), Alain Blieck and the organising team.**

<[Thomas.Servais@univ-lille1.fr](mailto:Thomas.Servais@univ-lille1.fr)>



### Lyell Meeting 2005: Applied Phylogeny

London 9 February 2005

The 2005 Geological Society of London Lyell Meeting, sponsored by the Joint Committee for Palaeontology, is to be organised by The Micropalaeontology Society (Joint Convenors Haydon Bailey & John Gregory). This prestigious one-day meeting, to be held at Burlington House, London is currently being planned for 9th February 2005 and this is the first call for papers on the theme of 'Applied Phylogeny'. It is intended that the meeting will comprise three sessions, arranged stratigraphically (Palaeozoic, Mesozoic and Tertiary), each session with an invited keynote speaker, with the opportunity to discuss a complete range of macrofossil and microfossil subject areas within the proposed theme.

Contributors are asked to consider a single phylogenetic lineage and to pursue its development and application, both stratigraphically, and to any other area of applied usage. It is intended to publish the proceedings of the meeting at the earliest possible opportunity as a Special Publication of the Geological Society (author's notes will be distributed prior to the meeting).

Proposed titles and abstracts should be sent to Haydon Bailey either via e-mail, or to the address below, as soon as possible so that a complete programme can be drawn up. Further details of this meeting will be made available once an initial programme has been established. Details will also be posted on TMS website at <<http://www.tmsoc.org/>>.

Haydon Bailey (Network Stratigraphic Consulting Ltd, Unit 60, The Enterprise Centre, Cranborne Road, Potters Bar, Hertfordshire <[haydonbailey@btconnect.com](mailto:haydonbailey@btconnect.com)>) and John Gregory (Kronos Consulting, 33 Royston Road, St Albans, Hertfordshire AL1 5NF <[john@jgregory.demon.co.uk](mailto:john@jgregory.demon.co.uk)>)

# Association Diary

2004	June	9–10	<b>Progressive Palaeontology 2004</b> Organisers: James Wheeley, Susannah Moore Location: School of Earth Sciences, University of Cardiff, UK. Contact: <WheeleyJR@cardiff.ac.uk>, <MooreS@cardiff.ac.uk>	2005	January	<b>Syposium on Body Plan Regionalization</b> Organisers: Nigel Hughes, David Jacobs Location: San Diego, California Contact: <nigel.hughes@ucr.edu>, <djacobs@ucla.edu>
		25	<b>Copy deadline</b> for Newsletter 56		February	9 <b>Lyell Meeting 2005: Applied Phylogeny</b> Organisers: Haydon Bailey & John Gregory Location: The Geological Society, Burlington House, Piccadilly, London, UK. Contact: <haydonbailey@btconnect.com>
	August		<b>Stem groups and the establishment of vertebrate bodyplans</b> (PA symposium) Organisers: Philip Donoghue (Bristol, UK) and Mark Purnell (Leicester, UK) Location: 7th International Congress on Vertebrate Morphology, Florida State University, Boca Raton, Florida, USA. Contact: <p.c.j.donoghue@bham.ac.uk>, <map2@le.ac.uk>		11	<b>Copy deadline</b> for Newsletter 58
	September	6–10	<b>Fossils, fakes and forgeries</b> Organiser: Mark Purnell (Leicester, UK) Location: BA Festival of Science, University of Exeter, UK Contact: <map2@le.ac.uk>		May	20 <b>Copy deadline</b> for Newsletter 59
	October	8	<b>Copy deadline</b> for Newsletter 57		October	14 <b>Copy deadline</b> for Newsletter 60
	December	17–20	<b>2004 Annual Meeting and AGM</b> Organisers: Thomas Servais (Lille, France) Location: University of Lille, France. Contact: <lille2004@palass.org>		December	18–21 <b>2005 Annual Meeting</b> Organiser: Derek Siveter (Oxford, UK) Location: University of Oxford, UK. Contact: <oxford2005@palass.org>
				2006	July	<b>9th Symposium on Mesozoic Terrestrial Ecosystems</b> Organiser: Susan Evans (UCL, UK) Location: University of Cambridge, UK Contact: <ucgasue@ucl.ac.uk>.
					December	17–20 <b>Annual Meeting</b> Organiser: Charles Wellman (Sheffield, UK) Location: University of Sheffield, UK Contact: <Sheffield2006@palass.org>
				2007	December	<b>Annual Meeting</b> Organiser: Maggie Cusack (Glasgow, UK) Location: University of Glasgow, UK

— OBITUARY —

**Emeritus Professor Leslie Rowsell Moore,  
DSc, PhD, FGS  
1912-2003**

Leslie Moore, former Sorby Professor and Head of the Department of Geology of the University of Sheffield, was a founder member of the Palaeontological Association.

The son of a miner in the Somerset Coalfield, Leslie grew up in the small mining and market town of Midsomer Norton. He was encouraged by his family to obtain a good education, and after winning a scholarship to the University of Bristol, Leslie decided to read geology with physics. At Bristol Leslie was awarded a 1st class honours degree in Geology (1934), a Ph.D. (1936) and later a D.Sc. (1948).



At Bristol Leslie came under the guidance of Professor Arthur Trueman, the influential Carboniferous stratigrapher and coalfield geologist. This prompted Leslie to remain in Bristol following his undergraduate studies, to undertake Ph.D. research on the structure, stratigraphy and economic geology of the Bristol and Somerset Coalfields, with Trueman as his mentor. Subsequently much of this research was published (e.g. Moore and Trueman 1937). Importantly, it was during this time that Leslie began to realise and explore the value of fossil faunal and floral evidence for regional correlation of the Coal Measures.

Leslie's first job was in teaching. However, he was soon appointed as an Assistant Lecturer in Geology at University College Cardiff in the University of Wales, where his research was expanded to embrace the South Wales Coalfield. It was during this period that he commenced his research on those aspects of palaeobotany that were subsequently to give impetus to the science of palynology. He noted that spores he recovered from the maceration of Carboniferous fructifications displayed a wide range of morphological variations, which he suggested were representative of a sequence of stages towards maturity, further noting that the same developmental patterns could be observed in fructifications from different plant groups (Moore 1946). These observations had implications for the morphological classifications of fossil spores which were then emerging, and resulted in the award of the Lyell Fund of the Geological Society in 1947. At this time Leslie moved to more senior positions, first in the University of Glasgow and then to a Readership at the University of Bristol, before accepting the invitation to become the Sorby Professor of Geology at the University of Sheffield in 1949.

On accepting the Sheffield appointment, Leslie was charged with the task of promoting the growth of the science at the university, a challenge that was to occupy much of the remainder of his working life. He oversaw expansion of the Department of Geology to the extent that by the late 1960s – early 1970s it was one of the largest in Great Britain. An excellent teacher, he always taught the major part of the first year courses, frequently lecturing to classes of more than 100, arousing interest and enthusiasm for geology from many generations of students. The heavy administrative burden of running a large university department for 28 years inevitably restricted the amount of time available for personal research, but it was never able to suppress Leslie Moore's commitment and enthusiasm, and he was able to establish a thriving research school.

Palaeontology was always an essential part of any course in Sheffield. The realisation of the potential that micropalaeontology and palynology might offer to stratigraphy led him to initiate development of a school of research in this area, which was later to acquire a global reputation, particularly in the field of palynology. In 1950 Leslie Moore appointed Charles Downie to the staff, and supervised his research on the Jurassic Kimmeridge Clay. Shortly afterwards he strengthened the team with the appointments of Peter Sylvester-Bradley, Roger Neves and Herbert Sullivan. Despite the ever-expanding demands on his time, he managed to remain active in personal research. Initially he concentrated on developing palynology in Sheffield. Since the inception of the Sheffield Palynology School, approximately 100 Ph.D.s have been awarded in this field, and over 200 students have graduated with the World famous M.Sc. in Palynology that was initiated by Leslie in the mid 1960s. In the latter part of his career Leslie turned his interests to micropalaeobiology, particularly to seeking evidence of fungal and bacterial attack on organic matter in sedimentary rocks. Relatively few of these studies were completed before his retirement, but he did document evidence supporting probable fungal and bacterial attack on Carboniferous miospores in the Palaeontological Association's journal (Moore 1963).

Leslie Moore's legacy to geological science might well be considered to be his impact in its organisation. He was a strong supporter of the Palaeontological Association from its inception, and in 1957 had the pleasure of hosting in Sheffield the first of its now traditional Annual Meetings. He was also influential in the establishment of the *Commission Internationale de Microflore du Paleozoique (CIMP)* as a component body of the International Carboniferous Congress, and hosted CIMP meetings in Sheffield on numerous occasions. In the late 1960s he was approached by the Geological Society of London to investigate the possibility of establishing a Micropalaeontological Working Group within the Society's framework. Following extensive discussions with all interested parties, including the Palaeontological Association, he recommended the establishment of a separate group that ultimately was to become the British Micropalaeontological Society (now The Micropalaeontological Society). He served as its first President (1970–1972). Leslie's concerns over the teaching of geology at all levels in education were reflected in his commitment to the establishment of the Association of Teachers of Geology.

Leslie retired in 1977 to the village of Curbar in the Derbyshire Peak District, from where he kept in touch with many of his former Sheffield students. Sadly his wife Peggy died shortly after his retirement, a blow which hurt Leslie deeply. With the progressive loss of mobility over the years, he decided that he would move to Birmingham to be closer to his son. He died peacefully on 13th November 2003 at the age of 91.



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- MOORE, L.R. and TRUEMAN, A.E. 1937. The Coal Measures of Bristol and Somerset. *Quarterly Journal of the Geological Society of London*, **93**, 195–240.
- MOORE, L.R. 1946. On the spores of some Carboniferous plants: their development. *Quarterly Journal of the Geological Society of London*, **102**, 251–298.
- MOORE, L.R. 1963. Microbiological colonization and attack on some Carboniferous miospores. *Palaeontology*, **6**, 349–372.

## —OBITUARY—

### Professor Pierre Hupé (1907–2003)

As an inspiring and devoted instructor (and later Professor) in Palaeontology in the University of Paris at the Sorbonne, Hupé first made known in 1953 the abundant and remarkable Cambrian trilobites of Morocco. This work was undertaken by invitation from the Service Géologique du Maroc (S.G.M.), and based on their great collections and his own field investigations. Between 1945 and 1955 he also published a series of shorter papers on trilobites, describing and discussing the panderian opening, macropleurial segments and other morphological features, as well as segmentation of the body, aspects of growth and the influence of paedomorphism. Hupé's extraordinary wide acquaintance with the literature was combined with these studies to propose a revised classification of trilobites given in volume 3 of the *Traite de Paléontologie* (1953) and in his longer account in *Annales de Paléontologie* (1954–55). At the 1960 Geological Congress in Copenhagen he put forward his views on the zonation of the Moroccan Lower Cambrian and its correlation with sequences in the Iberian region, Scandinavia and Siberia. This work was an astonishing achievement and its international significance was recognized by the U.S. National Academy of Science in the award of the C.D. Walcott Medal in 1957. The hoped-for further collaboration between Professor Hupé and his students with S.G.M. in Cambrian Studies was halted by the war of independence.



I had the privilege in 1953 of meeting Professor Hupé at the Sorbonne, and of seeing and discussing some of the specimens of Moroccan trilobites. In the early 1960s, when staying at a small hotel in the Montagne Noire district, I looked across the dining room to see a bronzed and very fit-looking Pierre Hupé. He told me he was mapping and studying tectonic problems in the area – a return to his original, early interest in tectonics. He was fond of the region, and retired to live there. His major contribution to the palaeontology of trilobites, particularly to their classification, is evident in the 1959 edition of the *Treatise on Invertebrate Paleontology, Trilobita*, and in the many references to his work in the 1997, volume 1, on the *Trilobita* (revised).

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## From our Correspondents

# The hold of hypothetical ancestors and the amazing appeal of annelids as archetypes

"In the beginning, all people lived around a great ironwood tree in the jungle, speaking the same language. One man whose testes were enormously swollen from infection with a parasitic worm spent his time sitting on a branch of the tree, so that he could rest his heavy testes on the ground. Out of curiosity, animals of the jungle came up and sniffed at his testes. Hunters then found the animals easy to kill, and everyone had plenty of food and was happy. Then, one day, a bad man killed a beautiful woman's husband, in order to get the woman for himself. Relatives of the dead husband attacked the murderer, who was defended in turn by his own relatives, until the murderer and his relatives climbed into the ironwood tree to save themselves. The attackers tugged on lianas hanging from one side of the tree, in order to pull the tree's crown down towards the ground and get at their enemies. Finally, the lianas snapped in half, causing the tree to spring back with tremendous force. The murderer and his relatives were hurled out of the tree in many different directions. They landed so far away, in so many different places, that they never found each other again. With time, their languages became more and more divergent. That is why people today speak so many different languages and cannot understand each other, and why it is hard work for hunters to catch animals for food" (Diamond, 2002).

Thus explains an origin myth of the small Sikari tribe of New Guinea the existence of different people living in different places, and all speaking different languages. I thought that this remarkable origin myth would be an apt introduction for a first column in the New Year; I hereby wish all readers a happy and productive 2004! However, it also serves beautifully as an entry into the topic of this essay, namely how we pinpoint the historical origin of diversity in the living world. Although hypothetical ancestors and archetypes in our theories about the evolutionary origins of animal diversity in geological time is the real meat of this essay, I thought that perhaps we can warm up by briefly addressing an analogous question on the shorter and more fully documented time-scale of human cultural history: how do different peoples construct theories about the origins of human diversity?

In his Pulitzer price winning book *On human nature* (1978: 169), Edward O. Wilson calls our "predisposition to religious belief" "an ineradicable part of human nature." Wilson (1998: 286) describes our "religious drive" in more florid prose as being fed by "a great subterranean river of the mind" that "gathers strength from a broad spread of tributary emotions." Aha! The universality of the human drive for religion is convincingly supported by the independent invention and elaboration of complex systems of religious belief by many different peoples at different times, and in many different places around the world. Interestingly, despite the unavoidable idiosyncrasies entailed by such independent origins, a set of remarkable similarities is shared among the many different beliefs. These include sets of rules or

formulae that allow one to attain a higher state of spiritual enlightenment, rites of passage, sacred places, and most important for the current discussion, at the core of each religion one will find creation myths to explain the origin of both the world and the people.

For example, the big ironwood tree in the Sikari origin myth, which provides lodging for the man with the enormously swollen testes, strongly evokes the Tower of Babel from the Bible's book of Genesis. After Noah's flood, the clans of the sons of Noah embarked upon building a city with a large tower that would reach up into the heavens. This would allow the people to make a name for themselves, and protect them from being scattered widely across the world. However, God realized that if man could fulfil this goal, nothing would be impossible for them to achieve. God therefore curtailed man's over-zealous aspirations by confusing the language of the people so that they could no longer understand each other and coordinate their efforts. Then God spread Noah's progeny to all corners of the globe. The New Guinean Sikari tribe, knowing that different peoples lived in different places, speaking different languages and respecting different customs, specifically constructed their origin myth to explain all these otherwise confusing facts. Therefore, despite their strikingly dissimilar imagery, the stories of the Tower of Babel and the ironwood tree fulfil a shared need to explain the origins of human diversity. In contrast, to explain the even more fundamental problem of the origin of the world, a surprising number of peoples invoke exactly the same image: an egg. The world hatches from an egg in the myths of people as diverse as Egyptians, Greeks, Celts, Siberians, Tibetans, and Chinese (Pinto-Correia, 1997).

Now, before you utter a mildly patronizing chuckle about this delightful, but of course hugely naïve New Guinean origin myth, please think twice. Considered superficially, the Sikari origin myth strikes us as just plain silly, and that was reason enough for me to post this origin myth on the message board in our lab a while ago (evoking some mixed feelings...). However, after reading and thinking a bit more, the Sikari origin myth started to make much more sense. We have to realize that it originated in a society and region of the world utterly unlike our own. Given that very unfamiliar context, how strange are the central ingredients of this New Guinean origin myth really? First, before the Europeans colonized this largest island in the Southern hemisphere in the late 19th century (Diamond, 1998), New Guineans were without exception non-literate, and literally living in a Stone Age world. Then, as well as now, the New Guinean jungle is teeming with filarial worms, which are parasitic nematodes that can cause lymphatic filariasis, better known as elephantiasis. It is a widespread and common disease of the tropics world-wide, with around 120 million infected people each year. Mosquitoes transmit the disease and many New Guineans suffer the gruesome symptoms. In males one of the most characteristic symptoms is the pronounced swelling of the scrotum, sometimes to a size large enough to fill a wheelbarrow, caused by clogged up lymphatic vessels. A man with painfully distended testes was therefore certainly not a rare sight in ancient New Guinea.

Second, although people have been living in New Guinea for at least 40,000 years, archaeological evidence of the origin of agriculture dates back only to about 7000 BC. This means that hunter-gathering has long been the dominant mode of life for New Guineans, and in some modern tourist brochures the Sikari people are still called expert crocodile hunters who can catch crocodiles by trapping them with bait. I don't know whether a poor tribesman with elephantiasis is commonly used as bait for the New Guinean hunt, but the concept is less fanciful than it might seem at first glance.

Third, contacts between different families of a tribe, or between different tribes in New Guinea, are not known for their diplomacy, especially not when a woman is at stake. For example, Diamond (1998: 277) describes it as a rather common situation for women of otherwise gentle tribes to have several sequential husbands. Remarkably, the succession of husbands was typically regulated by a sequence of homicides, with each sequential husband murdering the previous one!

Finally, and I don't know how relevant this may be to the Sikari origin myth, bungee jumping was purportedly invented by tribes on Pentecost Island in Vanuatu, which is a group of islands located roughly between New Guinea and Fiji, as a rite of passage into manhood. With lianas tied around their legs, the young man throw themselves from a height. Admittedly, bungee jumping from a tree is not the same as using a tree as a catapult, exactly the reverse in fact, but if nothing else, this indicates that perhaps New Guineans might not have been entirely naïve about different forms of arboreal aerobics.

These facts about New Guinean life at once make the Sikari origin myth much more intelligible, especially when compared with the logical structure underlying certain modern 'religions' that have recently gestated in the womb of Western civilization. Just for the sake of comparison let us have a quick look at scientology. On <[www.scientology.org](http://www.scientology.org)> you can read that "scientology constitutes man's first real application of scientific methodology to spiritual questions." This either sounds too good to be true, or too weird to be workable. And it is, both. For example, to enter the religious order of scientology, members have to sign a "billion year contract" as a vow of dedication to the shared cause. The fact that allegiance to the precepts of scientology apparently has an expiration date, admittedly a very distant one, is not the only peculiarity about this religion. It is only after long-term training that the most devout and experienced scientologists are finally allowed insight into the Holy Grail of their chosen religion, namely scientology's origin myth. But unfortunately, this part of scientology scripture is secret to everybody else inside or outside scientology because "premature exposure could impede spiritual development." That sounds rather mysterious. Luckily, nothing stands in the way of me and my Apple laptop with Internet connection to expose scientology's origin myth, which is child's play in a time when even parts of the secret source code of Microsoft Windows are freely available online. At <[www.clambake.org](http://www.clambake.org)> you can find why "premature exposure" to the secret parts of scientology's scripture can impede people's spiritual development. To lift just a tip of the veil, 75 million years ago the Earth was colonized by people (read: aliens) coming on board of space ships to solve an over-population problem in another part of the galaxy. After arrival on Earth, H-bombs were deployed to kill all invaders, whereupon the alien spirits were collected and imprinted with a false reality, before they were set loose on the Earth. You catch the drift. Although the imagery is strikingly modern compared to the Sikari myth, is it really more believable? I'm not too surprised that people might run away screaming after this revelation. But then again, perhaps it just depends on one's perspective. If you can stomach the pronouncements of scientology's spiritual founder L. Ron Hubbard that he has twice visited Heaven, a trillion years apart, but that on his second visit Heaven looked rather shabby, enclosed by plain wire fencing, then maybe the Earth's colonization story doesn't only sound possible, it sounds positively plausible!

This example about origin myths brings an important universal aspect of human reasoning into sharp focus, the explicit recognition of which is very important to the historical scientist.

Humans are quintessential storytellers, and all good stories have a clear beginning and end point with a continuous story line in between. However, data about the history of human culture and animal evolution are notoriously spotty, and clear beginnings and end points may not be readily identifiable. Nevertheless, to render a meaningful story we feel forced to fill in the factual gaps and assume or invent a beginning and an end point of our narrative. This is where the role of the narrator becomes crucial. For the Sikari tribesmen evidence that other people live in different regions and speak different languages constitutes a natural end point for a story. However, the origin of this situation remains a mystery. Consequently, they constructed an origin myth using logic and imagery familiar to them. By using strikingly dissimilar imagery other groups of people have constructed origin myths with different details. In analogy, when we are forced to construct an historical narrative about the origin of animal diversity, we need the equivalent of an origin myth to serve as a convenient departure point for stories of evolutionary divergence. Because the fossil record rarely reveals the details of the exact origin of a taxon, we embody our ideas about organismic origins in hypothetical ancestors or archetypes. As with the human origin myths, it is here where our influence as a storyteller may be most palpable. It therefore becomes interesting to ask ourselves whether our hypotheses about animal ancestors and archetypes principally reflect our parochial expectations, or certifiable evidence.

Our modern concepts of stem-species and ancestors can be traced back to the notion of archetypes in pre-Darwinian times (I base my statements about ancestors and archetypes mostly on the following works: Desmond, 1982; Hull, 1988; Richards, 1992; Nyhart, 1995; Asma, 1996; Gould, 2002). A prominent originator and disseminator of the notion of archetypes in botany and zoology was that great icon of 19th century German literature and biological science, Johann Wolfgang von Goethe (1749–1832). Apart from coining the word "morphology" (or at least being one of the very first users of the word, which is recorded in Goethe's correspondence with his friend Friedrich Schiller in the late 1790s), and standing at the cradle of the discipline, Goethe was an influential member of the school of *Naturphilosophie*, which can best be understood as the scientific incarnation of German romanticism. Two central intellectual commitments of *Naturphilosophie* were that nature is always in flux, changing in a unidirectional manner, and a belief in the unity of nature and natural laws, which binds the organic and inorganic world together into one seamless whole. In this context Goethe developed an archetypal theory of plant diversity, in which he conceived of an *Urpflanze* or archetypal plant that embodied an abstract Platonic blueprint or generating plan from which all observed angiosperm diversity could be derived. The central element in Goethe's botanical system was the generalized leaf, and he hypothesized that all the lateral outgrowths that we can find along a plant's stem are in fact more or less modified leaves. In zoology Goethe developed a theory of the archetype of the vertebrate skeleton, with the vertebra as a generalized central element. Goethe then attempted to explain the vertebrate skull as a fused series of modified vertebrae. It is important to note that at the core of both Goethe's botanical and zoological systems was a single generalized element, which through modification, could give rise to all observed derived forms. These ideas diffused with modification to England where Richard Owen, the conceptual father of the dinosaur, more fully developed an archetypal theory of the vertebrate skeleton. Owen attempted nothing less than to derive the entire vertebrate skeleton from a single generalized archetypal vertebra.



However, although it is often stated that the archetypal theories of Goethe, Owen, and others such as the French transcendental morphologist Geoffroy Saint-Hilaire, were intended as purely non-material, ideal, unchanging, abstract Platonic archetypes, in the case of at least Goethe this is not strictly true. True to the tenets of *Naturphilosophie* Goethe also tried to convey the importance of change in time for understanding form. Moreover, at some point Goethe was actually convinced that his conception of the archetypal plant had a real material existence on Earth (he did not always hold this view, however), a very non-Platonic notion. Incidentally, that archetypes could have a real material existence is further suggested by Goethe's nomination of granite as the *Urgestein* or archetypal rock.

With his emphasis on the importance of change of form with time, and with the material nature of certain archetypes, Goethe was already getting quite close to our modern evolutionary concept of a real ancestor. The famous note that Darwin scribbled in the margin of his personal copy of Richard Owen's *Nature of limbs*, Owen's 1849 monograph where he presented the full version of his archetypal theory of the vertebrate skeleton, neatly obviates the need to belabour the conceptual transition from imagined archetype to real (however hypothetical) ancestor: "I look at Owen's archetypes as more than idea(l) (Darwin's handwriting has been transcribed in two different ways in my sources), as a real representation as far as the most consummate skill and loftiest generalization can represent the parent form of the Vertebrata." However, irrespective of whether ideal archetypes or real but extinct ancestors are called upon, they can function as effective starting points from which to explain modern day organismic diversity. This heuristic value didn't escape Richard Owen, and using his archetype as a base line he could start to tackle the nature and direction of trends in the fossil record, such as the different degrees of specialization that animals exhibited through time. For example, Owen linked the specialization of horse limbs, with reduction in the number of their toes, to their increasing capacity for fast running. The use of an archetype made Owen's palaeontology a much more useful science than that of his archrival Thomas Henry Huxley, who for a long time was loath to entertain any heuristic notion of an archetype. Not having the benefit of a starting point, Huxley was consequently unable to admit any evidence for fossil specialization well into the 1860s, for example denying that the Eocene three-toed *Palaeotherium* was in any way more generalized than modern horses.

Of course, today biologists and palaeontologists generally accept the existence of real ancestors, and for many workers it is strangely tempting to speculate on the nature of distant ancestors. Modern phylogenetic methods now allow us to make at least logically sound inferences about past life. However, the origin of certain taxa remains hidden, even if we use the latest methods, or the biggest feats of our imagination. Just consider the recent flood of ideas on the nature of Urbilateria, with so far only one unambiguous result: we have absolutely no idea what it might have looked like! Or consider turtles. Recently, the phylogenetic position of these morphologically bizarre animals has been hotly debated. The great difficulty of relating the anatomically unique turtle body plan to any living or extinct group of vertebrates has generated many speculations about their ancestors, with proposals spanning the full panoply of vertebrate architecture, and ranging from frogs to plesiosaurs (Lee, 1995). However, similar to the situation with Urbilateria no consensus appears to be imminent.

In striking contrast, for certain taxa there are long-held and deeply entrenched ideas about the nature of their ancestor. For example, although the Mollusca have a very distinctive body



plan, attempts to derive them from an annelid-like ancestor can be traced back for more than a century, from Lankester (1893) to Ghiselin (1988), and Scheltema (1993). In fact, I know of no other living group of invertebrates that has so often, and for so many different groups of animals, been invoked as a hypothetical ancestor as the annelids. I think that the annelids are absolutely unique in the extent to which they have influenced and/or constrained our thinking about the evolutionary origins of many taxa in all corners of the animal kingdom. Ironically, unwittingly the same fate has befallen both Goethe and the annelids: over-zealous advocates have implicated them in far too many different cradles. Although the many great works of Johann Wolfgang von Goethe have rightly earned him the status of a literary and scientific icon (such a rare combination!), after his death Goethe has been over-used and abused many times in the service of many different ideologies to which he himself did not ascribe. In fact, the obsession to cite Goethe after his death in the service of everything ranging from German National Socialism to fascism has been called a "German disease" by the Dutch Goethe fanatic Boudewijn Büch (2002). Although the poor annelids have not been connected with the origin of anything as pernicious as the Nazis, for a long time they have been pressing an indubitable stamp upon evolutionary theories in invertebrate zoology, as I will illustrate in the final section of this essay.

The best place to start gauging the influence of ancestral annelids is to start local, that is with the origin of the molluscs, which after the dissolution of Cuvier's four *embranchements* that housed the molluscs and annelids in different groups, have always been regarded as somehow closely related to annelids. To get a first impression of the incredible hold of hypothetical ancestors, just consider the conceptual and pictorial stasis of the famous Hypothetical Ancestral Mollusc or HAM, which adorns the pages of so many invertebrate textbooks until right up to the end of the 20th century. Despite many new discoveries in malacology, the HAM in recent textbooks still looks basically identical to Lankester's original conception of the HAM in the late 19th century as a superficially limpet-like gastropod (see figure 2.6 in Bowler, 1996 and fig. 2 in Haszprunar, 1992). When we take one step back in time to the next ancestor in line, we can see that the first thoughts of deriving molluscs from segmented annelids or annelid-like ancestors has its origins in the late 19th century in the work of Berthold Hatschek, with continuing support throughout the 20th century by authorities like Karl Heider and Paul Pelseneer, right up into the molecular era where Michael Ghiselin (1988: 81) concludes that "the molluscs evolved from something like an annelid."

Annelids have been considered to be ideal candidates as ancestors of the arthropods for even longer than the molluscs. The close relationship between annelids and arthropods was first and most famously codified as the Articulata, one of Cuvier's four *embranchements* from the early 19th century. Since then it has been regarded as so commonplace to derive the arthropods from segmented annelid-like ancestors that any dissenting views are a precious oddity (as each other's closest relatives, or more recently sister groups, one could equally well use an arthropod to stand model for the ancestral annelid, but curiously, I think I have never encountered this hypothesis.). In 1876 T.H. Huxley regarded certain polychaete features as "foreshadowing" structures in the Arthropoda. It was with the recent advent of molecular systematics, which separated the annelids and arthropods in two different clades of protostomes, the Lophotrochozoa and Ecdysozoa, that we realized how ingrained our ideas about deriving arthropods from annelids had become. However, molecular data has not



(yet) convinced everybody, and in 2000 the noted malacologist Luitfried von Salvini-Plawen proposed to derive modern annelids, onychophorans, and the arthropods directly from oligochaete-like ancestors.

Others saw annelids as perfect ancestors of a very different, much more distantly related group: the vertebrates. The annelid theory of vertebrate origins was conceived by the fertile mind of Anton Dohrn, founder of the famous Stazione Zoologica in Naples. His hypothesis of the dorso-ventral inversion of the vertebrates has become a textbook example (Romer & Parson, 1986) of transforming seemingly disparate body plans into each other. Dohrn facilitated this dramatic evolutionary transformation by assuming the importance of the principle of change of functions of organs in evolution. For a man who could transform annelid gills into a vertebrate penis, no evolutionary scenario is beyond reason. The English physiologist Walter Gaskell, who in his 1908 book *The origin of vertebrates* traced the ancestry of the vertebrates back to the annelids, envisioned even more bizarre structural transformations. For example, Gaskell envisioned the transformation of the dorsal gut of arthropods (which he considered the direct descendants of the annelids) into the vertebrate brain and spinal cord, so that the brain ventricles in vertebrates should be regarded as the remnants of the arthropod stomach. Unable to defend such views against inevitable criticism, poor old Gaskell lost respect and students. Interestingly, the great polymath Karl Ernst von Baer, who's reputation as a critical thinker is well established, in fact welcomed the idea of the annelid origin of the vertebrates, because he considered the bag-like ascidians as a much less workable starting point (Nübler-Jung & Arendt, 1994).

However, the annelids have recently also been placed at the crib of more encompassing taxa. Gutmann (1981) used a functional-mechanical analysis to conclude that the chordates, hemichordates, and echinoderms must have been derived from a metameric annelid-like ancestor. Christoffersen & Araújo-de-Almeida (1994) used a Hennigian phylogenetic pencil and paper study to argue for the annelid origins of an even broader set of assumed deuterostomes, including phoronids, brachiopods, ectoprocts, hemichordates, echinoderms, chaetognaths, and chordates. Interestingly, rather than just rooting their phylogeny in an annelid-like ancestor, they derived all these taxa from within the polychaete annelids through the intermediate of the pogonophores. Strikingly, a decade later the first author of this paper is now second author on a paper that presents the results of a new phylogenetic analysis (now computerized) (Oliveira-Almeida *et al.*, 2004). The new phylogeny is even more arresting than the first. Not only does the previous conclusion hold up, deriving all those deuterostome phyla from within the polychaetes, but also in addition all the Ecdysozoa are derived from elsewhere in the polychaetes. Their definition of Ecdysozoa is somewhat broader than that currently accepted by most metazoan phylogeneticists, including acanthocephalans, rotifers, gnathostomulids, kinorhynchans, loriciferans, priapulids, gastrotrichs, nematodes, nematomorphs, tardigrades, onychophorans, arthropods, and pentastomids. With their analysis Oliveira-Almeida *et al.* (2004) manage to derive most bilaterian phyla directly from within the annelids. The well-known zoologist Claus Nielsen (2003) recently proposed a somewhat similar hypothesis. In an attempt to reconcile the conflicting results of available molecular and morphological phylogenetic analyses of the Metazoa, Nielsen proposed the Ecdysozoa as the sister group of the Annelida. Although Nielsen does not explicitly state the evolution of the ecdysozoans from an annelid-like ancestor, the optimisation of characters on his phylogeny creates a distinctly



annelid-like impression of the ecdysozoan ancestor. However, the danger of such an intuitive joining of conflicting molecular and morphological topologies is that the result may not be optimal by any quantifiable or logical criterion. Indeed, Nielsen's phylogenetic chimera is so far unsupported by any existing molecular, morphological, or combined data set. Finally, in an ultimate attempt to derive all but the non-bilaterians from an annelid body plan, Balavoine & Adoutte (2003: p. 144) write: "Clearly, the organisms which today resemble this hypothetical *Urbilateria* the most are the annelids. Obviously, annelids are not 'living fossils' but, in our view, they are the animals whose body-plan (and presumably life-cycle) has derived the least from *Urbilateria*."

With this we seem to have come full circle. Whereas Christoffersen & Araújo-de-Almeida (1994) and Oliveira-Almeida *et al.* (2004) derive a substantial part of invertebrate diversity directly from within the annelids, Balavoine & Adoutte (2003) instead envision a more abstract, archetypal role for annelid organization. For them, annelids are as close as one can get to a model of the real, ancestral *Urbilateria*. A very similar sentiment is expressed in the recently published second edition of *Invertebrates* by Brusca & Brusca (2003) (see my review of the book in Newsletter 54). Brusca & Brusca (2003: 395) write: "The annelid body plan is the classic example of the metameric, triploblastic, coelomate bilateria, and provides a good model for comparison with other protostomes."

But why is the annelid body plan so attractive as an archetype, a hypothetical ancestor, from which at one time or another almost every animal phylum has been derived? The only explanations that I could come up with are reasons for serious caution (if you have other ideas, please do send me an e-mail). First, annelids are the most conspicuous of worms, and for many of us, before we receive any formal training in biology, worms are therefore the quintessential invertebrates. Only molluscs and arthropods may rival the annelids in this status. So almost automatically annelids assume the role of unquestioned reference point with which to compare other animals. And although we, as professional scientists, all like to think that we are in conscious control of our thoughts and decisions, I can't help but wonder whether certain ideas or modes of thought that we acquire early in life might not be more difficult to modulate at a later time, than we might hope.

Unfortunately, I think it is even more likely that our professional training holds the key to this puzzle. When we are confronted for the first time in our lives with academic zoology, we are indoctrinated with all the received wisdoms of the discipline. One of the first steps that is taken to create some sense out of the chaotic data of invertebrate zoology, is to erect some age-old divisions. For example, first we separate the bilaterians from the non-bilaterians, the triploblasts from the diploblasts. Then we proceed to parse bilaterian diversity into non-overlapping domains of coelomate and non-coelomate animals. Then we distinguish segmented and non-segmented animals. Then we split the groups with and without larvae, in other words the indirect and direct developers. The distinction between microscopical and macroscopical animals has already been made when you were a kid; how many 14-year-olds have heard of a gastrotrich or a tardigrade? With these dichotomies in place, it becomes easier to understand the appeal of annelids as canonical invertebrates. When textbooks discuss animal body organization and life cycles, almost universally we are informed that the macroscopic, indirectly developing coelomates are somehow more typical, more primitive,

than the minuscule, direct developing non-coelomates that typically share a chapter as “minor phyla.” It is then perhaps not too surprising, however misleading and distorting the effect, that even competent professional biologists may fail to notice their ingrained biased views in the midst of their most precious scientific hypotheses. The most dramatic symptom of such a biased view of nature is when a scientific hypothesis is crippled because certain crucial taxa apparently have become invisible. Several studies that I discuss in Jenner (2000) conclude that Urbilateria may well have been a coelomate indirect developer. However, the authors didn’t even mention the potential effect that inclusion of the many ignored non-coelomate, direct developing, minor phyla could have on their conclusions. For all intents and purposes these phyla had simply ceased to exist.

To end on a brighter note, many of the ideas about ancestral annelids have not, or may not, stand the test of time. However, the status of annelids as legitimate ancestors may yet be salvaged on the basis of recent molecular phylogenetic insights. Accumulating molecular data now show that at least the echiurans and pogonophorans, and I bet in the future the myzostomids and sipunculids as well, can be derived from polychaete ancestors. However, especially when we are dealing with non-molecular data, we should be vigilant that annelids do not become equally constraining as religious origin myths.

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# Palaeo-math 101: Prospectus & Regression I

Phil Donoghue, the editor of this publication, recently wrote to inquire whether I would be interested in writing a regular column on quantitative data-analysis techniques for palaeontologists. My first reactions were amusement, concern, and then fear, in that order. Amusement because, as a field, palaeontology is no slouch when it comes to assimilating new quantitative methods. Among practitioners of the natural sciences, palaeontologists have often been among the first to employ new data analysis methods in innovative applied contexts (e.g., factor analysis, Monte Carlo simulation, bootstrapping, morphometrics) and our ranks boast several individuals who have played prominent roles in the development and popularization of both semi-quantitative and fully quantitative techniques (e.g., Imbrie, Reymont, Shaw, Raup, Marcus, Gould). Concern because palaeontologists also have a well-deserved reputation of being sceptical of mathematical results and generally don't conceive of their science as being mathematical. Far too often have I heard talented practitioners cite an antipathy toward mathematics as the reason they opted for the geosciences in the first place and palaeontology in particular. Indeed, I recall vividly when, at my first Geological Society of America meeting, after having spent some time patiently explaining my poster dealing with a morphometric analysis of radiolarian evolution, one of the grand old men of American palaeontology congratulated my advisor for having secured the skills of a young palaeontologist who 'can really make those numbers dance'. How can I hope to persuade a group that has made an overall indifference to numerical methods a point, not only of pride, but the imprimatur of a kind of folk wisdom, that numbers aren't only useful, but beautiful and fun?

Which leads me to fear. The fact is, with each passing year science becomes more quantitative. This should be welcomed. Quantification has been the hallmark of a maturing science ever since Descartes and Newton. Even the qualitative bastion of taxonomy will soon feel its effects in much the same way phylogenetic analysis did some two decades ago. But there is also danger here. As the tools of quantitative analysis become easier to use, and are employed more frequently, my experience has been that understanding of the fundamentals of numerical analysis becomes ever more important. Those who don't understand the difference between parametric and non-parametric approaches, correlation and covariance, and relative and principal warps not only put themselves at a disadvantage in examining their own data, they quickly surrender their ability to make informed decisions about the increasingly large number of studies that apply – or, in many cases, mis-apply – such methods. Taking responsibility for guiding a traditionally reluctant audience through such material, separating its core truths from the aficionado's love of detail, and providing a practical understanding that people can use to come to their own conclusions about their own data, is a daunting task. But that's what's needed and that's what I will try to provide.

In each essay I'll try to illuminate a corner of quantitative method and practice with an emphasis on practicality in a palaeontological context. These articles will not be written for specialists in quantitative analysis. Those with such experience should already be aware of

much of the material I intend to present, though I will try to juxtapose topics in novel and hopefully appealing ways. Rather, they will be written for those who always wanted to gain knowledge of this subject, but never had the opportunity to do so and haven't managed to make much progress through self-education. In addition, I'll try to illustrate the methods discussed with spreadsheets containing the various formulas and procedures rendered in a form acceptable to that indispensable piece of data-analysis software sitting on your computer desktops right now; the venerable MS-Excel. On occasions where the method exceeds Excel's abilities, I'll point you to inexpensive software you can use to perform the procedure.

But you must play your role too. If, in an essay, I say or do something you don't understand, please tell me. If there's some data analysis problem you're having and are stuck for a solution, please suggest it as a topic for a future article. Most of all, I'll need your forbearance. To my knowledge nothing like this has been attempted in the PalAss newsletter before. It may work. It may not. Regardless, it will be interesting to find out.

Let us begin with two columns of numbers representing measurements of glabella maximum length and width measurements from 18 trilobite species:<sup>1</sup>

Trilobite Glabella Data			
		Length (mm)	Width (mm)
1	<i>Acaste</i>	5.10	3.46
2	<i>Balizoma</i>	4.60	6.53
3	<i>Calymene</i>	12.98	14.15
4	<i>Ceraurus</i>	7.90	5.32
5	<i>Cheirurus</i>	12.83	12.96
6	<i>Cybantyx</i>	16.41	13.08
7	<i>Cybeloides</i>	6.60	6.84
8	<i>Dalmanites</i>	10.00	9.12
9	<i>Delphion</i>	8.08	10.77
10	<i>Narroia</i>	15.67	9.25
11	<i>Ormathops</i>	4.53	4.11
12	<i>Phacopdina</i>	6.44	6.94
13	<i>Pricyclopyge</i>	21.53	14.64
14	<i>Ptychoparia</i>	12.82	9.36
15	<i>Rhenops</i>	22.27	17.56
16	<i>Sphaerexochus</i>	4.93	6.21
17	<i>Trimerus</i>	16.35	15.02
18	<i>Zachanthoides</i>	13.41	8.51

<sup>1</sup> An MS-Excel spreadsheet containing all data, detailing all analyses, and presenting all results is available at <<http://www.palass.org/pages/Palaeomath101.html>>

I'm going to assume, for the purposes of this initial essay, that you are familiar with basic sample description indices (e.g., mean, standard deviation). These numbers describe your data and tell you things about the population from which the sample was drawn. Such parameters are used in data analysis, but they aren't analytic results themselves.

One of the basic data analytic tools is linear regression analysis, sometimes described as 'shooting a line' through your data. More precisely, one uses regression analysis to create a model of the manner in which one variable behaves relative to another. Such models do two basic things for the analysis. First, they provide a precise estimate of the specific relation between the variables. In a sense, you can regard this as making known that aspect of variability which all objects included in the analysis have in common. Second, they provide a measure of each object's uniqueness, in terms of its degree of deviation from the model. These two factors are expressed in the generalized equation for all linear regressions.

$$y_i = mx_i + b + \epsilon_i \tag{1.1}$$

In this equation, the regression line's slope ( $m$ ) expresses the aspect of between-variable behaviour that refers to the relative rates of change. Slope values of less than 0.5 ( $< 0.5$ ) mean that a unit change in the  $x$  variable engenders a less than unit change in the  $y$  variable. Slope values greater than 0.5 ( $> 0.5$ ) mean that a unit change in the  $x$  variable engenders a greater than unit change in the  $y$  variable.

While this estimate of change rates is often the practical target of a data analysis, the slope by itself does not specify the entire model. In order to do that, the position of the model in the space defined by the variables must be tacked down in such a way as to ensure that the model 'runs through' the data. This aspect of the model is determined by the  $y$ -intercept which is represented by the symbol  $b$  in equation 1.1. The  $y$ -intercept is a constant because it expresses the constant positional relation between the model and the data.

The third term in equation 1.1,  $\epsilon$ , represents the idea that real data deviate from the ideal. This term is left off many textbook regression equations, and aspects of the problem relating to this deviation factor are, consequently, seldom discussed. This is a great pity because the key to understanding what regression analysis is all about, and, more importantly, the key to avoiding the most common error palaeontologists make when undertaking a regression analysis, is embodied by the concept of  $\epsilon$ .

The mathematical point of any regression analysis is to create a way of calculating the values of  $m$  and  $b$  such that, when summed over the entire sample, the total  $\epsilon$  is minimized. Before we discuss what 'minimized' might mean in this context, let's do a simple experiment. Figure 1 contains a scatterplot of the Table 1 data with each symbol representing a different genus. Without recourse to any calculations—by 'eye', as it were—fit a straight line to these data. Don't worry about marring your perfect collection of Palaeontological Association Newsletters. Just get out a straight-edge and do it.

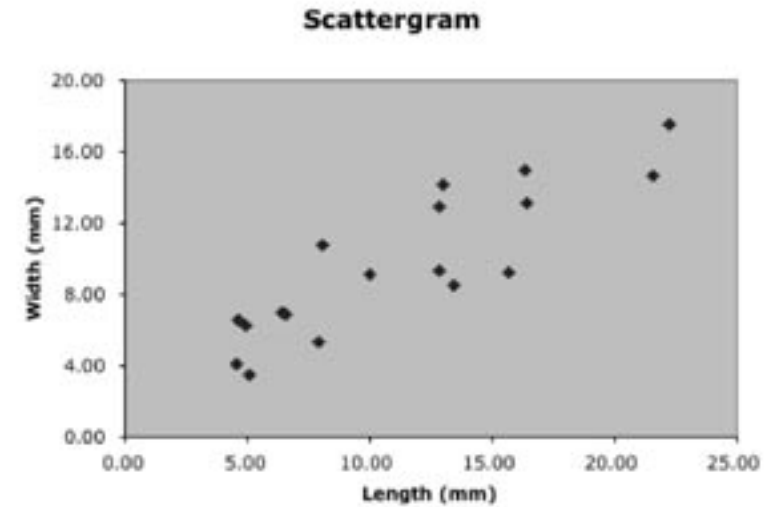


Figure 1. Scatterplot of the Table 1 trilobite data.

OK. That's your model of covariation between these two variables based on this sample of 18 trilobite glabella measurements. We could, but won't, determine the slope,  $y$ -intercept for your model, use that to calculate a set of predicted  $y$ -values based on the Table 1  $x$ -values, compare those predicted  $y$ -values to the measured values given in Table 1, and calculate the deviation ( $\epsilon$ ) of each point from the model. We could then compare everyone's model across the entire Association to determine how similar each was to every other. My guess is that they would all be pretty similar. It's a small, well-constrained data set with a clear trend. No problem.

Let's now try a standard regression analysis of these same data produced by, say, MS-Excel. This can be done in two ways. Either you can use Excel's 'Paste Function' button ( $f_x$ ) to find, and select, the appropriate parameters for the built-in statistical SLOPE and INTERCEPT functions, or you can first plot the data as I have done in Figure 1 and then use the 'Chart' Pull-Down Menu's 'Add Trendline...' function to specify and plot the linear regression on the chart. Either method produces the same results. Both methods are illustrated in the spreadsheet that accompanies this article. If you opt for the latter, or if you create a graphic model in another software application, your plot should look something like Figure 2 (over the page).

Compare your linear model with Excel's. Are they the same? Take a close look at Excel's model. Do you believe this line is really minimizing the deviation between each data point and the linear trace of the model? I don't. What's going on?



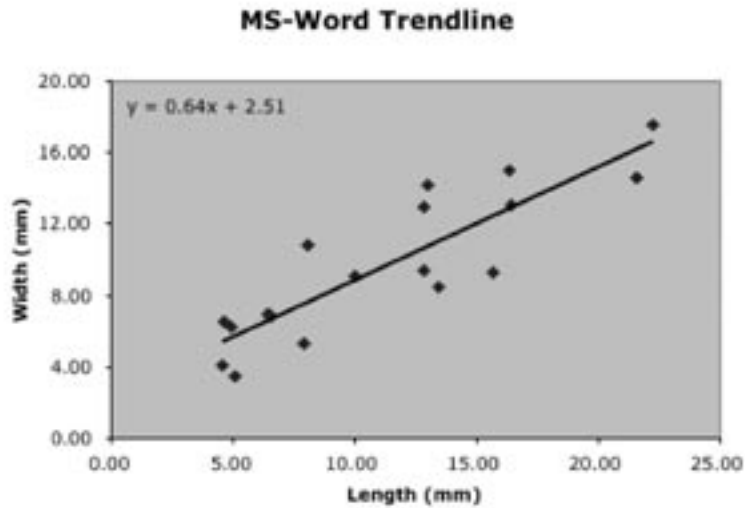


Figure 2. Regression model for the Table 1 data resulting from use of the MS-Excel default linear trendline function. The slope and y-intercept of this line are identical to those specified by Excel's built-in statistical SLOPE and INTERCEPT functions.

When you drew your model line, what were you trying to minimize? Excel uses what has come to be the standard error-minimization strategy termed, somewhat misleadingly, 'least-squares' (L-S). Specifically, Excel – along with virtually all software-based regression applications – constructs its model to minimize the square of the deviation of the points from the model line. Why do they use the square of the deviation instead of the raw deviation? It's really a bookkeeping convention that avoids having to deal with negative numbers in the form of deviations from points that fall below (rather than above) the model. The L-S convention itself isn't the problem. The reason why most L-S regressions differ systematically from 'eyeball' regressions is that this L-S convention is carried out over only one of the two variables (see Fig. 3). Consideration of  $\epsilon$  with reference to only one variable in this way has the effect of 'pulling' or 'rotating' the regression model to a position of greater alignment with the axis over which deviation is being minimized. If the deviation is minimized in terms of the y-variable, the regression is properly termed an 'x on y least-squares regression' whereas minimization over the x-variable is termed a 'y on x least-squares regression'. Because of the asymmetry of the minimization criteria, x on y regressions will estimate models that differ from y on x regressions.

The purpose of these types of regression is (1) prediction of a dependent variable in terms of an independent variable, (2) adjustment for a confounding variable, and (3) determination of a relation for use in assay analyses. In each case there exists a logical distinction between the two variables. One – usually the x-variable – is regarded as being the subject of the analysis and the other – usually the y-variable – the object of the analysis. Put another way, variation in one variable is conceived as being tied to, or best expressed as, variation in the other. Such

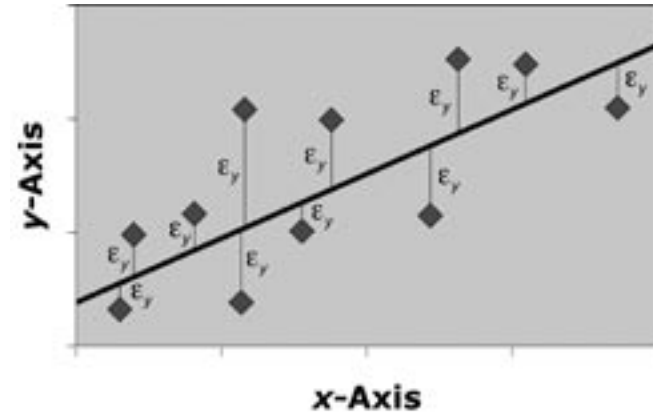


Figure 3. Error-minimization scheme used by the x on y least-squares linear regression method. Note this method only minimizes error with respect to the y-variable.

one-dimensional least-squares regression models can also be used to test for the existence of a non-zero trend in the data and will, of course, 'fit a line' to a set of data. In many cases, though, the priority of an approach that minimizes  $\epsilon$  over only a single variable is open to question. After all, one can easily think of other minimization criteria that could be applied to the Table 1 data; such as the one you applied when you drew your 'eyeball' model.

It would be one thing if one-dimensional L-S analysis was listed as an option in regression software packages. Unfortunately, it's not. The fact is MS-Excel, Statistica, SysStat, StatWorks, and so forth all offer x on y least-squares regression as the *only* programmed option for regression analyses. Indeed, in MS-Excel's short, on-line definition of the SLOPE function, we learn that this routine 'returns the slope of the linear regression line through the given data points' (emphasis mine); as if x on y L-S regression was the only minimization criterion available for linear regression.

Fortunately, other regression models exist that more faithfully capture the two-dimensional geometry of data such as those included in Table 1. In most palaeontological analyses there is no clear-cut need or desire to distinguish between the roles of different variables. Why should glabellar length measurements be regarded as fundamentally different from glabellar width measurements? What is to be gained from expressing  $\epsilon$  in our model only in terms of deviations on glabellar width?

One of the most useful of these alternative linear regression methods is reduced major axis (RMA) regression (Kermack and Haldane 1950; also called the relation d'allométrie, geometric mean regression, and the standard major axis). Reduced major axis regressions minimize the product of deviations from the model along both x and y axes (Fig. 4). Calculation of an RMA regression slope is unexpectedly easy, being the simple ratio between the standard deviations of variable x and variable y.

$$m = s_x / s_y \tag{1.2}$$

This slope also has a satisfying relation to L-S regression, being the geometric mean of the  $y$  on  $x$  and  $x$  on  $y$  regression slopes. The fact that the slope is calculated from the variable standard deviations is also useful in many (but not all) contexts insofar as this renders the regression insensitive to differences in the magnitudes of the numbers being used to represent the variables. In other words, RMA regressions can be used to compare apples and oranges (or, to be slightly more palaeontological, foraminifera and temperature, dinosaurs and rainfall, and so forth), as well as apples and apples (e.g., foraminifera and dinosaurs).

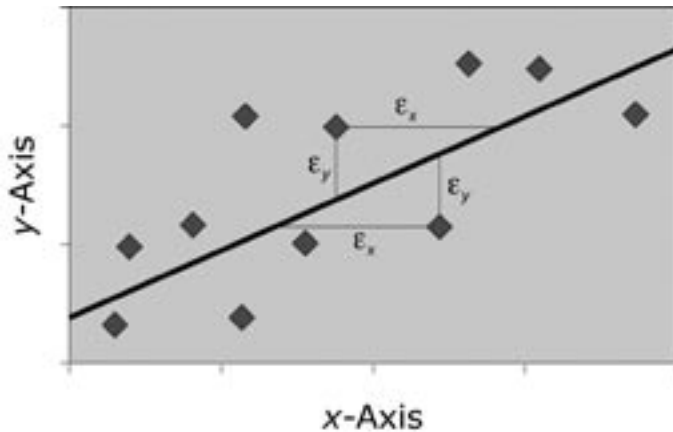


Figure 4. Error minimization scheme used by the reduced major axis regression method. This method minimizes error with respect to both  $x$  and  $y$  variables as a function of their joint product. This is equivalent to minimizing the area of the triangle formed by the projection of the data point's  $x$  and  $y$  coordinates and the regression model.

What about the  $y$ -intercept? There's only one standard formula for this that is used by all regression methods. It's the projection, onto the  $y$ -axis, of a line with slope  $m$  that is constrained to pass through the bivariate mean.

$$b = \bar{Y} - m\bar{X} \tag{1.3}$$

There's one more bit to the RMA calculation. Since the value of the standard deviation is always positive, the raw ratio of standard deviations will always return a positive number, even for variables whose regression line should have a negative slope. Unlike least-squares methods, the sign of the RMA slope is determined by a separate calculation. It's the sign of the sum of products, but not the raw sum of products.

$$SP = \sum x_{mc} y_{mc} \tag{1.4}$$

In order to get the correct sign you'll need to express your data in terms of each variable's deviation from its mean.

$$\begin{aligned} x_{mc} &= x - \bar{X} \\ y_{mc} &= y - \bar{Y} \end{aligned} \tag{1.5}$$

The correct answer will also be given by the corrected sum of products, but that equation is slightly more complex.

How does RMA stack up with respect to the trilobite data? Results of an RMA regression on the Table 1 data are shown in Figure 5. Compare that model to the one you drew at the start of this essay. Closer to your 'eyeball' estimate? Probably. When we estimate lines by eye we instinctively try to minimize error in both  $x$  and  $y$ , not with regard to just  $x$  (or just  $y$ ) alone. The programmers of statistical software select L-S regressions as their default because they are trying to do right by their main audience. Least-squares models are precisely what you would want to choose in a wide variety of business and manufacturing contexts. That's fine, even laudable. But it doesn't mean  $x$  on  $y$  L-S regression is the best choice for everyone in every instance. In particular, L-S methods are usually, if not the wrong choice, the less-than-obvious choice for many natural history applications of regression.

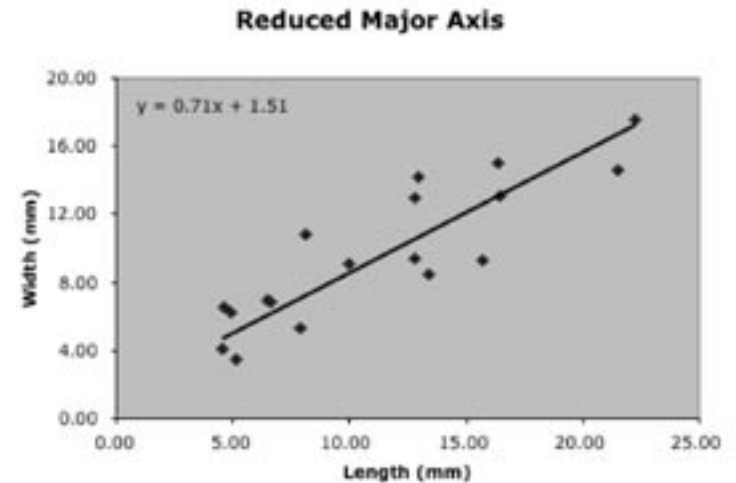


Figure 5. Regression model for the Table 1 data resulting from use of the reduced major axis regression method. Unlike, standard least-squares approaches, this model is invariant to the selection of which variable is portrayed on which axis, and to differences in variable type.

Of course, if all bivariate data points are clustered tightly around a line, the difference between these two types of regression will be small. For data that have a fair amount of scatter about the trend though – and here we're talking about most palaeontological data – the difference will be noticeable and possibly important. For the trilobite example, the angular deviation between the two regression models is only 2.5° and the conclusion that glabellar width is distributed in a linear manner, but at a lower overall rate than glabellar length, would be supported regardless of which model was accepted as correct. Nevertheless, the 'odd' trend of the LS regression is quite obvious once you look at it. Note also, this was an example calculation and we had no way of knowing that the regression models would be close (but noticeably different) at the outset.



Rather than run both models on all your data to see if model choice makes a difference, why not decide which model is most appropriate to your need and use that from the start? Only use L-S regression where there is a definite causality relation between your variables and in cases where you know which direction the cause-effect arrow is pointing. If you don't know these things, you're better off with RMA or an alternative method I'll discuss next time. Above all, never trust a statistics application to look out for your best interests or to give you the whole story about a method.

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#### Further Reading

*RMA regression is one of those topics that is rarely mentioned in statistical textbooks (even those which claim to be aimed at 'scientists') and, in those rare instances where they are mentioned, the discussion is usually incomplete. The following represent the sum total of discussions in textbooks of which I am aware, along with the original RMA reference. Caveat emptor.*

DAVIS, J.C. 2002. *Statistics and data analysis in geology* (third edition). John Wiley and Sons, New York. 638 pp. – *Contains a brief discussion of RMA regression, but neglects to mention how the sign of the RMA slope is determined. Previous editions contain no mention of RMA.*

KERMACK, K.A. and HALDANE, J.B.S. 1950. Organic correlation and allometry. *Biometrika*, **37**, 30–41. – *Where it all started for RMA regression.*

SOKAL, R.R. and ROHLF, F.J. 1995. *Biometry: the principles and practice of statistics in biological research* (third edition). W.H. Freeman, New York. 887 pp. – *The best discussion of non-least-squares regression methods available, including RMA. Pay careful attention to their symbol conventions.*

SWAN, A.R.H. and SANDILANDS, M. 1995. *Introduction to geological data analysis*. Blackwell Science, Oxford. 446 pp. – *Very brief mention of RMA, no discussion of how to find the correct sign of the RMA regression slope.*



## Acellular teleost bone: dead or alive, primitive or derived?

Amongst animal groups, rigid cellular skeletal structures are relatively uncommon, and may be restricted to the cartilages of non-vertebrates such as molluscs, arthropods and sabellid polychaetes (Cole and Hall, in prep.) as well as vertebrate cartilage and bone. However many animals have acellular skeletal tissues, for example molluscan shells, and annelid and arthropod cuticular exoskeletons. Even hemichordates have acellular skeletons derived from the hypertrophy of an epithelial basement membrane (Benito and Pardos, 1997). Our present column deals with a relatively unusual and yet intriguing instance where a cellular skeletal tissue appears to have secondarily evolved into an acellular skeletal tissue. The evolution of acellular bone is not merely a quirk restricted to a single group of organisms (teleost fishes), but as we shall see, has large-scale implications for the evolution of skeletal tissues in general.

The unlimited growth of bone in most vertebrates, its constant remodelling, and its response to mechanical and metabolic changes, define bone as a living tissue. Palaeontologists take advantage of information contained within the bone tissue in their structural analyses of fossilised skeletons to collect data about an organism's sexual maturity, age and growth rate (Castanet and Smirina 1990, Chinsamy 1995, Horner *et al.* 2000).

Bone as a tissue is characterized by three major cells types; osteoblasts, osteocytes and osteoclasts. Osteoblasts (bone-forming cells) are of mesenchymal origin, secrete non-mineralized bone matrix (osteoid), finally becoming entrapped in mineralized bone matrix as osteocytes. Osteocytes connect to other osteocytes and to osteoblasts on the bone surface via long cell processes. Osteocytes are considered to play an important role in strain detection and in the regulation of bone metabolism (Burger *et al.* 2003). Figures from human bone indicate that osteocytes constitute 95% of all bone cells and cover 94% of bone surfaces (Marotti 1996). Bone is resorbed by osteoclasts, which are macrophage-like cells derived from the haematopoietic cell lineage. In mammals and birds osteoclasts are typically multinucleated giant cells. Since regulation of osteoclast activity depends on osteoblasts and osteocytes, all three cell types together are regarded as a "basic multicellular unit" (BMU) (Frost, 1990). Finally, living bone tissue contains blood vessels, nerves and fat, and can accommodate haematopoietic tissue in late embryonic and postnatal tetrapods.

Taken together, bone is not just an inert mineralised hard structure, but a true metabolically active tissue. Nevertheless, in many (if not all) the osseous elements of the largest group of vertebrates, the advanced teleosts (Atherinomorpha, Paracanthopterygii, Acanthopterygii = Acanthomorpha, together representing approximately 16,000 species), the main cellular components of bone, the osteocytes, are missing. This phenomenon was first detected by Kölliker (1859) about 150 years ago and has since been described in detail. The osteocyte-lacking bone of advanced teleosts is called anosteocytic or acellular bone, in contrast to the osteocytic or cellular bone of tetrapods, basal teleosts, and primitive osteichthyans (Moss 1961; Meunier 1987; Meunier and Huysseune, 1992).

The lack of osteocytes has raised discussions whether acellular teleost bone is metabolically active, can be remodelled and ultimately mobilized for use as a mineral source. The reported lack, under normal conditions, of bone resorbing cells (osteoclasts) in teleosts with acellular bone (Glowacki *et al.* 1986) has further nursed the assumption that acellular bone is a “dead”, metabolically inactive, tissue. However, the presence of osteoclasts in acellular bone has been demonstrated (Sire *et al.* 1990), especially as essential elements during skeletal growth and tooth eruption (Witten and Villwock 1997, Witten *et al.* 1999). Furthermore, we now know that acellular bone can, at least under experimental conditions, participate in the animals’ mineral metabolism, even though phosphorous rather than calcium (the key factor in mammalian bone metabolism) seems to be the trigger for releasing minerals from the bone matrix (Witten 1997, Roy *et al.* 2004).

Osteoclasts involved in bone resorption in teleosts with acellular bone are usually mononucleated, and rarely create typical resorption lacunae (so-called smooth resorption) (Witten 1977). This is very different from typical bone resorption in mammals where multinucleated osteoclasts create deep resorption lacunae. The absence (or rarity) of multinucleated osteoclasts in teleosts with acellular bone may relate to the absence of osteocytes and haematopoietic bone marrow tissue, since both provide signals that are important for the formation and action of multinucleated osteoclasts (Burger *et al.* 2003). The inconspicuous appearance of osteoclasts in teleosts with acellular bone requires their detection through osteoclast specific enzymes (*e.g.*, tartrate resistant acid phosphatase, TRAP) or transmission electron microscopy (Witten *et al.* 2001, Sire and Huisseune 1993). Without such enzyme markers, proper identification of osteoclasts and sites of bone resorption in advanced teleost remains elusive (Witten 1997, Witten *et al.* 2001). Consequently, standard histological procedures alone do not provide the correct picture of resorption and bone remodelling in advanced teleosts.

The lack of easily recognizable indications for bone resorption and remodelling has important implications when it comes to the examination of fossilised bone structures from this group. Whereas in tetrapods and primitive bony fish, sites of bone resorption can be identified on the basis of typical resorption lacunae (as traces of the activity of multinucleated osteoclasts), this might not be the case for acellular bone in advanced teleosts. With this in mind it might be worth considering that structural analysis of fossilised skeletons from advanced teleosts does provide data about bone growth (commonly utilized elements include operculae, vertebrae, otoliths, fin rays) but that data about resorption and bone remodelling are likely to be overlooked or misinterpreted. A similar reason might also explain the lack of evidence for bone resorption in many groups of early gnathostomes (Donoghue and Sansom, 2002).

Apart from the debate about the degree to which acellular bone is metabolically active, there is a discussion about the first appearance of acellular bone in the course of vertebrate evolution (Ørvig 1964, Smith and Hall 1990).

With few exceptions (see Moss 1961, Meunier and Huisseune 1992), acellular bone in extant bony fish is restricted to advanced teleosts, which is a good reason to view acellular bone as a derived character within teleosts. On the other hand, acellular bone has also been reported from the base of chondrichthyan placoid scales (and teeth) and in the remarkable ‘spine brush’ of stethacanthids (Coates *et al.* 1998; Donoghue and Sansom 2002). This may indicate

that acellular bone did not evolve in advanced teleosts for the first time, suggesting that acellular, and not osteocytic, bone would be the primitive vertebrate bone type.

The occurrence of aspidine (considered to be a type of acellular bone) in the dermal skeleton of Heterostraci is often cited as an argument for acellular bone as the plesiomorphic condition (reviewed by Ørvig 1964 and by Smith and Hall 1990). Moreover, the simultaneous appearance of cellular bone in both the endoskeleton and dermal skeleton has been identified as a character of the stem group of gnathostomes (see Donoghue and Sansom 2002). Certainly, considerations of whether acellular bone is derived or primitive within vertebrates have to take into account whether one is dealing with elements of the dermal skeleton or of the endoskeleton, skeletal elements derived from neural crest or from trunk mesoderm, and/or intramembranous or endochondral modes of bone formation (see Palass Newsletters 53: 48–51 and 54: 17–21).

Comparative studies on bone development and structure in acellular- and cellular-boned teleosts might shed new light on the evolutionary origin of acellular bone in advanced teleosts. Indeed, in all instances examined, developing cellular bone in teleosts seems to go through a phase of acellularity, in which it much resembles acellular bone. Together with the sequence in which osteoclasts appear in cellular bone (first mononucleated, followed by multinucleated cells), these observations suggest that acellular bone might have arisen in advanced teleosts through a process of heterochrony (Witten *et al.* 2004).

The question then is how this interpretation could affect our view concerning the relation (developmentally, and/or evolutionary) of acellular bone to other acellular, or partly acellular skeletal tissues, like dentine, osteodentine, mesodentine, and aspidine (Smith and Hall 1990). Acellular teleost bone does not develop by cell processes retreating or by death of osteocytes (Ekanayake and Hall 1987, 1988). From a developmental perspective, there is thus no transitory tissue between acellular and cellular bone. Acellular bone contains no osteocytes (thus no lacunae) and no cell processes (Huisseune 2000); it is present both in the dermal skeleton and in the endoskeleton, it can be produced by both neural crest and trunk mesodermally derived mesenchyme (Hall 1978, 2004), and its appearance is not dependent on the presence of teeth. From an evolutionary perspective, these characters discriminate acellular bone from all other acellular skeletal tissues that have arisen in evolution. Basal plates of placoid scales/teeth, bone of attachment, and acellular cementum are dermal skeletal tissues that have arisen in relation to tooth/scale attachment and are restricted to the dermal skeleton.

In conclusion, acellular teleost bone is not static but an active tissue that is primarily remodelled by inconspicuous, mononucleated, bone-resorbing cells, without leaving easily identifiable traces such as deep resorption lacunae. Acellular bone appears to be a new feature of advanced teleosts that presumably evolved during the group’s long evolutionary period in a stable and mineral rich marine environment.

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**STEALING TIME**

Do you remember the things that scared you, when you were very young? Witches and dragons. Ghosts and skeletons, and bears under the stairs. With me it was each week’s new episode of Dr. Who, which I watched, hardly breathing, from under the sofa, peeping through my fingers, as a Dalek scuttled across the High Street and laid waste to the grocer’s. And, yet more insidious, those shadowy malevolences that could reach beyond mere life and death to steal Christmas, or put human souls into a bottle, or banish the letter ‘O’ so that neither love nor hope could exist.

Lately I’ve been feeling an echo of those old frissons. Only – and this is something the wide-eyed child of yore could not have predicted – I’ve become one of the storybook villains, complete with curled moustachios and pantomime leer. Part of a cabal (hisses from the



audience), that would banish time itself, the GrandFather of Time, the familiar deep time, the tick-tock of the earth itself. The Jurassic System, the Arenig Series (upon which I lavished three years of my youth), the Bathonian Stage – all stolen away. Your correspondent has flipped, finally? Well, perhaps. But the proposal is out there, in black and white (Zalasiewicz *et al.*, 2004), and in all seriousness.

There is a catch, of course. In geology, there is more than one type of time, or, at least, three ways of pinning down the inexorable passage of that same phenomenon which, on a human scale, is the begetter of nostalgia and the foundation of anti-wrinkle cream empires. You can simply use numbers of years – mostly large numbers, of course. This is formally termed ‘geochronometry’, the setting up of a numerical time-scale, usually by means of radiometric dating, but also lately by using Milankovitch cycles, tree-rings and such.

The early geologists, though, struggling along without the benefits of radioactivity, had to conjure up a relative time-scale armed only with rock (rock strata, mostly) and fossils, and the dawning suspicion that neither of these proxies could be entirely trusted. So what emerged was a dual time-scale, with on the one hand geological time itself, and on the other hand the rock successions from which the time scale was derived. This seemed rigorously and effectively to separate the inferences (time) from the evidence (the rocks).

Thus, there is what is officially termed ‘geochronology’ in stratigraphy text-books; this has to do with setting up and using the geological time units: Jurassic Period, Arenig Epoch, Bathonian Age and so on. Then, exactly parallel to this ‘geochronology’, there is ‘chronostratigraphy’, commonly referred to as ‘time-rock’, which is the physical manifestations of the geochronological units as strata: hence Jurassic System, Arenig Series, Bathonian Stage. And, in various incarnations, this dual terminology of time has been at the heart of geology virtually since its beginnings.

Is the dual terminology still necessary today? The Stratigraphy Commission of the Geological Society has wondered about this at some length, especially when trying to explain the differences between ‘time’ and ‘time-rock’ in compiling the latest guide to UK stratigraphical procedure (Rawson *et al.*, 2002). For, there are problems with the dual system today. Firstly, most geologists (and not just students) are unsure about, or forget, or are simply unaware of, the time/time-rock distinction, and use Late Cretaceous (of time) and Upper Cretaceous (of time-rock) quite interchangeably, to the continual chagrin of those whose grim task it is to prepare manuscripts for publication. A reflection of the sad decline in contemporary stratigraphical rigour, perhaps (a few years ago I would have pleaded guilty as charged, m'lud), for which the only cure is eternal editorial vigilance? Well, that might well be true.

There are other difficulties, though. Time-rock, if you think about it, can only refer to stratified rocks, deposits which have accumulated during a particular episode; by convention, it's the sedimentation events only that are considered (rather than, say, the diagenetic and weathering events which have also contributed to the make-up of the rock). Igneous and high-grade metamorphic rocks can't be so neatly pigeon-holed, for any such rock is typically the product of a succession of crystallization/recrystallization events which might well span millions of years. It's no problem of course, simply to place such crystallization events within a relative time framework of periods, epochs and so on.



There's also the formal use of the word ‘geochronology’, as applied to the definition of individual periods and series, mostly still by the use of fossils. Now I know a good many geochronologists; a subset of them would reach for the garlic and silver bullets at the mere sight of a stratigraphically useful petrified dead animal. They consider themselves scientists working on the age relationships of rocks, mainly by the very careful measurement of radiogenic isotopes, and they certainly don't call themselves geochronometricists. There is even a Geochronology Subcommittee (which occasionally Exchanges Views with the International Subcommission for Stratigraphic Classification on the use and ownership of the word ‘geochronology’). Now, whether you adopt a relatively narrow vernacular interpretation of the word ‘geochronology’ (*i.e.* more or less equal to ‘isotope geochronology’, with tree-rings and the like thrown in) or a broader one (working out time relationships in rocks generally), then you would still use the word differently than its formal sense implies.

The ingrained sloppiness of most working geologists, methodological awkwardnesses, ambiguous terminology: all these would be some of the many necessary evils inherent in geology if there was a real need for the dual time/time-rock terminology: either a conceptual need (it's necessary to keep time inferences and rock separate) or a practical need (we would struggle to communicate properly without the system/period distinction).

Conceptually, the separation of evidence and inference need not be necessary. Virtually all geological evidence comes from rocks, just as virtually all archaeological evidence comes from material objects, and yet there doesn't seem to be a ‘time-pot’ in archaeology in quite the way that we have ‘time-rock’. My archaeologist colleague Alun Salt, though, tells me that Palaeolithic is typically Upper while Meso- and Neolithic are always Late. These terms, like ‘Mousterian’ and suchlike, seem more akin to biostratigraphy in that they refer both to time (loosely) and culture (rather more tightly) and thus are diachronous.

Back to the thread. Has, in particular, the golden spike punctured the conceptual need for the dual system? Consider this: what's needed is a robust framework of time, within which geological events, of whatever sort, can be placed and correlated. Numbers of years would be fine if we could get precise, fool-proof numbers: say, place the K/T boundary at precisely 4.32 p.m. (Mexico time) on Friday 13th February, 64, 223, 516 million years BC. Well, we can't, and despite the temporal magic wrought by the geochronologists, it's unlikely that we will, not least because the various radiometric decay constants keep being refined (that is, changed). Thus, by and large, relative means of dating – particularly of events recorded by strata – are still, and are likely to be, better guides to time (for this particular purpose, that is) than absolute numbers, whether the latter are arbitrarily defined (such as the Archean/Proterozoic boundary at 2.5 billion years) or the best estimate of a particular stratigraphic horizon.

The time framework is therefore best defined in strata, simply because relative dating is mostly more precise than absolute dating, and is likely to stay so: think of those ammonite biohorizons, or the Carboniferous tonsteins, or magnetic polarity reversals. The golden spikes (or Global Stratigraphic Sections and Points (GSSPs) to give them their full title) simply pin moments in time within strata, that we then try to correlate, using the full plexus of recorded events in the strata above and below, by any means possible. This process we could term ‘chronostratigraphy’, so that the geochronologists can officially call themselves geochronologists, and then geochronometry can be gently laid to rest, remembered by few.



The whirring noise you may now hear in the background is that, as so often in geology, of a wheel being enthusiastically re-invented, and, in this case, gaudily repainted. For the idea that the practice of chronostratigraphy is in effect defining the time-scale of geochronology (in the formal sense of that word) isn't new. Brian Harland and his colleagues said as much when they published their '1989 timescale' in 1990, and went so far as to discuss problems of practical terminological unification (best to retain 'Stage' in the time-unit hierarchy, they said, rather than 'Age', as the latter word could thus be freed for general use).

Rather more surprisingly (and I'm indebted to Steve Walsh of the San Diego Natural History Museum for making me aware of this), Hollis Hedberg himself said, in 1973, that there really wasn't any pressing conceptual need for the dual time-scale. Thus:

"Comment: There is no need to have one set of terms for the rock strata formed during certain time intervals and another set for the time intervals themselves, e.g. Devonian System and Devonian Period."

"Response: Agreed. We could get along with only the stratigraphic term or with only the time term, and use 'time' or 'rocks' for the other. Thus we could say Devonian System and Devonian time, Albian Stage and Albian time; or conversely, Devonian Period and Devonian rocks, Albian Age and Albian rocks. However, we have inherited the two sets of terms, one chronostratigraphic and the other geochronologic, and they are already in common use so it seems simpler to go on using both rather than trying to suppress one. Certainly the two sets of terms do no harm."

It's a statement made with Hedberg's characteristic clarity and common sense. Yes, he said, the dual system did have built-in redundancy: the belt and braces of earth time, as it were, a mirror-image time framework where you could get by with either time or time-rock. But as the dual system had evolved for historical reasons, we were now stuck with it: it was familiar and harmless and anyway trying to get rid of it would likely cause more confusion than benefit. Why try to fix something that isn't exactly broken?

It's a persuasive argument. But, as persuasive today as a quarter-century ago? I wonder if time, as it were, hasn't moved on. Firstly, as argued above, time and time-rock can only be said to be mirror-images of each other as regards strata. You can't say that a polyphase metamorphic rock or slowly-cooled granite are 'Cenomanian' in the same way that you can say that a bed of sandstone is Cenomanian: all you can do is place various crystallization or closure temperature events into a time framework. And as the earth sciences have got more cross-disciplinary, with, say, extinction events being linked to things going bump deep in the mantle, stratigraphy as a science has moved well beyond the preserve of traditional stratigraphers. And so as stratigraphy makes the long trek into the territory of igneous geochemists and climate modellers, the dual time framework may be becoming less of a harmless quirk and more of an anachronistic irritant, as these other scientists find themselves coming up against the deep time equivalents of Lower January or Upper Tuesday.

Further, it's possible, with a bit of effort, to pick tiny holes in the absolute time/time-rock duality in stratified rocks, even if you accept the convention of rock=time as referring only to the rock's depositional age, and disregard the detrital and diagenetic components. Picture,



say, an open-framework gravel accumulating above a hardground on a current-swept sea floor; some time and a transgression later, silt and mud infiltrate down into the pore spaces as a matrix, to give one rock which thus combines two depositional ages. Or that common phenomenon, as the wonders of side-scan radar have shown us, the catastrophic slumping of a section of continental slope. Around the top of the scar, there are barely-moved slabs of strata, which we can say represent time interval A. Downslope, these gradually disintegrate into smaller, more disrupted slabs, which in turn give way into an olistostrome and finally, into a megaturbidite of depositional age B. At what point, precisely, does this variably transported and reworked stratal mass change from 'being' one time into 'being' another? But, of course, if all you have is a time framework, there is no problem in placing events within it: original deposition, slump and subsequent final settling. The whole complicated mess doesn't have to 'be' any individual age.

I can stand accused of being excessively picky here, and too devilish an advocate by far: probably justly. For the vast majority of rocks these sorts of special cases still don't matter. But, stratigraphy is increasingly being not just interdisciplinary, and evolving from a cataloguing of strata into a means of trying to understand all the Earth's intricate mechanisms of environmental cause-and-effect, but also looking (necessarily) at finer and finer time-scales. And just as Milankovitch-scale events, invented, as it were, in the Quaternary\*, are now enthusiastically being applied to older rocks, so the decadal and annual scale of modern Holocene studies aren't escaping the notice of envious and inventive geologists on a wider stage. So perhaps an effectively imperceptible terminological awkwardness today could become a distinctly perceptible hindrance tomorrow, as tiny windows of geology are picked from the long canvas of deep time and reconstructed in human-scale time.

Nevertheless, Hedberg's observation still holds good. Would we cause more harm than good in trying to unify the stratigraphy of time? I still don't know. Right now, a reasonable case can be made for unification. And as 'time' has a much wider reach than 'time-rock' in geology, it should therefore have the primary role, rather than sharing power as an equal. But, these arguments are, and I stress, *for discussion only*. There certainly have been enough changes in terminology already to make one's head spin (think of all the different uses of the word 'stage', for instance: Walsh *et al.*, in submission). But it would be interesting to try out such unification in practice. There's an acid test. Can one communicate, and write papers on stratigraphy or geology, using only a single hierarchy of relative geological time units, only Period and not System, and only Early and not Lower? Well, over the last couple of years, I've been quite attentive to this, both in manuscripts that I've been involved in, and in editing those of others. My impression (thus far into this personal experiment) is that single-track communication of time relationships is indeed possible. There are local problems of familiarity, as time-rock does provide a convenient short-hand for the age of stratified rocks. For instance the book title 'The Ordovician System' couldn't be directly translated as 'The Ordovician Period'. It would have to be 'Geology of Ordovician Strata' or some such. One positive spin-off in applying this process (which, incidentally, stratigraphers and palaeontologists are likely to be less comfortable with than other stripes of geologist) is that one has to be more attentive, not less, to precision of words, to the separation of rock evidence and time inference, to *what* happened *when*.



Can we really bid goodbye to the Jurassic System, and simply retain the Jurassic Period? If so, there would be a general sense of the loss of part of geological history (that I would share: those Arenig Series, you see). But if it would help communication, and make the language of stratigraphy easier to understand on a wider scientific stage (especially now that the subject of stratigraphy has attained an importance well beyond the scientific sphere) then it might well be worth the effort. Time, I suppose, will tell.

\* Yes, I am aware of Grove Karl Gilbert's observations on the Chalk, made way back in 1895: it's amazing work. And of Schwarzacher's work several decades later. But the *general point* holds.

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**NB** this essay is an extension of extended and marvellously stimulating discussions with fellow members of the Stratigraphy Commission, but owing to my usual inability to do more than only-just cope with even the flexible deadlines of the Ed., they can't be held in the least responsible for assorted *faux pas* in the above. If you want measured words and considered views, then you'll need to delve into the paper cited.



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## Geological Society Special Publication 217 Evolution and Palaeobiology of Pterosaurs

Edited by E. Buffetaut and J.-M. Mazin

Pterosaurs were a peculiar group of Mesozoic vertebrates, which acquired the ability to fly in an original way, using a membrane attached to a single finger of the hand. Ever since the first description of a pterosaur skeleton in 1784, these remarkable animals have elicited much discussion and controversy among palaeontologists, and many basic questions about their origin, evolution and biology remain disputed. In the last few years, interest in pterosaurs has been revived by numerous discoveries of new and sometimes remarkably preserved specimens, which have enlarged and changed our picture of this group. The volume begins with descriptions of several new pterosaurs from the Triassic, Jurassic and Cretaceous of Europe, North and South America, and Africa. Following this, alternative hypotheses of pterosaur phylogeny and evolution are put forward. Several papers discuss the functional anatomy of pterosaurs and its implications for aerial locomotion. The study of pterosaur footprints provides important new evidence concerning their terrestrial locomotion, and this approach is used in several contributions. A developing aspect of pterosaur research is bone histology, as shown by the final papers in this collection.

#### Contents

- Evolution and palaeobiology of pterosaurs • A Late Triassic pterosaur from the Northern Calcareous Alps (Tyrol, Austria) • New morphological observations on Triassic pterosaurs • A new rhipidognathid pterosaur from the Upper Jurassic Morrison Formation of Wyoming, USA • A new crested ornithomimid from the Lower Cretaceous of northeastern Brazil and the unusual death of an unusual pterosaur • A new species of tapejard pterosaur with soft-tissue head crest • Pterosaur of *Tetanodontosidea*, *Pterodactyloidea* scapulo-coracoid from the Early Cretaceous of Venezuela • A new azhdarctid pterosaur from the Late Cretaceous phosphates of Morocco • Giant azhdarctid pterosaurs from the terminal Cretaceous of Transilvania (Western Romania) • Pterosaur phylogeny and comments on the evolutionary history of the group • On the phylogeny and evolutionary history of pterosaurs • Morphological evolution of the pectoral girdle of pterosaurs: myology and function • The detailed anatomy of *Rhamphorhynchus*: axial pneumaticity and its implications • New specimens of Pterosauria (Reptalia) with soft parts with implications for pterosaurian anatomy and locomotion • Middle- and bottom-decker Cretaceous pterosaurs: unique designs in active flying vertebrates • Pterosaur tracks from the latest Campanian Cerro del Pueblo Formation of southeastern Coahuila, Mexico • Ichnotaxonomic evidence for quadrupedal locomotion in pterodactyloid pterosaurs: trackways from the Late Jurassic of Crayssac (southwestern France) • Pterosaur swim tracks and other ichnological evidence of behaviour and ecology • The systematic problem of tetrapod ichnotaxa: the case study of *Pteractonus Stokes, 1957* (Pterosauria, Pterodactyloidea) • The John Quekett sections and the earliest pterosaur histological studies • Histovariability in bones of two pterodactyloid pterosaurs from the Santana Formation, Araripe Basin, Brazil: preliminary results



# THE MYSTERY FOSSIL

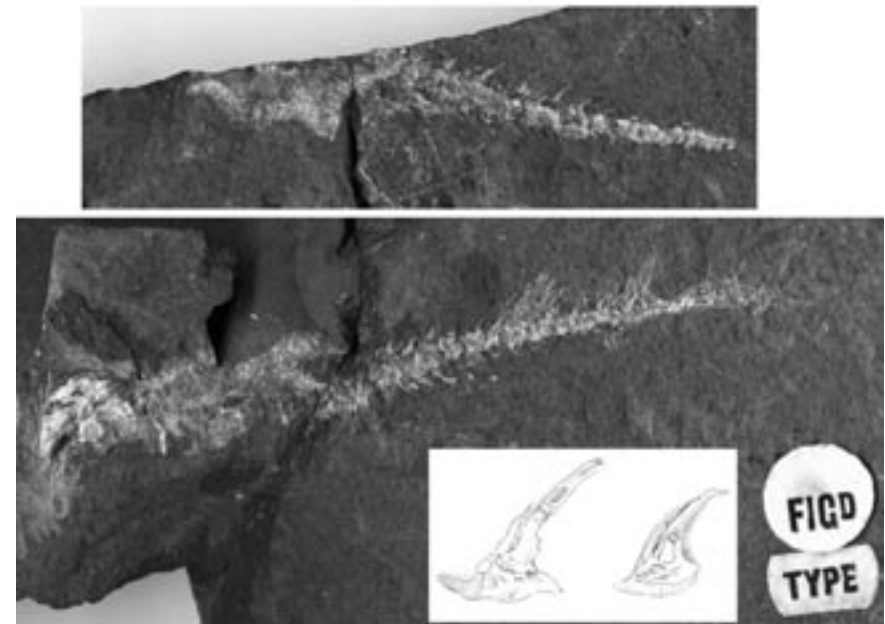
Mystery Fossil Numbers Two and Three remain a mystery. However, good news to report on Mystery Fossil Number One. Further SEM photography on the specimen at different angles has shown the beast has a bivalved shell and is indeed a polycopid ostracod, as initially suggested by John Whittaker at The Natural History Museum. Well done John! Further to this John reports that: “polycopid ostracods (including the genus *Polycope* itself) are all benthonic swimmers, but having said that, they can turn up on all sorts of substrates and in environments from quite shallow water down to several thousand metres.”

Mystery Fossil Four comes from Mike Coates (University of Chicago, USA), courtesy of the NMS, Bobby Paton and Lyle Anderson (who drew it to Mike’s attention). Like mystery fossil number three, this too has a name (*Eucentrurus paradoxus* Traquair 1905), a muddled history leading to no satisfactory conclusion, and, oddly enough, like mystery three, most of this has also been interpreted as a chimaeroid notochordal sheath. The type and only specimen (NMS 1950.38.52) is from the Calciferous Sandstone series of Ardross, Fife, (Lower Carboniferous), total length about 60mm. It was described by Traquair (1905) as an ‘extraordinary little organism’; by Moy-Thomas (1937) as ‘a remarkable little fossil fish’ with chimaeroid affinities; and by Lund (1982) as ‘calcified rubble’ (but resembling a fish with ‘toothplate’, ‘ring centra’ and ‘unicuspid denticles’: 2 per vertebra). In fact, it is difficult to identify any convincing vertebrate affinities. Rubble and ‘toothplate’ (left of figure) obscure the end of the ‘vertebral column’, structured like a gently tapering pagoda (shown horizontally in this instance). Some of the rubble preserves a partly symmetrical pattern (see counterpart in upper panel) consisting of tiny white spicules. But perhaps the most diagnostic parts of this fossil are the apparent neural and heamal spines. These turn out to be double-crowned denticles – two examples are sketched and inset. Each has a broad base, which when broken or worn appears fluted – suggesting infolded interior morphology. The larger crown has a collared base; the smaller always flanks the convex margin of the curved larger example. Crowns include translucent core material, but each is otherwise composed of opaque white material. No dentine tubules were identified. There are more than two of these double-crowned units per segment: broken bases suggest that in life these ringed each ‘centrum’ (projecting in and out of the bedding plane), perhaps four or six in total per segment. The two dorsal (?) fins are tool-scrapes. Another conodont-bearing animal? Seemingly not.

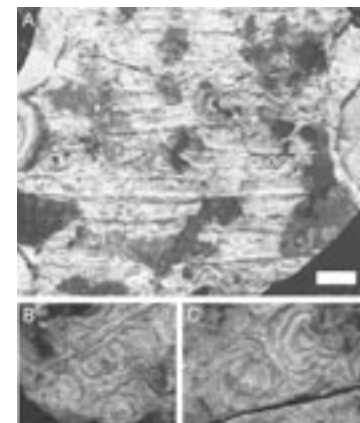
As ever, please send your opinions, considered or otherwise, to Cris Little, using the email address given below. The most convincing answer wins you a Pal Ass field guide of your choice. As always, please also get in touch with Cris if you have a mystery fossil.

**Cris Little**

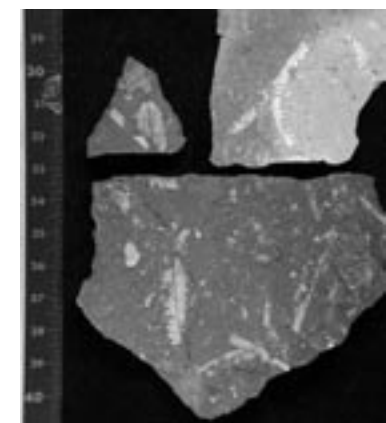
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(Mystery Fossil no. 4)



(Mystery Fossil no. 2)



(Mystery Fossil no. 3)

# Meeting REPORTS



**London Evolution Research Network 1st Annual Student Conference**  
 Natural History Museum, London 12th September 2003

LERN (the London Evolutionary Research Network) was established in October 2002 by students based in a number of London's academic institutions. The primary motivation of the Society is to encourage communication between postgraduate evolutionary researchers in London. The Society brings together students not only from different institutions, but also from different scientific backgrounds, including genetics, ecology, palaeontology, anatomy, zoology, and anthropology.

The Society held its first student conference at London's Natural History Museum, on 12th September 2003. Although much of the conference took place in the stately Museum Boardroom, the atmosphere remained relaxed and informal throughout. A number of posters were also presented at the conference, and were displayed in the nearby Gavin de Beers Room.

The day opened with an introductory address given by the LERN President, **Marc Jones** (University College), who detailed the Society's activities throughout its first year. An opening guest talk by **Richard Fortey** followed, on *The Biology and Evolution of Trilobites*. The talk included a review of an amazingly spiny Devonian Moroccan trilobite fauna. Special mention here must go to *Erbenochile*, a trilobite with eyes that have to be seen to be believed. Having been introduced to these unusual animals, it is hard to know whether to be more impressed by their impressive anatomy or by the obvious preparatory skill involved in their removal from the matrix!

The morning session continued with **Ursula Smith** (Imperial College) discussing the application of geometric morphometrics to gastropod species identification. Soft anatomy or genetic data, useful to aid in species recognition, is absent in many biodiversity and evolutionary studies. Ursula described how morphometric techniques may be used to distinguish extremely similar species using shell morphology alone. **Stefan Gabriel** (Queen Mary College) outlined how the jaw structure of shrews differs from that of other mammals, before revealing that this might be due to factors other than those involved in chewing. Next, **Gareth Fraser** (Kings College) focused in on the teeth, comparing the regulatory genes involved in the formation of teeth in rodents with those in Chondrichthyan and Osteichthyan fishes.

Lunchtime afforded an opportunity for the delegates to explore the Museum, and to view the poster presentations. Among these, **Emily Clare Ashford** (University College) detailed evidence of hunting in human populations at Hoxne and Boxgrove from an analysis of the bone elements preserved at these sites. Emily reported an over-representation of upper limb bones in sites occupied by humans when compared to sites with no evidence of human occupation. She suggests that the human removal of meat from these bones rendered them less appealing to scavengers, who would otherwise remove them at a similar rate to other bone elements.

**Elizabeth Caldwell** (University College) considered the differences in the salivary amylase genes in human populations with distinct histories of cereal agriculture to search for human adaptation to high starch diets. **Daniel White** (University College) presented his work regarding linkage disequilibrium in the SERT gene of two Latin American populations. Other poster topics included the lizard pelvis (**Brian Ruth**, University College), postmetamorphic frog ontogeny (**Marc Jones**, University College), Jurassic echinoid diversity (**Colin Barras**, University of Birmingham), insect wing morphometrics (**Debi Linton**, University College) and the surprising significance of crinoid ossicles (**Aaron Hunter**, Birkbeck College).

The first afternoon session was devoted to research into hominids in general, and *Homo sapiens* in particular. **Ashley Hazel** (University College London) showed how 3D geometric morphometrics can be used to analyse the contribution of mandible and facial bone articulation to overall facial prognathism. She has used this technique to compare the patterns of facial prognathism in Miocene populations of fossil hominids and apes with those of present day apes. **Julian Pender Hume** (The Natural History Museum) gave an account of the plight of the Mascarenes parrots. A once diverse population on the three islands has now been reduced to a single species on the Island of Mauritius, largely through the action of man. A number of these species are now known only from the often exquisite drawings of early naturalists, and through the accounts of the first sailors to visit the islands. **Steven Stuart** (Imperial College) showed how portions of the Y-Chromosome may be used to examine the patterns of human migration into the Americas from Asia, and to identify a number of distinct migratory episodes. He also demonstrated that a number of Amerind populations have effectively remained isolated since these first colonisation events. **Majid Haji Faraji** (Kings College) rounded off the session with an investigation into dietary Chromium intake.

The third and final session began with **Christopher Phennah** (Imperial College), who detailed his genetic study into the evolutionary history of the rodents. Using a Bayesian analysis of both nuclear and mitochondrial sequences, Christopher proposed a new group, the Beckoidea, comprising the Cricetinae, Arvicolinae and Myospalacinae. **Oliver Thatcher** (Institute of Zoology) spoke on his research into the population structure of the Harbour Porpoise *Phocoena phocoena* around the British coast from the study of stranded porpoises. The day finished with **Catherine Bridge's** (University College London) well-presented research into the struggle for dominance within populations of the primitively eusocial wasp *Liostenogaster flavolineata*. There is a well-established age-based queuing system for dominance in the majority of populations but, interestingly, she recorded examples of individuals 'queue jumping' to gain dominance at an earlier age. This is, of course, preferential for the 'jumping' individual, but may have detrimental effects on the colony, if other individuals are injured during the 'jumping' episode.

The conference was a success, attracting over 40 research students, a number of whom stayed on for an evening reception and prize giving ceremony. The prize for best oral presentation went to **Catherine Bridge**, while **Elizabeth Caldwell** was awarded the prize for the best poster presentation. The evening was rounded off with a post-conference trip across the road to the Imperial College Student Union, and many cheap drinks!

A huge number of people helped to make the conference possible and thanks go to all of them, with special mention to the C.E.E. (Centre for Ecology and Evolution) and the Natural History Museum Science Group Education Committee, for funding the event. Thanks also go to the staff

at the Natural History Museum for providing the vital support necessary for the smooth running of the conference.

For those interested in joining LERN or finding out more about its activities, the Society's president, Marc Jones, can be contacted at <[marc.jones@ucl.ac.uk](mailto:marc.jones@ucl.ac.uk)>. The Society runs its own website, at <<http://www.anat.ucl.ac.uk/research/lern/>>. More details of the conference can be found here, together with a complete listing of the conference abstracts.

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**Palaeontological Association 47th Annual Meeting**  
Leicester 14th – 17th December 2003

I can't say I have ever envisaged my home town of Leicester being promoted as a tourist destination: Thomas Cook began the package holiday industry here in the 19th Century, but he was enabling people to leave the place, rather than bringing them in. However, some bright sparks in authority decided recently that it should be, and set about selling the city to anyone who might be listening. An agency named Leicester Shire Promotions was created, and [WARNING: ad-speak gibberish ahead] 'took the initiative, nurtured partnerships and developed ideas ... which would generate media attention and the involvement of local people.' Part one of their scheme was to slap a series of posters on bus shelters and billboards around the town.

Thus, a December visitor was confronted with adverts proclaiming 'Boring, Boring Leicester!', 'There's Nothing To Do In Leicester!' and 'No-one Ever Comes To Leicester!', the intention presumably being to provoke a furious response from the natives, and with it a swathe of publicity. If so, it worked to an extent, as enraged Leicestrians reeled off the legendary contributions their city has made to human history. Unfortunately, many residents appear to think that the Leicester City football team is one of them. Even worse, the ad agency agreed, and used the club as a major selling point (along with Walkers Crisps, Engelbert Humperdinck and Gary Lineker). Having been a supporter for over 20 years, I am certain one thing the Foxes will not do is bring visitors flocking.

All of which is rather a pity, because if the copywriters' myopic gaze could be diverted away from that most transient of extant species – the celebrity – they would discover that the city has some genuinely interesting stories to tell (or sell). And, of thankful relevance to this report, in no field is this truer than that of natural history. Back in the 1840s, for example, the success of their beetle-hunting trips around town led a hosiery's son and a local schoolteacher to head further afield. Henry Bates and Alfred Russel Wallace ended up in the Amazonian rainforest, where they identified hundreds of species new to science. Many of them were insects, and Bates recognized the phenomenon now known as Batesian mimicry, where harmless taxa come to resemble

poisonous or noxious forms. Wallace, after moving from Amazonia to South-east Asia, ended up formulating the small matter of his theory on natural selection. But is anyone in Leicester aware of any of this? Not as far as I can tell.

Slightly more recently, the flora, fauna and, in particular, the fossils of a Leicestershire childhood germinated an enduring fascination with nature in a young gent who has done a fair job of explaining the natural world since then. In his autobiography, 'Life On Air', Sir David Attenborough happily describes the thrill of ammonite-hunting in the Jurassic limestones which outcrop to the east of Leicester. He also wishes fervently that he had been Roger Mason, the Leicester schoolboy who, in 1957, discovered remnants of life where none was known to exist: the Pre-Cambrian sediments of Charnwood Forest, a few miles north-west of the town. Mason's astonishing finds, including the genera *Charnia* and *Charniodiscus*, soon became recognized as of immense palaeontological significance. The type specimens, on display in the New Walk Museum, seem as exquisitely unlikely today as they must have done nearly half a century ago.

And still the research goes on, with the University of Leicester one of the leading centres of geological and palaeontological investigation in the UK. So dubbing Leicester 'boring' is at least a little unjustified, and its choice as venue for the 2003 PalAss Annual Meeting was an entirely appropriate one. Furthermore, the huge number of delegates from across the UK, Europe and far beyond showed not only that 'There's Something To Do In Leicester (Occasionally)!' but also that 'Someone Sometimes Comes To Leicester!' too.

#### SUNDAY 14th DECEMBER

Living only a few miles from the campus, I foolishly assumed I had a major advantage over other delegates in terms of getting to the talks easily and on time. However, I'd forgotten just how much fun one can have with a Sunday bus service. Couple this with an underestimation of the time required to march from the town centre out to the University, and you have a perfect recipe for arriving at the Bennett Building about half a minute before the Stem Groups Seminar is due to start. Still, I made it, and was thus able to see the sextet of talks.

First to take the stage was **Dick Jefferies** (NHM), examining stem and crown groups in relation to the early evolution of deuterostomes. Dick argued that, although Ockham's Razor is an important and useful concept (and possibly the first interesting thing said by an Englishman), it is a dangerous principle to apply phylogenetically if extant taxa alone are used as its basis. Echinoderms are the only living organisms with a skeleton formed of optically continuous calcite ossicles, so one might expect the presence of this feature in an extinct group to indicate they too were echinoderms. However, the bizarre Palaeozoic carpoids place doubt on this assumption, as detailed examination has revealed features that Dick interprets as gill slits, suggesting a close affinity with other deuterostome groups, such as tunicates. Indeed, Dick argued that within the mitrate carpoids can be found members of the stem group craniates, tunicates and acraniates, leading to the conclusion that all primitive chordates possessed an echinoderm-like calcite skeleton. The next question is thus: is the same true of hemichordates? I await further developments, intrigued to see whether Dick's crown group concept remains 'the only thing I've done that has met with any approval.'

Next up was **Phil Donoghue** (Bristol) and, since I have yet to see any sign of the plastic dinosaur and half pint of shandy he promised me as payment for this report, I do not feel duty bound to



give his presentation a glowing review. Annoyingly, though, Phil's talk on the problems of dating the origins of metazoan clades and, in particular, the discrepancies between palaeontological and molecular clock evidence was really quite interesting. Although molecular dates agree on the whole with the fossil record, there are some pronounced mismatches, especially when it comes to the evolution of metazoan crown groups. Within the mammals, molecular dates of origin deal with total groups, whilst the fossils are better at giving times for the diversification of crown groups, producing something of a discrepancy. For birds, meanwhile, the fragmentary nature of most fossils makes reliable palaeontological dates difficult to achieve, and Phil suggested that greater clarity would be achieved if only complete or near-complete specimens were used.

**Graham Budd** (Uppsala) was third to speak, and by now I had noticed a strange audience phenomenon. With every cladogram presented, there would be rows of people sitting with their heads tilted at 90 degrees, trying to decipher the name of each clade. Thankfully, Graham made his talk on the Cambrian explosion neck-friendly by simplifying the taxa into 'weird things' and 'normal things'. The weird things are the problematical Cambrian taxa that do not show an obvious relationship to extant crown groups (*i.e.* the normal things), but, irrespective of their precise positions, the weirdos must belong to stem groups. The question is then: which ones? Graham also pondered the nature of the Cambrian explosion, suggesting that the large number of problematical taxa is probably the result of poor taxonomy rather than unique evolutionary mechanisms, although he noted that extinctions at the base of a clade are more important than extinctions within the crown, since they generate greater disparity between the surviving taxa. As to why there are so many Cambrian weirdos when compared with other parts of the Palaeozoic, perhaps there was elevated extinction *and* origination in these early faunas.

And then there was greenery, as **Paul Kenrick** (NHM) discussed the origins of land plants. How do you go from green algae to liverworts to giant sequoias, evolutionarily speaking? Charophyte algae are the sister group of land plants, but Paul stated that there is no fossil that we can

unequivocally place in the land plant stem group. Useful characters are hard to define, not least because green algae are morphologically very variable, and also because most plant organs (*e.g.* wood, seeds, leaves) evolved on land. Additionally, leaves themselves are not homologous, as it transpires (no botanical pun intended) that megaphyll and microphyll forms evolved independently from different plant organs. And, as if that wasn't enough, many of the informative characters of living plants do not preserve well, if at all, in the fossil record.

So, how about vertebrates? Can we unravel the evolutionary sequence from aquatic to terrestrial taxa in tetrapods? **Mike Coates** (Chicago) brought us up to date, noting that fragmentary specimens can be very informative (Dr. Donoghue!). However, despite its importance, such material (*e.g.* *Kenichthys*) won't make it onto the front page of *Nature*, because its state of preservation is 'a bit rubbish'. In the transition from fins to limbs, Mike informed us that the evolution of pentadactyly appears to coincide with the appearance of complex wrist structures, but that forelimbs and hindlimbs did not change in synchronicity. In fact, analysis shows that hindlimb morphological change is derived with respect to that of the forelimbs. Thus, one must be careful in using body parts to interpret evolutionary sequences, especially in fossils that are incomplete.

To complete the seminar, **Dave Unwin** (Berlin) went bird-watching. Crocodiles are the closest living relatives of our fine feathered friends, but there are no living intermediates, so an examination of living taxa only isn't very informative. This can mean only one thing – palaeontology to the rescue! Skeletally, theropod dinosaurs have a lot in common with birds, but the precise relationships had never been resolved. However, the recent discoveries in China of stunningly preserved 'fuzzy raptors' has helped to fill in a lot of the gaps, and experimental studies strongly suggest that feathers did not evolve for flight. Instead, wings enabled the ancestors of birds to climb inclines, and only from that did true flight evolve.

And after all that information had been thrown our way, the only proper response was to partake in a thorough cogitation over a pint or three of fine ale. Even better, add a traditional Leicester curry to the equation and the world will soon be put to rights. At least, that is, until you realise that you aren't staying with everyone else in University accommodation and have to dash back into town to catch the last bus home.

#### MONDAY 15th DECEMBER

It was an early start for the first full day of talks, but surely the absence of an audience at the scheduled 8.45am start couldn't be due to everyone refusing to get out of bed? No, it turned out that the buses were misbehaving, refusing to deliver most of the delegates to the Bennett Building on time. But eventually the lecture theatre was filled, and **Mark Sutton** (Oxford) was able to get the programme underway with some strange Silurian starfish. Exceptional material from the Herefordshire Lagerstätte shows for the first time that tube feet were unequivocally present in Wenlock asteroids, and papulae are also preserved. The pointed morphology of the tube feet is similar to that of extant paxillosid starfish, and suggests that suckers are a derived feature.

**Sarah Gabbott** (Leicester) then investigated the preservation of the Chengjiang fauna, introducing the recipe for pyritizing a carcass, one of Delia Smith's less well-known specialities. Firstly, you need some sediment with a low organic carbon content, to which you need to add

porewaters with a high quantity of Fe<sup>2+</sup>. Then find a suitable dead Early Cambrian organism, and decay it quickly to produce pyrite framboids, or more slowly for euhedral crystals. All this and more will feature in Delia Cook's *The Cambrian*, coming to BBC2 soon.

Last year, I got into trouble within my own research group for managing to miss the main point of **Lauren Tucker's** (Birmingham) presentation on Permo-Carboniferous tetrapod trackways. So, for fear of doing it again, I shall state only that it is critically important to use trackways in combination with body fossils in order to build a complete picture of early terrestrial ecosystems. This is a terrible cop-out, I know, but I can't think of a better solution. **Clive Trueman** (Portsmouth) then told us that palaeontologists are antipathetic towards new analytical techniques, especially in geochemistry, and that we should make a conscious effort to remedy this. Given that I had enough difficulty with the terms (e.g. MALDI-TOF-MS with PSD), let alone the techniques, I'm not sure I'm the man to begin the revolution, however useful it could be.

Tree-rings and palaeoclimate were the subject of **Howard Falcon-Lang's** (Bristol) talk, who revealed that scientists carrying out Quaternary tree-ring studies take their samples at breast height on the tree trunk. Assuming that trees do not have breasts, this led me to wonder whose breast height was defined as the standard unit, because should the pneumatically enhanced tabloid favourite Jordan ever decide to become a palaeobotanist, her results could well be a little skewed. None of which leads to **Norm MacLeod** (NHM) and his research into whether computers can be programmed to recognize species using morphological characteristics. With systematists a dying breed, approaches such as PalaeoDAISY are becoming more important, and Norm's forum study showed that it is a fast, efficient, reliable identifier, which spots useful specific characters. Could this be the way forward for species diagnoses in the future?



And, talking of the future, it was time for The Great PalAss Experiment, also known as a session consisting solely of ten-minute talks. First to get the chance to try it was **Cris Little** (Leeds). Cris explained that filamentous jaspers are the ancient equivalent of sea-vent iron oxides, showing that bacteriogenic oxide formation has occurred for at least 490 Ma. This was supported by **Oliver Lehnert** (Prague) who documented shallow water, stromatolitic vent communities from the Ordovician of the Prague Basin. **Marc Laflamme** (Queen's, Ontario) took us further back, into the Precambrian, with his study of that local favourite, *Charniodiscus*. Specimens from Newfoundland display two morphologies, one long-stemmed, the other smaller and spined, suggestive of ecological tiering. Silurian borings in gastropods, probably bioerosional, were the theme of **Jan Ove Ebbestad's** (Uppsala) presentation, followed by **Stefan Gabriel** (QMC, London) and his study of the jaw morphology of shrews.

**Maria McNamara** (UCD) then gave a fascinating talk on Spanish Miocene frogs. Two dominant forms of soft-tissue preservation – bacterial and phosphatic – are present, varying in degree across different parts of the frog, enabling Maria to produce a 3-d diagram of tofography, sorry, tapostratigraphy. And from frogs to spiders, as **David Penney** (Manchester) showed that arachnids were not affected by either C-T or K-T extinctions, and then **Jason Dunlop** (Berlin) described the first Baltic mites and camel spiders, which together indicate that the amber forests of the time must have been at least partly arid. **Rachel Moore** (Bristol) uncovered muscle fibres in Silurian horseshoe crabs, and **Una Smith** (Los Alamos) informed us that a fossil HIV strain is any more than five years old, before **Bill Fone** (Staffordshire) took us to the lunch break in the company of a strange Ordovician mitrate.

As often happens at the conferences I've attended, our pub lunches took a good deal longer to arrive than anticipated, ensuring that I missed the first four talks of the afternoon session. Given that the fifth was by my internal examiner – **Ivan Sansom** (Birmingham) – I magically reappeared in the auditorium, sneaking in to hear all about bizarre Silurian sinacanthids. The problematical brachiopod *Tropidoleptus* was then re-examined by **Dave Harper** (Copenhagen), who suggested it might be most closely related to spiriferids and terebratulids, and **Alex Nützel** (Erlangen) tried to unravel the patterns of gastropod diversity across the Palaeozoic-Mesozoic boundary. The session was brought to a close in related fashion by **Alistair McGowan** (Smithsonian), who looked at why three ammonoid superfamilies cross that boundary, but only one leads to later families. Alistair emphasized the value of statistical techniques such as the Spearman-Rank Correlation Coefficient but, looking at my notes, I am rather concerned by the fact I had actually written 'Spearmint Rhino Correlation Coefficient'. For those of you who have no idea what Spearmint Rhino is, I recommend you don't ask.

That may have been the end of the day's sessions, but it wasn't the end of the talks, because, after a short intermission, we moved to the Rattray Lecture Theatre for the Annual Address. This year's speaker was **Mike Benton** (Bristol), who was giving a presentation intriguingly titled 'Palaeontology and the future of life on Earth'. The human race is undoubtedly responsible for the extinction of many species, but one can only put present-day goings-on into context by a detailed examination of life in the past. Thus, Mike argued persuasively for the importance of palaeontology in understanding what might happen to the Earth in the future, particularly in the case of terrestrially originated events such as the end-Permian mass extinction. As that tricky little Chinese full-back, Confucius, once said: 'study the past if you would divine the future'.



And on that note it was time for a few drinks before heading back to Beaumont Hall for the annual dinner. Pheasant was dish of the day, before **Derek Briggs** gave a presidential speech of customary entertainment and then presented the Hodson Fund to **Charlotte Jeffrey** (Liverpool). Thence, the well-practised migration to the bar began in earnest and, for a few hardy souls, carried on until the cleaners threw us out. But not before Howard Falcon-Lang was able to introduce the delights of The Box Game (incriminating photographs are in circulation) to a mildly inebriated gathering.


**TUESDAY 16th DECEMBER**

Pleas of mitigation were in abundance on Tuesday morning, especially upon arriving at campus with the first two talks of the day having been presented, but time and tide (and the bus) waits for no man, particularly in this privatized age. So my notes began with **Sarah Stewart** (Glasgow) and the biodiversity of Ordovician faunas from Girvan, followed by late Eocene-early Oligocene summer water temperatures in southern England, which **Margaret Collinson** (Royal Holloway) and her team had calculated with the help of rodent teeth and fish otoliths. **Liz Harper** (Cambridge) then asked why molluscs appear always to have been a much more popular food source than brachiopods. Little previous work has been carried out on the subject, but it may be that brachiopods have a low nutrient content as well as (presumably) not tasting quite so pleasant as mussels and oysters. Perhaps flavour could be used as a phylogenetic character, pondered **Lars Holmer** (Uppsala), as he reappraised the systematic position of *Heliomedusa*. Long thought to be a hydrozoan, new specimens with a punctate, setae-bearing shell suggest that *Heliomedusa* was actually a stem-group brachiopod, belonging to the Mickwitziidae.

**Phil Wilby** (BGS) opened the post-coffee session with another problematical beast. The Silurian *Dawsonia* has been interpreted as an alga, a graptolite and a phyllocarid, but it is now thought to be an armoured polychaete annelid, possibly a member of the chrysopetalids. Staying in the Silurian, **Dave Gladwell** (Leicester) gave us an update on the re-excavated Ludlow beds of Leintwardine, before **Mark Purnell** (Leicester) presented some astonishing, articulated conodonts from the Wenlock of Canada, some of which might even have preserved eyes. Hopping back in time to a slightly more famous Lagerstätte, **Jean-Bernard Caron** (Toronto) looked at the taphonomy of the Burgess Shale, showing that assemblages were often a combination of dead and living specimens, indicating autochthonous burial of the fauna. And then we returned to the Silurian, as **Lyall Anderson** (NMS) rediscovered the Gutterford Burn eurypterid beds.

The phylogenetics of Ordovician ostracods were assessed by **Tonu Meidla** (Tartu), before 'brachiopods again and setae again' with **Uwe Balthasar** (Cambridge). Setae are often found in stem-group brachiopods, such as *Micrina* and *Mickwitzia*, and may have served a sensory function. Personally, I wondered whether *M. muralensis* represented a stem-group Sri Lankan spin bowler, though this might just be my cricketing fixation coming to the fore. Ashgill chitinozoans were next to the crease, as **Thijs Vandenbroucke** (Ghent) used Cambrian material to define seven biozones, all of which tie in well with the existing graptolite and shelly fossil biozones. Now, way back in the last century, I did undergraduate fieldwork on some Jurassic oysters of the area around Weymouth, and spent a few days studying an extraordinary shell bed at Langton Herring. In doing so, I became the first L. Herringshaw to stand on the L. Herring shore, which tickled me no end. So it was good to see someone else had been there too, as **Andrew Johnson** (Derby) compared the growth patterns of the taxon *Praeexogyra hebridica* in Dorset and Rutland. It appears that the two areas had different salinity and different rates of productivity, enabling the Rutland forms to grow faster and form thicker shells.

An epic pre-lunch programme was brought to a close with the tenth and eleventh talks of the session. First, **Seyed Naser Raissosadat** (Birjāt) looked at the patterns of ammonite distribution in relation to sea-level in the Cretaceous of Iran. In most cases, the first appearance of a new

taxon occurs in transgressive or highstand systems tracts. And finally, **Oive Tinn** (Tartu) found that 13 ostracod assemblages are present in the Middle Ordovician of Baltoscandia, many of them strongly facies- or time-specific. The lunch interval gave delegates the opportunity to peruse the posters on display, or for those interested in the march of technology, there was a workshop on digital publication. I decided not to risk a trip to any nearby hostelry, and sampled instead the delights of the Charles Wilson building canteen. And, stuffed full of carbohydrates, I waddled back to the auditorium for the last two sessions of the conference.

**Paul Selden** (Manchester) continued proceedings with a few Permian spiders, including the first funnel web-building member of the Mesothelae. Next, **Natalie Thomas** (Leicester) analysed the taphonomy of the Bear Gulch Lagerstätte, showing that a variety of preservation styles are present, and **Elizabeth Boulter** (Cambridge) unveiled the wonderfully named *Perplexia* as a member of the enteropneust hemichordates. **Bjorn-Gustaf Brooks** (Iowa) found evidence of early terrestrial arthropods in the Silurian of Newfoundland, **Alberto Perez-Huerta** (Oregon) used Nevada brachiopods to examine changes in climate and geography during the Carboniferous, and **Bjarte Hannisdal** (Chicago) utilized some fascinating new statistical and computer-based approaches to analysing the fossil record. **David Polly** (QMC, London) pointed out the difficulties in distinguishing populations within a species from separate species, then **Fiona Gill** (Leeds) suffered for her craft, having to go to Barbadian beaches in order to study Tertiary cold seep communities. **Heather Wilson** (Yale) found plenty of problems in millipede phylogeny, especially the taxonomic wastebasket Archipolypoda, and discovered that adding fossil millepedes to a cladogram of extant taxa made the whole tree fall apart. It now appears likely that millipede cladogenesis began in the Ordovician, although there are possible myriapod trackways in the Cambrian of the Grand Canyon.

**Bernard Lefebvre** (Bourgogne) brought us back to the mitrates, finding finger-like structures in various species that might be the imprint of a complex nervous system, followed by **Jason Hilton** (Birmingham), who compared the Carboniferous coal swamps of China with those of Euramerica to see if they told the same story. Intriguingly, many diagnostic Euramerican plants are also present in China, and some taxa did not die out at the end of the Carboniferous (*i.e.* there was no worldwide extinction of these floras). **Mike Bassett** (Cardiff) documented numerous strange Middle Eastern brachiopods with unusual opening and closing mechanisms, and **Dima Grazhdankin** (Cambridge) brought the meeting to a close with the revelation that at least some Ediacaran 'fossils' are not organisms but actually microbial mat structures.

So, the presentations complete, that left the small matter of prize-giving, with Derek Briggs once again given the difficult task of choosing the best talk and best poster by a delegate under the age of 30. In the poster category, Derek commended Lucy Wilson (Cambridge), Federica Manon (Manchester) and Joe Botting (Cambridge), but jointly awarded the Council Prize to **Jenny England** (Glasgow) for her work on the role of proteins in calcium carbonate biomineralization, and **James Whealey** (Cardiff), who had captured Carboniferous aragonitic molluscs not normally preserved in the rock record. In the President's Prize for best presentation, Derek made the point that many talks, whilst interesting and promising, had the feel of work in progress rather than of a complete story, but picked out Bjarte Hannisdal's novel approach for praise. However, the prize itself was presented to **Maria McNamara** for her excellent presentation on Miocene frog preservation.



And that, for another year, was that, except for those who attended the fieldtrip to Charnwood the next day, and who got to hunt Ediacaran organisms in amongst the deer and the bracken. It was another thoroughly enjoyable annual meeting, and good that the timetablers were able to avoid parallel talks (even if one or two sessions were a little on the lengthy side). Congratulations must be passed on to Mark Purnell and the rest of the organizing team for their extremely hard work in putting everything together so well, and with no glitches whatsoever. I look forward to crossing the Channel for Lille 2004.

*Photo credit: Kay Hawkins, Department of Geology, University of Leicester.*

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**13th International Conference of the International Bryozoology Association**  
Concepción, Chile 11 – 16 January 2004

For the second time in its 36 year long history, the IBA ventured into the southern hemisphere for a triennial conference that brought together a high proportion of the scientists currently active in the study of fossil and Recent Bryozoa. The 2004 conference was hosted by Hugo Moyano (Universidad de Concepción) and Juan Cancino and María Cristina Orellana (Universidad Católica de la Santísima Concepción). Concepción is a city of some 325,000 inhabitants in central Chile, 45 minutes flying time south of Santiago. Originally built on the coast, the current city is located inland and protected from the effects of tsunami that destroyed earlier incarnations, although earthquakes still regularly take a toll on the city and its people.

Seventy bryozoologists registered for the conference, delivering 64 lectures and displaying 25 posters, a commendable level of active participation, especially as many of the papers were co-authored by two or more delegates. The abstracts have already been published as Volume 74 (2003) of the *Boletín de la Sociedad de Biología de Concepción*, and the full papers are scheduled to be published by Taylor & Francis. My review of the conference can cover only a selection of the excellent talks that were given during four days of formal sessions.

As is usual for this kind of non-thematic conference, the presentations, ranged across a wide variety of topics that, like the Bryozoa themselves, defy easy classification. **Claus Nielsen** again drew attention to the conflicting and sometimes bizarre results of molecular phylogenetic research, some of which, as explained by **Jo Porter** (with **David Skibinski & Peter Hayward**) may be due to erroneous sequencing of microbial symbionts or the effects of pseudogenes. **Tim Wood** and **Michael Lore's** 18S RNA analysis of the phylogenetic relationships of phylactolaemate bryozoans suggested that this freshwater class may not be closely related to the marine bryozoans, raising the possibility of a diphyletic origin for the Phylum Bryozoa. They also found that, contrary to expectations, phylactolaemate genera with simple statoblasts (seed-like asexual resting and dispersal bodies) and branching colony-forms seem to be more advanced than those with complex statoblasts and 'integrated', gelatinous colonies. If the phylactolaemates are eventually split-off from the Bryozoa *sensu-stricto*, they will join the Entoprocta, a small phylum of solitary and colonial animals formerly included within the Bryozoa. Entoproctologists have always been welcomed at IBA conferences; this year **Tohru Iseto** spoke about entoprocts that live as 'commensals' with other invertebrates, entertaining the audience with some stunning video clips of tiny entoprocts clinging to the gills of polychaete worms, and others moving across settlement panels using the tentacle crown and adhesive 'foot' in a looping motion.

It has been known for some time that the surfaces of living bryozoan colonies can become profusely fouled by biofilms, but there has been little understanding of the specificity of these biofilms to particular species of bryozoans, or of the positive and negative effects that the biofilms have on their hosts. **Sandra Kittelmann** tackled the first of these issues by studying the molecular biology of the biofilms associated with four cheilostome species in the North Sea, finding (a) more diverse bacterial communities on the bryozoans than on control surfaces, and (b) indications of specificity for three of the four bryozoan species.

The great majority of bryozoan species secrete skeletons of calcium carbonate but the details of the structure and chemistry of these skeletons has not received the attention it deserves. **Priska Schäfer** and **Beate Bader's** comparative study of stable light isotopes in a variety of polar and temperate species showed disequilibrium effects in the isotopes of both oxygen and especially carbon. Kinetic disequilibrium in  $\delta O^{18}$  was more prevalent in high than low latitude species. Such information will prove invaluable as spatial precision of isotope sampling improves and the thin walls of bryozoan colonies become amenable to analysis. A foretaste of what will be increasingly possible was provided by the work of **Marcus Key et al.** on some gigantic Permian trepostome bryozoans from Greenland. Their study tested the previously published idea that gigantism was due to algal symbiosis. A one micrometre spatial resolution was achieved using a computer-driven micromilling device which could sample the walls with minimal contamination from cements filling the zooidal chambers. They were able to show

no appreciable vital effect. This, in combination with the fact that the fossils were found in sediments estimated to have been deposited beneath 200 m of water at a palaeolatitude of 35-40°, makes the hypothesis of algal symbiosis untenable. Isotopic profiling by **Beate Bader** and **Priska Schäfer** of the Recent Antarctic bryozoan *Melicerita obliqua* confirmed that the conspicuous growth bands in this peculiar lanceolate species represent annual checks, with colonies living for 45 years or more. **Marcus Key** and **Abby Smith** presented a preliminary exploration of the relationship between bryozoan mineralogy and marine geochemical supercycles (Calcite vs Aragonite Seas), stimulated by the work of Stanley and Hardie that proposed a strong link between ocean chemistry and the evolution of biomineralizing organisms. However, they could detect no relationship between the dates of first appearance of cheilostome families and their skeletal mineralogy, although this is a topic clearly demanding further data for analysis.

Bryozoan ecology was the focus of several interesting papers. **Maja Novosel et al.** reported flourishing populations of the bushy cheilostome *Pentapora fascialis* close to karstic freshwater springs in the Adriatic Sea. Here, at depths as shallow as one metre, nutrient levels are 10-50 times greater than normal sea-water, and colonies have an average diameter of 20 cm, despite salinity levels of only 0.8-2.0‰, showing that even heavily calcified cheilostomes can sometimes be euryhaline. We know astonishingly little about predation on bryozoans, as **Scott Lidgard** emphasized. Heavily calcified frontal shields, often explained functionally as having an anti-predatory role, are probably ineffective against many groups of predators (*e.g.* echinoids, chitons) which produce mechanical forces that are too great for them to resist. Lidgard showed two examples of promising targets for research on fossil predation: small circular boreholes that penetrate the frontal shields of various bryozoans and may be due to drilling predation by tiny gastropods; and the intramural budding of new zooids within the zoecial chambers of dead zooids perhaps killed by single-zooid predators.

Competition for substrate space continues to be a major focus of ecological studies. Generally this results in partial or total overgrowth by the dominant competitor and the death of some zooids or the entire colony. However, **Juan Cancino** and **Maria Cristina Orellana** reported examples of small colonies surviving total overgrowth and subsequently resuming their growth. The ability to survive overgrowth depended not only on the identity of the overgrown species (*e.g.* *Celleporella* survived better than *Umbonula*) but also that of the overgrowing species (*e.g.* overgrowth by *Cauloramphus* was more likely to be fatal than by *Alcyonidium*). A high proportion of competitive interactions for space between bryozoans in the Antarctic are intraspecific according to **David Barnes** and **Piotr Kuklinski**. This is especially true in areas of high ice scour where frequent disturbance means that diversity is low and the only species present are pioneers. In a study of boulder-encrusting bryozoans from Svalbard, the same authors were able to find no relationship between numbers of species or individuals attached to the boulders and sampling depth down to 12 m. As in the Antarctic, disturbance levels are high – ice can flip boulders at depths as great as 40 m. **Kuklinski** reported a second study of bryozoans in four Arctic fiords in Svalbard where glacial meltwater results in high rates of sedimentation. Here dropstones form oases for colonization by two erect cheilostome genera, and muddy sea-beds adjacent to glaciers are populated by the peculiar free-living ctenostome *Alcyonidium disciforme*. **David Barnes** pointed out that high polar bryozoans can actually



grow as quickly as their low latitude relatives but have much shorter growing periods and therefore do not achieve the same annual growth rates or sizes. In the discussion of this paper, Barnes made the important observation that Antarctic bryozoans (and other organisms) reared in aquaria become functionally incapable if the temperature of the water rises by only 2°C. Global warming may exceed this rise during the next 100 years, with potentially catastrophic consequences for Antarctic biotas.

**Roger Hughes** summarized the results of his group's important research on cryptic speciation in the cheilostome *Celleporella hyalina* – supposed *C. hyalina* at the present day was found to consist of about 15 genetically distinct species. A cluster of clades, each characterising a major geographical region, is thought to have diverged during the Miocene, with subsequent subdivision of these clades in the Plio-Pleistocene. Mating experiments and SEM of skeletal morphology back-up the genetic results. Comfortingly for palaeontologists, most of the genetic species are recognizable from their skeletal morphology. If these findings for *C. hyalina* are typical for cheilostome bryozoans as a whole, then we may be underestimating the diversity of modern cheilostomes by an order of magnitude, and the true diversity of Recent bryozoans may be nearer 50,000 than the oft-quoted figure of 6,000 species.

**Patricio Manriquez**, in a paper with **Roger Hughes** and **John Bishop**, assessed the capacity of *Celleporella hyalina* colonies to fuse, an indicator of their genetic relatedness. Importantly for studies of fusion based on skeletal evidence, as in fossils, some examples of apparent fusion are false. This can be shown in *C. hyalina* by applying a thermal shock to one of the colonies – if the two colonies are really fused this stimulates production of male zooids in both colonies, if they are not fused, males appear only in the shocked colony. **Steve Hageman** and **Chris Todd** sampled *Electra pilosa* colonies from different stations and substations along a 1.5 km long marine channel (Clachen Seil Sound) in western Scotland to address the question of whether microenvironmental variation can be greater than macroenvironmental variation in skeletal morphology. Using nested ANOVA they found no differences between stations or substations along the channel but significant differences between colonies from the same substation and even between patches of zooids within the same colony. The source of this variation (genetic, environmental, or gene/environment interaction) is unknown in *E. pilosa*, but this is one of relatively few bryozoans with long-lived larvae so it would be interesting to see whether these results are atypical.

Several years ago an interstitial fauna of tiny bryozoans was discovered encrusting coarse sand grains at Capron Shoal, Florida. To this previously unique occurrence **Judy Winston** (with **Alvaro Migotto**) has now added another interstitial bryozoan fauna living off Sao Paulo, Brazil which contains many genera in common with the Floridan fauna. The discovery of this second fauna shows that sandy substrates are not always 'deserts' for bryozoans. Careful scrutiny of both modern and ancient sands for interstitial bryozoans is clearly called for.

A few papers focused on bryozoans in ancient reefs. **Roger Cuffey** was not at the conference but his paper on bryozoan roles in Carboniferous mud mounds from the US mid-west was read by Marcus Key. Sixty-two bryozoan species were identified in these small mounds, none being restricted to the mounds. They appear to have been important in mud sedimentation, acting as sediment baffles and stabilizers, as well as supplying skeletal material to the mounds. Messinian

microbial-bryozoan-serpulid buildups from Sardinia described by **Pierre Moissette** *et al.* Other Mediterranean Messinian buildups are dominated by hermatypic corals and contain abundant coralline and green algae but the Sardinian buildups are very different. Analogies were made with Palaeozoic mud mounds, with the upwelling of cold, nutrient-rich waters favouring microbial communities containing abundant suspension feeders.

In the final paper of the conference, out-going IBA President **Dennis Gordon** talked about two biodiversity initiatives, *Species 2000* and *OBIS* (Ocean Biogeographic Information System). Bryozoology needs many more hands on the systematic deck if it is to make full use of these initiatives and close the knowledge gap on some of the more intensely studied phyla.

Chile was definitely not chilly and the temperate rain forest was bone dry during our mid-conference excursion to Nahuelbuta National Park. This is an area of native forest dominated by araucarian trees. Having been accustomed to seeing lonely monkey puzzle trees in the gardens of English suburban houses, it was a real treat to observe them in their natural habitat, along with tarantulas and fine views of the snow-capped volcanoes of the distant Andes. Altogether, a memorable excursion befitting a well-organized and stimulating conference.

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**Lyell Meeting 2004: Dinosaur Palaeobiology**

Geological Society, London, UK 11th February 2004

The 47th Lyell Meeting was a symposium held jointly by the Geological Society of London, the Palaeontological Association, the Micropalaeontological Society, the Palaeontographical Society (collectively the Joint Committee for Palaeontology) and, for the first time, the Linnean Society of London. It was professionally convened by Mike Benton and Paul Barrett and hosted in the majestic surroundings of Burlington House, with its excellent Audio Visual facilities. There were over 140 delegates from all over the UK and as far afield as France, Germany, Canada, USA (and, of course, the Isle of Wight). A wide variety of backgrounds were also represented (undergraduates, postgraduates, amateurs, press, botanists, petroleum companies). It's clear that the 'd' word has lost none of its attraction or popularity. However this attention also brings with it the responsibility to promote the image of palaeontology as a whole.

**David Norman** opened the meeting with an overview of dinosaur evolution and diversity. He concentrated particularly on the locomotory specialisations of dinosaurs and the affinities between dinosaurs and birds, the latter with reference to the recent exciting finds of Chinese feathered dinosaurs. David also included a summary of the history of palaeontology and dinosaur research, acknowledging the contributions of Charles Darwin, Richard Owen, Thomas Henry Huxley and John Ostrom. Oddly Gideon Mantell's name was left out, at least until Paul Barrett's talk later on. **Paul Upchurch** discussed the virtues of cladistic biogeography: scenarios compiled from pattern repetition within time-sliced cladograms. He compared his results through the Mesozoic with current tectonic hypotheses and discussed both the areas of

correspondence and the areas of conflict, referring to such problems as epicontinental seaways. He also stressed the importance of vicariance for dinosaur evolution, indicating that the diversification of many dinosaur groups occurred prior to the break up of Pangaea, much earlier than currently recognised from the fossil record. **Angela Milner** elaborated on the evidence for the dinosaurian origin of birds. The highlight was a breathtaking animated presentation of a digital reconstruction of the *Archaeopteryx* braincase constructed in collaboration with Patricio Dominguez-Alonso, using slice data from the amazing high resolution CT lab in Austin, Texas.

After lunch **Chris Cleal** briefly launched the Global Geosites framework, an important international geoconservation initiative that aims to compare candidate localities fairly.

**Paul Barrett** asserted the merits of studying herbivorous dinosaurs, not least due to their huge ecological importance and diversity during the Mesozoic. He discussed the range of methodologies available for inferring feeding behaviour and the benefits of synthesizing them. He also outlined the possible impact of dinosaurs on angiosperm radiation and described correlated progression in relation to ornithomorph character acquisition. **Emily Rayfield** cautioned against making functional inferences based on superficial similarities and highlighted the importance of testing such ideas using new technologies. She presented recent results of Finite Element Analysis applied to theropod skulls, including impressive animations of biting and skull kinesis. These 3-D models reveal the stress distributions that might be expected during feeding and prompted reassessment of cranial osteology in this context. She showed that anatomical features can be related to stress reduction during various types of feeding behaviour. **Don Henderson** explained his ground-breaking work on sauropod locomotion, running through the methods used to calculate weight, centre of mass and buoyancy, as tested against extant animals such as crocodiles and elephants. He demonstrated that increased body size in theropods was coupled to allometric shape changes that would have helped to maintain manoeuvrability.

**Eric Buffetaut** described the history of dinosaur egg palaeontology, the ease of misinterpretation in such studies, the prevalence of 'known unknowns', ootaxonomy and egg microstructure. Notably he also pointed out that Jean-Jacques Pouech was the first to describe dinosaur eggs from the French Pyrenees in 1859, long before the famous Roy Chapman Andrews and his 'caravan' of Dodge automobiles touched sand in the Gobi. **Mike Benton** rounded off the meeting with a talk about the K-T extinction. He started with an extensive and humorous historical introduction to previously proposed theories (praising Alvarez's bravery), continued with a discussion of recent studies, and ended with the much-versed plea for unbiased primary data collection and consideration of environments prior to spectacular speculations. The meeting ended in the Geological Society library with wine and enthusiastic conversation. There were also three posters presented by: **Richard Butler** (South African ornithischian material); **Jon Noad** (dinosaur taphonomy and sedimentological applications); and **Remmert Schouten** (meticulous mechanical preparation of *Thecodontosaurus*).

Overall this was an extremely enjoyable, well-balanced meeting. There were no 'technical hitches', all the speakers kept well to time, the Powerpoint presentations were all of a high standard, and only one mobile phone interruption. The substantial meeting abstract booklet deserves a mention too. Importantly, several talks emphasised the range of new technology becoming available and the application of simple but also highly informative novel

methodologies. These approaches are opening up a whole new set of avenues for research (e.g. assessing and comparing morphology, testing of biomechanical models, constructing rigorous palaeobiogeographic scenarios). Promoting these innovative techniques, which provide testable hypotheses, as the Lyell Meeting did, is vital if we want to compete in the current hostile climate of funding. The next few decades promise to continue these exciting times for dinosaur palaeobiology and vertebrate palaeontology as a whole.

The next Lyell Meeting will be on the theme 'Applied Phylogeny', organised by the Micropalaeontological Society under the usual aegis of the JCP, and is currently scheduled to take place on 9th February 2005, at Burlington House, London. For further information please contact the convenors Haydon Bailey <[haydonbailey@btconnect.com](mailto:haydonbailey@btconnect.com)> and John Gregory <[john@jgregory.demon.co.uk](mailto:john@jgregory.demon.co.uk)>. Details will appear soon on the TMS website: <<http://www.tmsoc.org/>>.

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## >> **Future Meetings of Other Bodies**



**Seventh International Organization of Paleobotany Conference**  
Bariloche, Argentina 21 – 26 March 2004

This conference takes place at the Llao Llao Hotel and Resort on the Andean Range. The VII IOPC is open to all those interested in fossil plants as well as scientists linked to plant biology and geology disciplines. For additional information, please check the meeting Web page at <<http://www.iopc2004.org/>> or contact the organizer by e-mail to <[info@iopc2004.org](mailto:info@iopc2004.org)>.



**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](mailto: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, e-mail <[Mike.Bassett@nmgw.ac.uk](mailto:Mike.Bassett@nmgw.ac.uk)>).



**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 who 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 palaeontological content of the Patagonia. Congress sessions will be held from 19th April to 23rd 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/>>.



**10th International Symposium on Early Vertebrates/Lower Vertebrates**  
Gramado, RS, Brazil 24 – 28 May 2004

Subjects covered will include intercontinental and interhemispherical stratigraphic correlations based on lower/early vertebrates (Palaeozoic); palaeoenvironments/geochronological dating based on early vertebrate faunas, correlations of marine/non-marine fish-bearing strata, systematics and evolution of fossil and extant agnathans and fishes and basal tetrapods, IGCP business meetings, oral presentations and posters. There will be a post-Meeting field trip to Devonian, Carboniferous, Permian and Triassic vertebrate localities of the Paraná Basin. An abstracts volume and a special volume of selected papers will be prepared for the Meeting.

For further information visit <<http://www.ufrgs.br/geociencias/evento.html>>.



**2nd London Evolutionary Research Network Fieldtrip 2004**  
Yorkshire Coast (UK) June 2004 (exact date tba)

The next L.E.R.N. fieldtrip is to the Yorkshire Coast this coming June. Planned events include visits to local Museum collections, dinosaur foot prints, collecting fossils, and looking at the surrounding coastal wildlife. This is intended to provide an opportunity for fieldwork experience and to bring together students from London who are interested in all aspects of evolutionary research.

The first L.E.R.N fieldtrip, last June, was to the Isle of Wight; it was co-organised by Julia Heathcote and Ursula Smith. A party of nineteen people between the ages of 20 and 75 went on the trip; they represented five different academic institutions in London (UCL, NHM, Imperial College, Birkbeck, Queen Mary), encompassing eight different scientific departments (e.g. Earth Sciences, Biology, Anatomy and Physiology). The trip included fossil collecting at Alum Bay, a guided walk from the Dinosaur rich Wealden deposits to Whitecliff Bay (Tertiary Molluscs collecting), a visit to Dinosaur Isle Museum, and rock pooling at Hanover point. For a more detailed account visit our website <<http://www.anat.ucl.ac.uk/research/learn/>> and for more information on this year's trip, please contact Aaron Hunter <[aw.hunter@geology.bbk.ac.uk](mailto:aw.hunter@geology.bbk.ac.uk)>.



**XI International Palynological Congress (IPC2004)**  
Conference and Exhibition Centre, Granada, Spain 4 – 9 July 2004

This international conference will bring together all those people actively involved or interested in the study of pollen from a wide variety of standpoints (botany, biology, environmental sciences, medicine, palaeontology, sedimentology, archaeology). Symposia include: Pollen biology, Pollen and spore morphology, Aerobiology, Pollen and allergy, Entomopalynology and melissopalynology, Forensic palynology, Palaeopalynology and evolution, Quaternary palynology and World pollen databases. The meeting includes a number of pre- and post-congress fieldtrips to Andalusia, south-eastern Spain, Morocco, central Spain, Camino de Santiago-Picos de Europa, Canary Islands, Balearic Islands.

Further details can be obtained from the Technical Secretary (tel +34 958 208650, fax +34 958 209400, e-mail <[eurocongres@eurocongres.es](mailto:eurocongres@eurocongres.es)>), and on the Congress website at <<http://www.11ipc.org/>>.



**Predator-prey interactions:  
experimental and field approaches in biology and paleontology**  
University of Washington, San Juan Islands, USA 19 July 19 – 21 August 2004

Predation, which plays a key role in many ecosystems and may have been critical in shaping the evolution of life on our planet, provides a rich source of data of interest to biologists and paleobiologists. This course provides training in experimental and field approaches used to study predator-prey interactions and is designed broadly and flexibly to include diverse organisms from various environments. The students will be trained in a wide range of research methods, including both biological and palaeontological perspectives. The lectures will review behavioural models (ESS, OFT, *etc.*), ecological aspects of predator-prey interactions, the long-term evolutionary consequences of predation, experimental/field methods used to study predation in modern environments, and data acquisition strategies used by palaeontologists in the fossil record. Lectures, laboratory exercises, and field activities will be explicitly integrated. Students will also be required to conduct a small, independent research project during the course. Several field trips (including boat dredging) will be included to acquaint students with

practical aspects of research on predator-prey interactions. The field trips may also serve to obtain data for individual student projects. The class is at the graduate student level, but exceptionally qualified undergraduate students will also be considered. We also encourage applications from foreign institutions. Enrollment limited to 12 students. Applications are due on 1st March and financial aid is available for qualified applicants (anticipated expenses may include tuition, room and board, travel and other education or living expenses). To download forms and obtain more information visit <<http://depts.washington.edu/fhl/classinfo.html>>. If you have any questions regarding application and financial aid procedures, please contact FHL at <[fhladmin@u.washington.edu](mailto:fhladmin@u.washington.edu)>. Find out more about Friday Harbor Laboratories at <<http://depts.washington.edu/fhl/>>. Should you have any questions regarding this course, its content, logistic aspects, and its educational and research goals, please contact the instructors, Michal Kowalewski <[michalk@vt.edu](mailto:michalk@vt.edu)> and Lindsey Leighton <[leighton@geology.sdsu.edu](mailto:leighton@geology.sdsu.edu)>.



**32nd International Geological Congress**  
Firenze, Italy 22 – 28 August 2004



**Computer techniques in the modelling and analysis of biological form,  
growth and evolution**

This is the first of the general symposia planned in section G17 (Palaeontology) of the Congress, and will encompass the following five topics:

- Theoretical morphology of biological skeletons: This topic includes all techniques for generating and displaying models of biological skeletons. Different approaches will aim at modelling morphology alone, or at modelling the growth and constructional processes that govern skeletal morphology.
- Morphogenesis of colour, relief and structural patterns: Unlike the foregoing topic, which has long been the domain of palaeobiologists, this aspect has been largely studied by biologists. It deals with smaller-scale patterns on or within skeletal parts. Of special interest to palaeobiologists are the modelling of morphogenetic programmes producing surficial patterns on shells that grow by marginal accretion, and the modelling of the genesis of microstructures in these shells.
- Modelling of evolutionary processes: This is a little developed area of computerized modelling but one that has a high potential. It embraces all aspects of the modelling of evolution, and contributions integrating evolutionary and morphological modelling will be especially welcome.
- Computer-assisted statistical and morphometric techniques: This topic is concerned with applications of geometric morphometrics to problems in the analysis of shape-variation in organisms, though with particular emphasis on advances in Geometric Morphometrics in the spirit of Bookstein, Dryden, Kendall, Kent and Mardia.
- Computer-assisted imaging techniques applied to palaeobiology: This topic will embrace applications of results accruing from image-analytical aspects of morphometrics. Although connected to the foregoing topic, this field involves a different area of expertise.

The symposium will take place over half a day, and will consist of approximately six to eight oral contributions, some from invited speakers. A poster session in connection with the symposium is possible, and can be used to host contributions that cannot be accommodated in the oral part of the symposium.

Since the International Geological Congress is very large, funds will not be available to subsidise symposium organisers and invited speakers. However, a Geohost program will be available, mainly to help individual scientists from developing countries to help cover their attendance costs. Information on this will be available on the Congress website at <<http://www.32igc.org/home.htm>>. Contact the organizers for more information: Enrico Savazzi (Uppsala University <[enrico.savazzi@pal.uu.se](mailto:enrico.savazzi@pal.uu.se)>) and Richard A. Reymont (Swedish Museum of Natural History <[richard.reymont@pal.uu.se](mailto:richard.reymont@pal.uu.se)>).



**Chemosynthetic communities through time (32nd IGC)**  
Session T-18.4 at the International Geological Congress

The aim of this session is to gather together researchers interested in the evolution of chemosynthetic faunas, both microbial and macrofaunal. The convenors are Crispin Little <[c.little@earth.leeds.ac.uk](mailto:c.little@earth.leeds.ac.uk)>, Roberto Barbieri <[barbieri@geomin.unibo.it](mailto:barbieri@geomin.unibo.it)> and Kathy Campbell <[ka.campbell@auckland.ac.nz](mailto:ka.campbell@auckland.ac.nz)>.

The session will have a half-day duration, and will include up to ten standard oral presentations (including invited presentations). Standard oral presentations have a 15 minute duration, including time for questions. Invited speakers include Crispin Little (Leeds University), Jack Farmer (Arizona State University), Lisa Levin (Scripps Institution of Oceanography), Antje Boetius (Alfred Wegener Institute for Polar and Marine Research) and Marco Taviani (Consiglio Nazionale delle Ricerche). Deadline for submission of abstracts and initial registration is 10th January 2004.

Through the generous sponsorship of NASA Astrobiology Institute the registration cost (€430) will be covered for up to six individuals whose submitted abstracts are selected by the convenors to give oral presentations. Costs will be reimbursed after the conference.

The second circular for the 32nd IGC is now available on the Web at <<http://www.32igc.org/home.htm>>. This lists registration details and deadlines for submission of abstracts and various payments for the Congress. The circular also has details of a post-congress fieldtrip P 07 – Fluid expulsion and authigenic carbonates in Miocene foredeep and satellite basins (northern Apennines) that may be of interest (see <[http://www.32igc.org/circularN-field05\\_1.asp](http://www.32igc.org/circularN-field05_1.asp)>). The Organizing Committee will help individual scientists mainly from developing and East-European Countries to attend the Congress by partially subsidizing their expenses via the GeoHost Program <<http://www.32igc.org/circular-gen07.htm>>.



**Paleobiodiversity and major biotic changes in Earth History**  
(Session G-17.3, International Geological Congress)

Palaeontological research on biodiversity has concentrated on global-scale patterns of diversity of taxa and of broad ecological groups, especially with respect to mass extinctions. However, biodiversity was originally defined to include all biological levels from genetics to ecosystems and landscapes. Here we invite papers that address any biodiversity level, or relationships between levels, with an emphasis on radiations and background trends through time.

Palaeontology provides historical perspectives from long-term patterns, and therefore complements studies of living biodiversity. After several decades of research however, there is still no satisfactory universal model for taxonomic biodiversity that integrates ongoing ('maintenance') and historical processes. Therefore we particularly encourage papers that identify problems which currently hinder our progress towards an integrated theory of biodiversity and suggest ways forward.

Papers may be based on any group(s) of organisms. Possible subjects include: measurement and analysis of biodiversity; development of open-access databases; sampling controls; phylogenetic constraints, including molecular vs palaeontological patterns; modelling (e.g. causal links between earth system processes and life processes); methods for investigating controlling factors; problems of scale (e.g. relative importance of ecological, regional and global factors); roles and relative importance of tectonic, eustatic, climatic, oceanographic and biogeochemical factors; proxies for, and possible roles of, nutrients; Adaptive innovations, including role of symbioses.

For further information feel free to contact the convenors: Francesca Bosellini <[frabos@unimore.it](mailto:frabos@unimore.it)>, Gian Luigi Pillola <[pillolag@unica.it](mailto:pillolag@unica.it)>, or Brian Rosen <[B.Rosen@nhm.ac.uk](mailto:B.Rosen@nhm.ac.uk)>.



**10th Meeting of PhD students in Evolutionary Biology**  
Preston Montford Field Centre, Shropshire, UK 29 August – 3 September 2004

The meeting will bring together PhD students from all over Europe to discuss current topics in evolutionary biology. Students are encouraged to present their research, which can be at any stage. The conference is open to 100 PhD students and registration has begun. Topic sessions will include: Palaeobiology, Experimental and Microbial Evolution, Population Genetics and Genomics, Phylogenetics, Coevolution, Life-history Evolution, Behavioural Ecology, and Ecology and Conservation. Please see our website <<http://students.bath.ac.uk/bspght/>> or contact Jessica Pollitt <[bspjrp@bath.ac.uk](mailto:bspjrp@bath.ac.uk)> for further details.



**4th International Bioerosion Workshop (IBW-4)**  
Prague (Czech Republic) 30 August – 2 September 2004

The aim of the workshop series is to combine the knowledge of biologists (working mainly in reef ecosystems) with the experience of palaeontologists interested in bioerosion of all types of substrates (reefs and other calcareous matters, wood, bone, *etc.*). All participants should communicate their results or problems as talks, posters or presentations of specimens. The workshop will be held at the Czech National Museum in Prague. Several additional days of field trips are planned during and prior to the meeting (*e.g.*, Devonian and Jurassic reef facies, Cretaceous and Miocene rockgrounds and hardgrounds, Miocene bored mollusc deposits, recent wood borings). For information please contact: Dr Radek Mikuláš, Institute of Geology, Czech Academy of Sciences, Rozvojová 135, CZ-165 00 Praha 6; e-mail <[mikulas@gli.cas.cz](mailto:mikulas@gli.cas.cz)>.



**64th Annual Meeting of the Society of Vertebrate Paleontology**  
Denver, Colorado, USA 3 – 4 November 2004

The Meeting will be held at the Adam's Mark, Denver, and the Denver Museum of Science and Nature. For further details visit the website: <<http://www.vertpaleo.org/meetings/>>.



**Geoscience in a Changing World**  
Colorado Convention Center, Denver, USA 7 – 10 November 2004

Details of the 2004 GSA Annual Meeting & Exhibition are on the conference website at <<http://www.geosociety.org/meetings/2004/>>.



**Society of Integrative and Comparative Biology**  
San Diego, California 4 – 8 Jan 2005

See <<http://www.sicb.org/meetings/2005/index.php3>>. The following two items are part of this meeting.



**Symposium on Terminal Addition, Segmentation, and the Evolution of Metazoan Body Plan Regionalization**

Recent insights into the developmental basis of body plan specification provide a new perspective upon major patterns of Metazoan diversification. Terminal addition, a process by which the body of bilaterian animals grows at a posterior growth zone that is most clearly displayed in segmented animals, is a common condition found among disparate metazoan groups. Terminal

addition is both a morphologic and a developmental phenomenon. Consequently, it can be examined through the study of development of modern organisms where molecular tools are available for the comparison of developmental process among taxa. The symposium aims to balance discussion of developmental mechanisms against historical evidence chronicled in the phylogenies of both living and fossil groups. We hope that it, and the resultant volume, will play a significant role in emphasizing the strengths of an integrated approach to the evolution of posterior body patterning. Sponsored by: SICB Divisions of Evolutionary Developmental Biology, Systematic Biology, Vertebrate Morphology and Invertebrate Zoology, the Paleontological Society and the Palaeontological Associations. Organizers: Nigel Hughes <[nigel.hughes@ucr.edu](mailto:nigel.hughes@ucr.edu)> and David Jacobs <[djacobs@ucla.edu](mailto:djacobs@ucla.edu)>



**Evolution and Development of the Vertebrate Dentition**

The programme includes the following speakers: Moya Smith (KCL, UK; *Developmental models for the origin of vertebrate dentitions*), Philip Donoghue (Bristol, UK; *Evolution and development of the skeleton in the earliest vertebrates*), Anne Huyseune (Ghent, Belgium; *Patterning of development in tooth replacement in osteichthyan dentitions*), Robert Reisz (Toronto, Canada; *Origin of dental occlusion in tetrapods, signals for terrestrial vertebrate evolution*), Tim Mitsiadis (KCL, UK; *Recovery of teeth in birds*), Renata Peterkova (Czech; *Phylogenetic memory of developing mammalian dentition*), Todd Streebman (New Hampshire, USA; *Genetics and development of the cichlid dentition*), Ken Weiss (Penn State, USA; *Evolutionary genetics of dental development*), Paul Sharpe (KCL, UK; *Development and evolution of dental pattern*) and Jukka Jernvall (Helsinki, Finland; *Mammalian dental diversity*). Sponsored by SICB Divisions of Evolutionary and Developmental Biology, Vertebrate Morphology, Cell Biology, and Systematic and Evolutionary Biology (primary). Organizer: Moya Smith <[moya.smith@kcl.ac.uk](mailto:moya.smith@kcl.ac.uk)>.



**Geologic problem solving with microfossils**  
Rice University, Houston, Texas, USA. 6 – 11 March 2005


The aim of the meeting is to draw together a diverse array of geoscientists to showcase the problem-solving power of microfossils in a variety of geologic settings. Call for abstracts via the website from 1st April to 14th October 2004. Registration begins 6th September 2004, via the website. For further details visit the conference website <<http://www.sepm.org/microfossils2005.htm>>, or contact <[garry.jones@unocal.com](mailto:garry.jones@unocal.com)>.



**Tracking Dinosaur Origins: the Triassic/Jurassic terrestrial transition**  
Dixie State College of Utah, St. George, Utah 22 – 24 March 2005

(Followed by the Utah Friends of Paleontology Annual Meeting, 25–26 March). The Triassic/Jurassic transition is a critical time in Earth history, recording the origins and early radiation of dinosaurs, pterosaurs, crocodylians, mammals, and several other significant Mesozoic vertebrate clades.

Additionally, a major interval of faunal stepwise extinction is recorded in both the marine and terrestrial environments that may be linked to impact events, setting the stage for the ascendance of dinosaurs to a position of dominance for the remainder of the Mesozoic. Current research in this area is dynamic, with important implications for a number of areas in palaeobiology and geology. A number of recently discovered fossil localities in a little researched area of southwestern Utah preserves a thick sequence of rocks spanning the Triassic/Jurassic interval. These localities are proving to be a catalyst for new studies on this time period. Many of these studies have centered on the basal Jurassic St. George Dinosaur Tracksite at Johnson Farm. This remarkable new site preserves an extraordinary series of track levels along the margin of a Hettangian lake ("Lake Dixie"); associated fossil plants, invertebrates, fish, and dinosaur remains make it particularly significant. These discoveries, along with a new interpretive centre slated to open in the Summer of 2004, provide an impetus to bring scientists together to discuss terrestrial faunas across the Triassic/Jurassic transition in a dramatic geologic setting unfamiliar to most attendees. A proceedings volume to be published by the New Mexico Museum of Natural History and Science, and a full colour overview volume, are planned by the Utah Geological Survey for initial distribution to attendees at the conference. This volume will include short review papers on areas of critical interest regarding the Triassic/Jurassic terrestrial transition in various areas of the world, summary papers on these rocks, and their preserved fossils in southwestern Utah. Preliminary programme: March 22 – plenary papers; 23 – general conference papers; 24 – field trip: Triassic/Jurassic geology and palaeontology in the St. George and Zion National Park areas. Conference participants may fly into St. George, Utah directly, or speakers may fly into Las Vegas, Nevada and then be transported by volunteers to St. George. Conference participants are invited to remain for the Utah Friends of Paleontology Annual Meeting, which will include additional afternoon field trips on March 25 and 26. Information on the St. George tracksite may be viewed starting on page 4 of Survey Notes v. 34, no. 5. <<http://geology.utah.gov/surveynotes/snt34-3.pdf>>




**North American Paleontological Convention**  
Dalhousie University, Halifax, Nova Scotia, Canada 19 – 26 June 2005

The meeting will include field trips to Horton Bluff (Dev/Carb boundary-early tetrapod trackways), Wassen's Bluff (Tri/Jur-link fossil between dinosaurs and mammals), Joggins (Carboniferous-world heritage site), and Arisaig (a world class Silurian invertebrate site). Major field trips will include the Gaspé Peninsula (Quebec).


The local organizer is David B. Scott (Centre for Environmental and Marine Geology, Dalhousie University, Halifax, Nova Scotia B3H3J5 Canada).

The meeting website is at <<http://www.dal.ca/~es/staff/dbscott/scott.htm>>.



**Fourth International Symposium on the Cambrian System**  
Nanjing, China 18 – 24 August 2005

More than thirteen years after the successful *Third International Symposium on the Cambrian System* in Novosibirsk, former Soviet Union (1990), the time has come to focus on a new target and to create a platform for all scientists working on the Cambrian to meet and calibrate their information. This meeting will accumulate not only the most influential colleagues but create the intellectual guidelines for the next decades. The symposium will focus on (i) meetings to discuss latest research findings relating to the System, especially in the global context, (ii) discussions and workshops of the IUGS Subcommittee of Cambrian Stratigraphy and related geosciences, and (iii) field trips to examine the best exposed Cambrian rocks in China and South Korea. Further details can be found on the symposium website <<http://www.nigpas.ac.cn/cambrian-conference.htm>>.



**15th International Symposium on Ostracoda**  
Freie Universität Berlin 12 – 15 September 2005

Ostracodology – linking bio- and geosciences. Visit the symposium website for further details <<http://userpage.fu-berlin.de/~palaeontiso15/iso15-main.htm>>



**9th Symposium on Mesozoic Terrestrial Ecosystems**  
Cambridge, UK July 2006

The 9th Symposium on Mesozoic Terrestrial Ecosystems (sponsored by the Palaeontological Association) will take place at the University of Cambridge in July 2006. The scientific programme will run over three days, with a short pre-conference field trip to Lower Cretaceous localities on the Isle of Wight, and a longer post-conference field trip to explore the Mesozoic succession of southern England. Further details will be posted later this Spring and in the next issue of the PalAss Newsletter. Preliminary enquiries can be made to <[ucgassue@ucl.ac.uk](mailto:ucgassue@ucl.ac.uk)>.

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Please help us to help you! Send announcements of forthcoming meetings to <[newsletter@palass.org](mailto:newsletter@palass.org)>.

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# Book Reviews

## Life on a Young Planet

A.H. Knoll, 2003. Princeton University Press. £19.95, ISBN 0-691-00978-3

“Science is a richly social endeavour”. So says Professor Andy Knoll in *Life on a Young Planet*. The author, an eminent Harvard palaeobiologist, brings considerable empathy to the turbulent history of research into the early biosphere, telling it as seen through his own eyes. In this respect, it shares something of a gameplan with the *Cradle of Life* by Bill Schopf, in which the rewards and dangers of self-promotion in palaeontology were also explored at length. No love is lost between Professors Knoll and Schopf, of course, and the latter’s putative 3.5 Ga old Apex chert ‘microfossils’ are examined in some depth and are here rejected. “My own guess,” he writes, “is that the Warrawoona structures are mineral chains draped by an organic film.” As the book makes clear, Knoll was witness to our first intensive investigations into the Apex ‘biota’ and shared in our very great puzzlement about the meaning of it all.



The author stands firmly besides a biogenic explanation for the carbon isotopic fractionation in the early Archaean, and lays out his belief in the early predominance of photosynthesis. I am not convinced by this, however, nor am I satisfied that any of the so-called ‘microfossils’ reported from South Africa are acceptably biogenic, including the rather humble object shown in Figure 4.6 herein. And even Rasmussen’s hopeful filaments from the 3.2 Ga old Sulphur Springs black smokers (accepted by Knoll as “convincing”) surely need much more critical scrutiny – they also look like mineralic filaments.

The problem of telling biogenic from abiogenic complex structures is a major concern for astrobiology today, though it doesn’t really get much of an airing in this book. But there is a truly superb and ironic example of abiogenic self-organizing structures on the front cover. It is a painting by the German expressionist Max Ernst in which drops of black paint have been laid over miscible layers of damp yellow paint, to give the impression of a landscape with thorn bushes. But here the seeming biology is really a kind of physics – a form of dendrite known to Materials scientists, I think, as the coffee ring effect. (For pretty digital artefacts of this kind, take a look at Stephen Wolfram’s book *A New Kind of Science*.)

Knoll also questions the biogenicity of that other icon of Precambrian palaeobiology, the Gunflint chert (c. 2 Ga). He suggests that the macromorphology of the stromatolites is simply that of siliceous sinters onto which microbes have dropped. He also challenges the plausibility of Schopf’s

so-called Volkswagen syndrome (*i.e.*, that external stasis conceals internal evolution), suggesting that morphology does indeed equate with biology. This view takes him, again, to the point where cyanobacteria and their metabolic machinery are imagined to have evolved very early.

Later chapters lucidly explore the ongoing debates about the origins of life, Archaean habitats, the earliest eukaryotes, the Ediacara biota (turning the latter into a sock in a rock), and the Cambrian explosion (here conjured up by oxygen). There is, however, no over-arching theme to tie these various threads together, although the book ends with nodding genuflections to Popper and Gaia (fair enough) and even, according to my reading, towards the prevailing American theocracy (Stephen Jay Gould, his late Harvard colleague, would never have done that, bless Him).

Professor Knoll explores early life on Earth with considerable elegance and insight, bolstered by his usual peerless scholarship. The book, which is excellent value for the money, should be recommended reading for anyone studying early biosphere evolution, and is likely to remain the most influential summary for many years to come.

**Martin Brasier**

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## Celebrating the Life and Times of Hugh Miller: Scotland in the Early 19th century

Lester Borley (ed.) 2003. Cromarty Arts Trust and Elphinstone Institute of the University of Aberdeen, Cromarty, 352 pp. ISBN 0 906265 33 9. Soft cover, £13.50.

*The Cruise of the Betsey and Rambles of a Geologist*, introduction and notes by Michael Taylor. National Museums of Scotland, Edinburgh, 576 pp., 2003. ISBN 1 901663 54 X. Soft cover, £20.00.

So much has been written about Hugh Miller (1802–1856) recently that the reviewer can no longer wonder at how such a noted public figure of the early Victorian era could have been entirely forgotten. And yet that was the case some years ago. I remember buying his popular works on geological and palaeontological topics – *The Old Red Sandstone*, *Asterolepis, or the Footprints of the Creator*; *Cruise of the Betsey*; *Testimony of the Rocks* – for a few pounds in second-hand bookshops. Even now, various editions of these works may be bought quite cheaply, which probably reflects the sheer numbers in circulation. There is no question that Hugh Miller was a popular author in his lifetime, and his wife Lydia made sure that his books remained in print long after his death.

The first book of the two books under review is unusual. It stems from a three-day meeting held in Cromarty in October, 2002, a meeting that I would love to have attended. There were contributions from geologists and palaeontologists of course, assessing Miller’s scientific achievements, but also from historians, folklorists, ministers of religion, politicians, and noted Scots worthies. The thirty chapters are divided into four sections, representing sessions at the meeting, on Miller in the 19th century context, ethnography and folklore, geology and natural

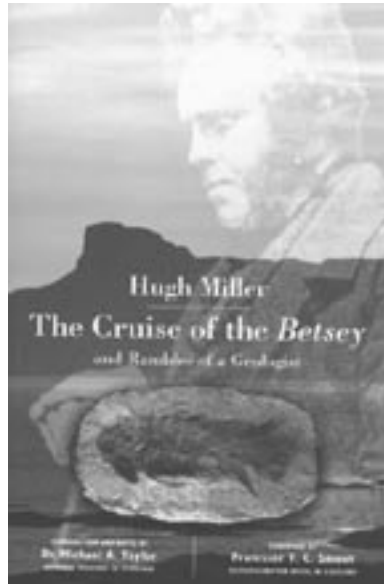


history, and church and society. This diversity represents Miller's diversity of interests. The broad range of the contributors allows us to appreciate Miller's impact, but there is one question that none of the authors can tackle.

In setting the scene, the first three chapters introduce such topics as the decline of Gaelic speaking, the Highland clearances, the Scottish enlightenment, industrialization and urbanization, the growth of natural history as an acceptable pursuit, and the crisis in the Scottish church. We hear a little of Prince Albert's and Queen Victoria's growing fascination with Scotland, but not much about the preceding establishment of the Scottish myth by Sir Walter Scott in the 1820s. Perhaps this was an Edinburgh phenomenon that was largely complete by 1839/1840 when Miller moved to the capital city.

The eight chapters on ethnography and folklore recount aspects of Hugh Miller's life that are perhaps least familiar to modern readers. And yet it appears that Miller can be seen to have been a leading figure in that field. He was one of few to record the old stories and myths of his part of Scotland, and these were some of his first published works, sent by him as a young man to the *Inverness Courier*, and later published in *Scenes and Legends of the North of Scotland* and *A Noble Smuggler and Other Stories*. Some of the stories were recorded by other writers, but most are unique to his collections. He contributed more than other folklorists of the time since he was scrupulous in recording the locations of the supposed events, some of them supernatural, and in rendering the stories with graphic detail and writerly verve. His enthusiasm was to record everything he could about his native Cromarty, and to get the details right, but also to engage his reader. The one surprise throughout is that Miller apparently never learned Gaelic. Although Cromarty is a coastal town, and in Miller's day English-speaking, he was emotionally attached to the Gaelic-speaking Highlanders he encountered there and on his wanderings. Indeed he was one of the leading voices to speak for the Highlanders in his famous attacks on the Government and on the Duke of Sutherland, in *Letter from one of the Scotch People* and *Sutherland as it was*.

The nine chapters on geology and natural history include assessments of Hugh Miller's place in the history of geology with respect to contemporaries in England, and especially a comparison of his role as provincial collector versus the metropolitan science/philosophy of his fellow Scots Lyell and Murchison. Miller was a stonemason; they were gentlemen. Miller was well regarded, like all collectors, but patronized; it was somehow not his role to philosophize or present his own scientific descriptions. He could be seen as a popularizer of the subject in his books, but being located far from London, he could hardly have worthwhile views. This was perhaps partly to do with social class, but not entirely, since many other provincial enthusiasts were definitely not from the working class, but, like Gideon Mantell, suffered from the fact that they had to earn



their living and could rarely visit the scientific meetings in London. Nigel Trewin and Philippe Janvier show us how clear Miller was in his observations on the Old Red fishes he collected. John Hudson gives a fascinating account of the geology of the island of Eigg, telling the story of how he re-traced Miller's footsteps in the 1960s and pieced together a modern interpretation of Miller's observations in the 1840s. Simon Knell and Mike Taylor describe Miller's work as a collector, and Michael Collier reconstructs some of his dealings with contemporary scientists.

The fourth section of the book, on church and society, includes eight chapters on the disruption in the Church of Scotland in 1843, and Miller's role. Trouble had been brewing since the late eighteenth century, especially on the issue of patronage. The law insisted that local landowners had the authority to select a minister and present that person to their future flock. The parishioners had little or no say. The dispute was about democracy, but also about language – the Gaelic-speakers had been poorly served by the established Presbyterian Church – and authority – freelance evangelists were having a huge impact in the north of Scotland, drawing people away from the established, lowland, moderate, metropolitan Church. Miller was summoned to join the fray in 1839. He had been noticed by the opponents of the established Church in Edinburgh for his journalism and especially for his *Letter from one of the Scotch People*, and he was appointed as editor of a paper he launched in January 1840, *The Witness*, which was to be the campaigning mouthpiece of the rebels. Thanks to Miller's tireless efforts – he wrote most of the paper himself, sometimes working frenziedly for 18 hours a day – and the political manoeuvrings of the paper's wealthy supporters, nearly half the Presbyterian Church seceded in May 1843, the Disruption, titling itself the Free Church. Throughout the Highlands and Islands, whole parishes seceded. In other areas, parts of congregations followed their ministers, and new churches were built. Church-building proceeded apace, both sides vying to have the larger, grander building. That is why many Scottish towns and villages boast two substantial churches, often glowering at each other from neighbouring sites.

How did Miller regard his move from Cromarty to Edinburgh? The invitation to *The Witness* must have fulfilled his dream, of wide acceptance and of a definitive move upwards socially. His social status in Cromarty was fluid, and was probably of no concern to him. Social status was more important in Edinburgh, with clear distinctions indicated by dress, by location, by clubs. And yet, in Edinburgh, Miller made a point of emphasizing his lowly origins as a stonemason – the famous photograph taken in 1843 was posed, and taken long after Miller had seriously put chisel to rock. He hurtled up and down the Grass Market in an anachronistic Highland plaid and bonnet. Perhaps he was confident that his writing placed him on a par with the gentlemen and University scholars, and he could create a sensation by reminding people of his exotic provenance.

Miller was indefatigable. He wrote on a huge breadth of subjects. He was a journalist at heart, preferring to write fast and abundantly on issues of huge moment. Many of his writings – most notably his journalism in *The Witness* – are forgotten. Only an enthusiast for Scottish church history could make anything of the day-to-day disputes to which he turned his robust prose. But the books are a fascinating legacy. No-one was quite like him, combining acute observations of geology and natural history with profound religious essays, but also, surprisingly, historical narrative with seemingly credulous accounts of supernatural happenings. I learned from this book that Miller had in mind a *magnum opus* to crown his earlier books, on the geology of Scotland. It is perhaps just as well he never wrote that: his descriptions of geological phenomena

on the small scale, and of specimens he collected, are superb, but he did not engage in many of the larger-scale geological debates. He had only limited contacts with geologists in London, Cambridge and Oxford, and almost none with scientists elsewhere in Europe. In Edinburgh, he could have had access to the books and journals of the learned societies, but there is no evidence that he read these. Miller was indeed a provincial scientist, but unlike others of that kind, he turned his local observations into something special and fascinating.

The first book under review, *Celebrating the Life and Times of Hugh Miller*, is an excellent work, notable for the eclectic mix of chapters, and for its reasonable price. Some of the chapters could have been omitted without loss, but most are useful. I regret the absence of an index, and of a full bibliography of Miller's works.

Mike Taylor has added to the revival of interest in Hugh Miller with a reprint of *The Cruise of the Betsey*, perhaps the most accessible work to modern readers. The *Betsey* was a yacht that belonged to the Free Church, and it toured the Hebridean islands with Miller's boyhood friend John Swanson, Minister for the Small Isles, on board. Swanson stopped off at each of the inhabited islands, and performed his ministry, giving services out of doors, or in someone's house. Mike Taylor provides a 64-page introductory section in which he provides a thorough overview of Miller's life and enthusiasms, as well as comments on retracing Miller's steps. Taylor has also added footnotes to the facsimile text, explaining allusions to people, rocks, fossils, plants, dialect terms, and Gaelic locations, and a 36-page glossary, longer notes, and an index.

The one question about Miller that cannot be answered is whether he was an agreeable and engaging companion. I think this lies behind much of the current fascination with his work. His portraits, with his scowl, his broad face, and his vast mutton-chop whiskers, suggest he was serious, perhaps dour and harsh. His writings on political and religious debates can be blunt and sometimes brutal in their demolition of opposing views. And yet, limited contemporary accounts suggest he was a fascinating companion, free in his conversation with all the educated women in Cromarty. His humanity shines through in *The Cruise of the Betsey*. So why did he shoot himself?

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### The Cretaceous World

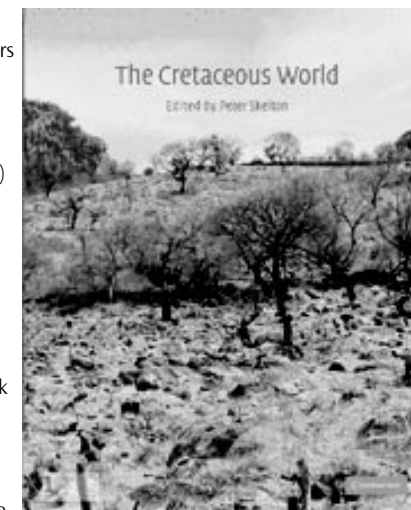
Edited by Peter Skelton. 360 pp. illustrated. The Open University.  
Paperback, ISBN 05215 38432, £27.95

This is an attractive, well-illustrated volume packed with information and ideas. The basic justification for the compilation is that the Cretaceous world had significantly higher global temperatures and sea levels and hence is an example of a 'greenhouse world' quite different from the present day world with which we are familiar. Studying the Cretaceous may give us insights into the likely effects of global warming. Furthermore, of course, the Cretaceous ended in a major extinction event, which it is increasingly being accepted was probably due to the impact of a large extra-terrestrial body 65 million years ago. Thus studying the upper

boundary of the Cretaceous gives us insights into mass extinctions and the controversies that still surround them. However, although specifically aimed at the Cretaceous, the arguments used to reconstruct the Cretaceous world, especially the discussions of geochemical cycles, are relevant to all past environmental reconstruction, so this is a generally useful book, not just one for Cretaceous specialists. Furthermore, many chapters place Cretaceous phenomena in a longer historical context, thus enabling comparisons of the Cretaceous with older and younger geological periods.

*Cretaceous World* falls into three broad sections. The first and largest is devoted to reconstructions of what the Cretaceous world was like, covering topics such as palaeogeographic reconstructions of Cretaceous continental positions and seaways, Cretaceous sea levels, Cretaceous climates and their effects on marine and terrestrial biotas. The topics are introduced from first principles and generally very clearly explained. Section two covers biogeochemical cycles, especially of carbon and sulphur, effects of volcanoes, a review of the major carbon sinks and modelling of the Cretaceous climate. Again these chapters work up from general principles to quantitative modelling, with adequate discussion of the limitations of the models used. The final section is devoted to the end-Cretaceous, or K-T, mass extinction. It starts by looking at how mass extinctions are recognized and discussing the evidence for, and controversies surrounding, the K-T mass extinction in particular. A review of ideas about the causes of mass extinctions prior to the impact hypothesis for the K-T mass extinction follows. Finally the evidence that the Chicxulub crater is the impact site and the likely effects of the Chicxulub impact are covered, these two chapters concentrating more on the evidence of impact than on the effects on the world's biota. In these reviews, alternative ideas about causes, such as effects of major volcanic episodes in the earth's history, are adequately covered. All chapters are well illustrated and include 'boxes' covering specific topics in more detail.

Inevitably I have one or two niggles. On p. 33 it is shown that published estimates of the age of the Aptian stage are anything but 'absolute', so why are phrases such as 'absolute dates' or 'absolute ages' used throughout the book to refer to estimates based on radioactive decay? 'Absolute' ages, that is accurate ages in years, are a theoretical concept for all but the last 30-40,000 years of Earth's history. All other dates are radiometric estimates, so why not call them radiometric dates? At first glance I thought that all diagrams in which time did not proceed up the page (as in graphic logs) had time going from left to right across the page. Although there is no absolute convention, to me this seems logical for all languages which are read from left to right. Sadly a few diagrams (e.g. figure 4.63) are reversed. This may seem a trivial point but the necessary mental flips in comparing such diagrams do not aid comprehension. Indeed a quick glance at a figure (and how many of us do just that) can give exactly the opposite impression to the one intended if the scale has been reversed with respect to a previous figure. In other cases where there is no



convention at all, one might still expect consistency within a book such as this. So I was surprised that figures 3.8 (c) and 3.9, which show sea-level curves, have the positions of highstands reversed with respect to each other. Similarly, figures 4.56 and 4.61 show the percentage of species of plants with entire-margined leaves plotted against present day mean annual temperature and inferred Cretaceous palaeolatitudes, respectively. But why is the percentage plotted on the X-axis for figure 4.56 and the Y-axis for figure 4.61? Errors and misprints are exceedingly rare. However, on p. 245 the estimate of lava production from the Deccan traps should be  $200 \text{ km}^3 \text{ yr}^{-1}$ , not 20, so it really is about an order of magnitude greater than that for the Laki eruption ( $14 \text{ km}^3 \text{ yr}^{-1}$ ). On the same page, why is the estimate of  $\text{SO}_2$  production from Laki given as  $12.5 \times 10^{10}$  but that for the Deccan traps as  $1.8 \times 10^{12}$ ? At first glance these figures seem to differ by two orders of magnitude, but in fact it is only one.

However, these are minor niggles in an otherwise excellently produced book. I found 'Cretaceous World' extremely informative, easily readable and good value for money. It is perhaps worth emphasizing again that much of the information presented is applicable to all geological periods, not just the Cretaceous. I thoroughly recommend 'Cretaceous World' for professional geologists, students and interested amateurs. There is something for everyone.

**Chris Paul**

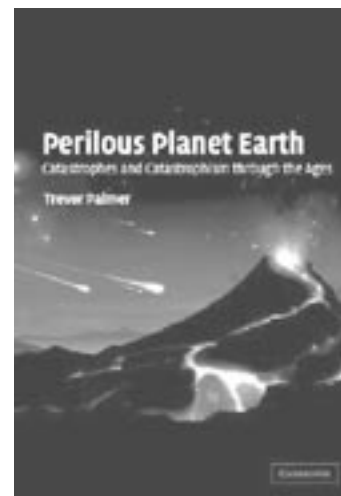
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### Perilous Planet Earth: Catastrophes and Catastrophism through the Ages

Trevor Palmer Cambridge University Press, 2003, 522 pp., ISBN 0 521 81928 8; £45 hardback

This is an unusual book, mainly historical, but with a good leavening of material on modern geological and palaeontological views, and then with some substantial forays into the parascientific literature. It follows closely after a similar, earlier work (Palmer, 1999). Palmer's main thesis is that catastrophism of one kind or another has a major role to play in our understanding of the history of Earth and of life, and indeed of the early history of humans. He recounts how early catastrophic 'theories of the earth', which held sway through the 18th century, and in the work of savants such as Cuvier and Buckland, went into abeyance for over a century following the work of Lyell and others, and re-emerged in the 1950s and 1960s, in the face of much opposition and criticism. The book is a good, and comprehensive (522 pages), overview of the field, although it is marred I feel by some matters of style, and for its inclusion of parascience virtually on a par with mainline scientific writing.

The book consists of 30 chapters in four sections, arranged roughly in historical order. In the first section, from ancient times to 1899, Palmer reviews early catastrophic views about the history of the Earth and of life, then covers the familiar story of the debates through the 1820s and 1830s, the role of Lyell and of Darwin, and the 'triumph' of gradualism. Most of this is well-known material, recounted in many books over the years, and it is well enough summarized. Palmer misses the timing of the debate about extinction though: 'the first faltering steps' in discussing the possibility that species and genera might become extinct (page 27) did not begin with Cuvier; they ended with him.



In the second section, from 1900 to 1979, we hear about neo-Darwinism and gradualism in palaeontology, especially in human evolution. Palmer covers here the minority role of 'neocatastrophists' such as Otto Schindewolf and Digby McLaren, but also Immanuel Velikovsky, and others of that ilk. Here, the author fails to stress the major role of Gene Shoemaker in establishing impact geology as a genuine branch of earth sciences. I am also rather uncertain about linking the punctuated equilibrium debate to the broader theme. Punctuated equilibrium and catastrophism need not go together, and Palmer is wrong (page 181) in claiming that 'evidence for punctuated equilibrium continues to accumulate', indicating that phyletic gradualism has been rejected.

In Section C, from 1980 to the present day, and Section D, an overview of current views, Palmer takes the Alvarez *et*

*al.* paper as his starting point, and argues that catastrophic explanations for many phenomena are now paramount. But here, while I would endorse his general point, that catastrophism is acceptable again (impacts on the Earth have happened, one at least caused a mass extinction (KT), dramatic eruptions and earthquakes have had strong effects in human history), I think he stretches the point too much, too often – there is little, if any, evidence for impact at the PTR, TrJ, or JK boundaries (pages 264–5, 286); periodicity of mass extinctions has been rejected ('undeniable periodicity', page 286); and it's not clear how impact triggered the Pleistocene ice ages (pages 302–3), or their termination (page 307).

The book shows an immense breadth of subject matter, from the origin of life to the debate about Atlantis, Darwinian evolution to classical allusions to comets, the origin of the Universe to the punctuated equilibrium debate. The author has read widely, providing some 129 pages of footnotes in support of his main text. However, he is tentative in too many areas, providing us with lists of quotations from papers and books around a central theme, but often not giving a firm, analytical conclusion. The quotations may lead in a particular direction, hinting, and suggesting, and then the conclusion is assumed later. The conclusion is often right, but the technique does not always work (see above). There are always forceful, but heterodox writers, who provide ample ammunition in support of a generally rejected view (*e.g.* impact at the PTR boundary, rejection of Chicxulub, periodicity of mass extinctions, non-dinosaurian origin of birds), and the technique of cutting-and-pasting quotations from a variety of sources can lead one astray.

Whereas the author is careful in his presentation of former, and current, views in palaeontology and geology, we detect more of himself in the chapters about marginal, or parascientific, topics, such as Velikovsky, the debates about Atlantis, mystical arrangements of the pyramids and other great structures, and catastrophes in archaeological time. We hear about the Society for Interdisciplinary Studies (SIS), of which Palmer is a leading part, which exists to discuss such parascientific topics, and appears to debunk most of them. However, I imagine most people might consider it better not even to lend credence to the ill-thought through claims of people

such as Velikovsky and the searchers after Atlantis. Although of course they used to say that about Heinrich Schliemann and Otto Schindewolf... But then I note from the SIS website that they support Velikovsky's radical re-dating of the Egyptian dynasties, and give links to all kinds of crazy websites that claim that the pyramids were built by little green men, and that human remains have been found entombed in Carboniferous coal... Where does one draw the line between renegades who challenge orthodoxy and crackpots?

PALMER, T.R. (1999) *Controversy: Catastrophism and Evolution*, Kluwer Academic, New York, 452 pp.

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### **Ichnology of a Pennsylvanian Equatorial Tidal Flat – The Stull Shale Member at Waverly, Eastern Kansas**

M. Gabriela Mángano, Luis A. Buatois, Ronald R. West, and Christopher G. Maples. 2002. *Kansas Geological Survey Bulletin 245*. Lawrence, Kansas. 133 pp.

These authors have published together previously on various aspects of the Waverly ichnofauna of eastern Kansas (e.g. Mángano *et al.*, 1998, 1999, 2000), but here they present an authoritative account which integrates ichnological, sedimentological, and stratigraphical data to help interpret the palaeoecology of the ichnofossils, depositional history and regional context of the site, and also its implications for classic ichnofacies models. This paper is not only of interest to ichnologists, but also to sedimentologists because it sets the standard for what can be achieved when these two disciplines are used to complement each other.

From the outset it is obvious that this is going to be a comprehensive account: the aims of the paper are set out in the introduction and range from straightforward descriptions of the ichnofossils to an analysis of the importance of tidal-flat ichnofaunas from an evolutionary perspective. Each of these aims is dealt with in turn and all are fulfilled, although some to a slightly fuller extent than others. Along the way there are also several refreshing discussions on taxonomic philosophy and the role of substrate on the morphology of trace fossils.

The paper begins with a very detailed section of descriptions and interpretations of the sedimentary units of the lower interval of the Stull Shale Member at Waverly (which wouldn't look out of place in a sedimentology journal). Six major subenvironments are identified: sand flat, mixed flat, mud flat, supratidal palaeosols, intertidal runoff channels, and fluvial channels. However, the depositional model, and analyses of palaeocurrent data, and palaeotidal range are left until later sections. The sedimentary structures described in the text are illustrated with numerous, very high quality black and white photographs; however, the legends for these figures often mention particular noteworthy structures or trace fossils, and it would be better if these were indicated in some way in the actual figures.

The vast majority of the paper is devoted to the description of the Waverly ichnofossils. At the beginning of this section there is a short prelude on taxonomic philosophy. The problem

of “lumpers” and “splitters” in body-fossil taxonomy is also present in ichnotaxonomy, with “splitters” erecting a host of new names based on slight differences in morphology whereas “lumpers” tend to group similar forms. Mángano *et al.* agree with most other ichnologists in that the morphology of the trace fossil is the basis for the name; they also emphasise the point that some morphological variations may be due to extrinsic factors, such as substrate type, rather than any behavioural differences, so they should not be used in ichnotaxonomy.

The authors therefore adopt a conservative ichnotaxonomic standpoint in this paper, grouping specimens that show slight morphological variation into one ichnospecies. Twenty-five ichnogenera are identified with generally only one ichnospecies ascribed to each. Some specimens were only diagnosed to the ichnogeneric level or have been left in open nomenclature because poor preservation or lack of bedding plane expression of the structures precluded their ichnospecific assignment. The ichnogenera are described alphabetically; for each there is a discussion on synonymous ichnotaxa, as well as the inferred tracemakers, depositional settings they have been documented in, and stratigraphic ranges. Each identified ichnospecies is then described along with its associated ichnofauna; however, there is no mention here of which unit or subenvironment they are found in. Each ichnospecies is illustrated with several very good quality black and white photographs, which demonstrate the preservational variations, both between and within specimens, and they also allow the non-ichnologist to become familiar with the different ichnofossils. The sheer number of quality figures should make this a useful reference for any future comparative studies. One new ichnospecies is erected, *Protovirgularia bidirectionalis*, which the authors consider is morphologically distinct enough to warrant this; and also represents a unique behavioural pattern, interpreted as a bivalve feeding/grazing trail. On a personal note, the layout of this section should be commended because the description and figures for each ichnospecies are invariably on the same page, and not in some other location that you have to keep flicking back and forth to.



The latter sections deal with the distribution of the ichnofossils, their palaeoecology, the sedimentary environment, sequence stratigraphy and regional context of the site, and also the implications for classic ichnofacies models and evolutionary palaeoecology.

Ichnofossils are only found in three units, which are interpreted as having been deposited in a mixed- to mud-flat environment, intertidal sand flat, and the fill of an abandoned fluvial channel. These occur in a general shallowing upward trend and the highest ichnodiversity is found in the sand flat facies. There is a good discussion of the spatial heterogeneity of the trace fossils in terms of a zonal distribution over the different facies; as well as on a smaller scale within each environment, which may be due to partitioning of resources or local microtopography. The distribution of the ichnofossils is also discussed in terms of their

palaeoecology and environmental controls. Environmental controls such as temperature and salinity are discussed separately, although it is stressed that these factors are intimately linked.

What stands out about this paper is that it includes a discussion on the role of substrate in the resultant morphology of trace fossils. The Waverly site offers a unique opportunity in this respect because the variations in microtopography over the tidal flat produce variations in substrate conditions. Several types of ichnofossils, in particular the bivalve locomotion structures, span these changes in substrate; in some cases chevroned *Protovirgularia* trails grade into bilobate or smooth trails. The authors stress the point that substrate consistency played the main role in producing the variation found in the morphology of the ichnofossils.

The beauty of trace fossils is that they are preserved *in situ*, so they represent a snapshot of a community at a particular point in time. The authors reconstruct the palaeoecology of the ichnofossils by analysing tiering in the sediment, and grouping them into ichnoguilds. The Waverly ichnofauna represents a diverse and complex community of both epifaunal and infaunal animals. Four ichnoguilds are identified: subsuperficial, vagile, deposit-feeding structures of worms and molluscs; very shallow, vagile to semi-permanent, deposit-feeding structures of ophiuroids and arthropods; shallow, vagile, deposit-feeding and predaceous structures; and relatively deep to semi-permanent traces from deposit feeders, suspension feeders, and predators.

The Waverly ichnofauna is also placed in a regional context. The Stull Shale Member outcrops in several other localities in Kansas and the sedimentology and ichnology of the other sites are reviewed. The variation in ichnofossil types, diversity, size, and the degree of bioturbation found at these localities are interpreted as reflecting salinity gradients, with an estuarine setting in the northeast and an open marine setting in the southwest. The high diversity, density, abundance, and, tiering of the ichnofossils in the Waverly tidal-flat are interpreted as indicating that it formed under normal marine salinities and was connected to the open sea.

At this point, the authors challenge the application of traditional wave-dominated shoreline ichnofacies models to tide-dominated shorelines. At Waverly, the *Cruziana* ichnofacies occurs inshore of the *Skolithos* ichnofacies, which is opposite to that found in wave-dominated shallow-marine settings. The *Skolithos* ichnofacies is typical of higher energy settings than the *Cruziana* ichnofacies; and the authors make the point that energy increases towards the shore in wave-dominated shorelines, whereas in tidal setting, energy increases away from the shore. The authors make the case that this is the norm in tide-dominated settings, presenting numerous examples documenting the presence of the *Cruziana* ichnofacies in tidal flats; and that tidal deposits interpreted to have formed in subtidal settings based on the presence of the *Cruziana* should be revised.

Finally, the authors give a brief discussion of tidal flats as sites of evolutionary innovations. Tidal flats are harsh, heterogeneous and unstable environments which are argued to promote adaptive innovations, and this is evidenced by the association of deep-dwelling structures of suspension feeding bivalves, and body fossils of their inferred producers. This suggests that these bivalves were exploiting deep infaunal tiers long before the Mesozoic radiation of the bivalves (Mángano *et al.*, 1998).

For sheer volume of topics covered, this paper is exemplary; and the descriptions and figures of the ichnofossils, as well as the sedimentological analysis, should make it indispensable for future comparative ichnology studies. The discussion on the role of substrate on the final morphology of ichnofossils and challenge to traditional ichnofacies models also make this paper stand out. This paper sets the benchmark for future ichnological studies, and demonstrates what can be achieved when sedimentological, stratigraphical and ichnological data are integrated.

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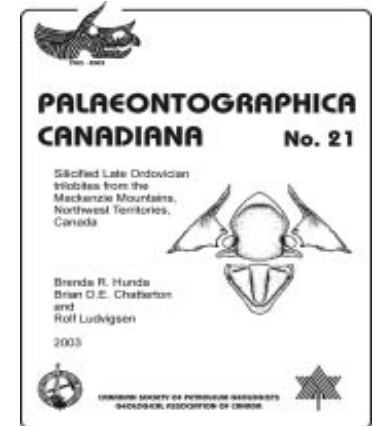
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**Silicified late Ordovician trilobites from the MacKenzie Mountains, northwest Territories, Canada**

Brenda R. Hunda, Brian D.E. Chatterton and Rolf Ludvigsen. 2003. *Palaeontographica Canadiana* no. 21, 87 pp., including 21 pls. ISBN 0-919216-84-6

The Lower Palaeozoic rocks of the southern MacKenzie Mountains have yielded a succession of rich graptolitic and shelly faunas, the latter commonly silicified. Over the last twenty-five years, these have formed the basis for a whole series of publications by Chatterton, Ludvigsen and their co-workers. The present monograph is a welcome addition to knowledge in this field, and deals with a sequence of Cincinnatian (Upper Caradoc-Ashgill) trilobite faunas, extending up to the Ordovician-Silurian boundary. These faunas span the extinction events that occurred in the Rawtheyan and at the base of the *persculptus* Biozone, both of which were probably related to the major environmental changes associated with the Late Ordovician glaciation. These broader issues are not dealt with in detail in the present paper, however, the purpose of which is to document the trilobite faunas that occur and to revise and extend the local trilobite-based biostratigraphy.



Thirty-five trilobite species (thirteen newly named) belonging to fourteen families are described. Cheirurids are most taxonomically diverse, but the trinucleid *Cryptolithus* is numerically dominant. Part of the reason that the fauna is so varied is that the Ordovician trilobites of the region are subject to strong biofacies differentiation, and the faunas described span the Nearshore, Open shelf and Upper Slope biofacies. The degree of differentiation is such that three parallel biozonal schemes are needed, one for each biofacies. The authors integrate their new data with information already published, producing a local biozonal scheme that spans the Whiterockian-Cincinnatian (Llanvirn-Ashgill).

Both the authors and the *Palaeontographica Canadiana* series are known for the high quality of their illustrations. By these standards, I think the authors will be rather disappointed by the quality of reproduction of some of their plates: resolution is good throughout, but some plates have been printed with insufficient contrast.

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### History of insects

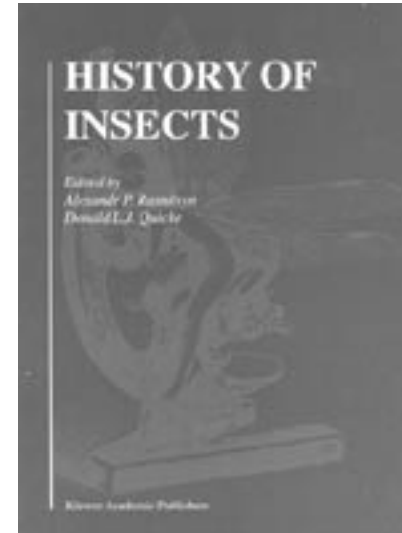
Rasnitsyn, A.P. & Quicke, D.L.J. (eds) 2002. xii + 517 pp. Kluwer Academic Publishers, Dordrecht. ISBN 1-4020-0026-X, US\$264

This is the defining work of the Arthropod Laboratory and its associates in the Russian Academy of Sciences (RAS) plus colleagues in Russian universities; it replaces *Istoricheskoe Razvitie Klassa Nasekomykh*, 1980 (Moskva). The new volume is larger, with contributions by 22 authors (regrettably two of them are now dead: Vladimir Zherikhin and Viktor Novokshonov). The present work is also helpfully in English unlike the earlier tome.

The book is divided into three main sections followed by an appendix, references and indexes. The first section (introduction to palaeoentomology) covers a wide range of topics including systematic methodology, global stratigraphy and locality maps; the study and history of palaeoentomology; and taxonomic and ecological considerations. Nomenclature is also explained, especially the Russian practice of extending the International Code of Zoological Nomenclature above superfamily level (for which there is no international agreement). The result of this has been the numerous replacement names for well-known insect orders and other higher taxa. Confusion or clarification? Only time and usage will tell.

One of the outstanding features of this book is its sheer comprehensiveness with no less than 3,000 references and four indexes – general, systematic, stratigraphic and geographic. Not surprisingly, you will find some unusual topics mentioned in section one, including pterosaur sick with dragonflies; insectan collectors, vandals and contaminants; and the vexed question of viable spores in amber!

The large section two is essentially about the systematics of fossil insects down to superfamily level. 42 orders are recognised which is about right in total number. (The additional order Mantophasmatodea was published shortly after this book). The Class Insecta is, however, taken



to exclude the entognathous hexapods (but will they be successfully included in the Myriapoda as suggested?). The Russian School's phyletic approach admits both holophyletic and paraphyletic groups. Thus Cimiciformes ('bug orders') is paraphyletic with respect to Holometabola (the majority of insects). Polyneoptera ('cockroach-grasshopper orders') becomes the sister group of the rest of the Pterygota (winged insects). Paleoptera are, however, not recognised as a group: the extinct palaeodictyopteroids are hived off to Cimiciformes, and the paleopteran rump (including dragonflies and mayflies) forms the Libelluliformes. Look out for unhighlighted stat. novs or even fam. novs in the text (p. 117). Section two also covers insect trace fossils as well as body fossils and broader evolutionary issues. Skimming is rejected as the origin of insect flight and the paranotal theory supported instead; but pterosaur

and other Mesozoic flea reports are treated with caution.

Section three (general features of insect history) discusses taxonomic diversity, ecological history and palaeobiogeography across the Phanerozoic. Momentary (instantaneous) counts are used to help overcome the effects of variable stage durations and rich fossil sites in family palaeodiversity. Nevertheless, non-linear curves still result. 'Insects are not dinosaurs' comment the editors in the Preface, but they could not entirely avoid the P/Tr (or more exactly Tr) extinction whereas tropical 'faunogenesis' is linked to periods with strong climatic zonation. Curiously, there is no direct evidence of fresh water insects prior to the Permian. The Asian Mesozoic assemblages including lacustrine will be of particular interest to western readers.

The short final section (4) summarises the world's top 161 fossil insect localities, including amber as well as rock fossil sites. 'Localities' are interpreted in the broad sense – some of them are the size of entire countries! It is therefore impressive that no less than seven are reported from the UK.

The book is amply illustrated with B/W photographs and line drawings and there are comparatively few production errors; e.g. the range of Triplosobida is omitted in key figure 1 (should be C3); the Purbeck insect beds are Berriasian; insects also occur above the Westphalian C in the UK Coal Measures; and records of UK Pliocene insects are doubtful. It is usefully augmented with the Proceedings of the 2nd Congress on Palaeoentomology, 2003 (Kraków).

The history of insects is also human history. Since the 1920s, the RAS has consistently worked on fossil insects, producing a unique dynasty of palaeoentomologists in spite of the sociopolitical and economic upheavals of twentieth-century eastern Europe. The Russian Federation is vast and with the restrictions on travel imposed during the communist era, the Arthropod Laboratory simply turned its attention to the fossil wealth of Mongolia, producing major monographs on Cretaceous insects. When Siberia beckoned, classical works on the Jurassic followed.

Insects are the most palaeodiverse class in the fossil record and, working as a team, Russian palaeontologists individually specialised in particular orders to facilitate progress. Thus they published the *Osnovy* volume on insects thirty years ahead of the equivalent *Treatise*. In the early twenty-first century, the Arthropod Laboratory is already a key player on the now international palaeontomology scene. Congratulations to Alex Rasnitsyn (RAS) for overseeing the Moscow end of this magnus opus and Donald Quicke (Imperial College) for ensuring its availability to all non-cyrillic readers.

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Palaeontology

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# The Lyell Meeting 2004

## Dinosaur Palaeobiology

The Geological Society,  
Burlington House, London

Wednesday 11th February 2004

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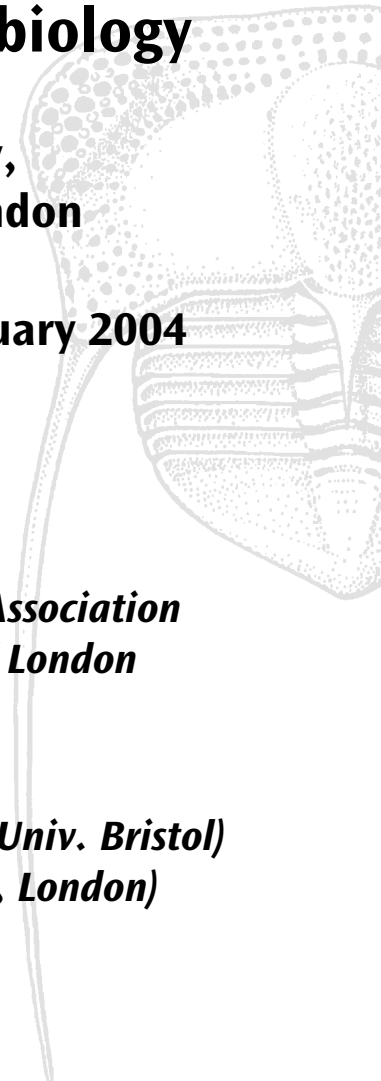
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# ABSTRACTS





## Dinosaur herbivory: from functional morphology to macroevolution

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In terms of species-richness and biomass, herbivorous dinosaurs were the dominant terrestrial vertebrates of the Mesozoic Era. Dinosaurs were primitively carnivorous (inheriting this condition from their archosaurian ancestors), but herbivory appeared in multiple dinosaur lineages early in the evolution of the group and may have arisen via various omnivorous intermediate stages. Plants are a difficult food source and require either significant oral or digestive processing to release the meagre amounts of nutrients that they contain. In order to deal with these problems, dinosaurs possessed a wide range of adaptations to herbivory. Many of these were concentrated in the skull and dentition, but herbivory also affected the postcranial morphology of these animals.

The levels of structural organisation displayed by the functional complexes associated with dinosaur herbivory ranged from rather simple feeding systems that were not too dissimilar from those of living herbivorous lizards (such as those seen in prosauropods and stegosaurs) to those that approached or surpassed those known in extant herbivorous mammals (such as those of ornithomimids). These adaptations included: complex jaw movements; development of dental batteries; presence of a precise occlusion; cheeks; and changes in limb proportions and neck function. Dinosaur herbivores occupy a much broader range of morphospace than their carnivorous relatives.

In addition to providing information on functional morphology and palaeobiology, the varied character complexes associated with herbivory offer the potential for macroevolutionary and palaeoecological insights. These include: possible coevolutionary interactions with food plants; effects of feeding adaptations on the diversity and evolution of various dinosaur groups; and also investigation of more general macroevolutionary phenomena such as correlated progression, 'key adaptations' and 'major adaptive zones'.

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## Extinction of the dinosaurs

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According to many, the extinction of the dinosaurs is now fully known. However, not much has changed since 1980 in fact.

Of course, the impact hypothesis of Alvarez *et al.* (1980) has not been rejected, and in fact has been reinforced by substantial, and unpredicted, evidence – shocked quartz, glass spherules with the geochemistry of sedimentary rocks, stishovite, direct evidence of flash freezing, zoning of the impact products in concentric circles leading out from the proto-Caribbean, and indeed



a crater. The Chicxulub crater is of the predicted size, it is in roughly the predicted place, and the fallout and tsunami materials are as would be predicted. So the impact model is multiply confirmed, and the hypothesis in the Alvarez *et al.* (1980) paper turns out to have been one of the most daring scientific hypotheses ever – the authors took a huge risk, laying themselves open to easy refutation – and yet they have not been successfully refuted, despite numerous efforts to do so.

The simple impact story is weakened by suggestions that the extinctions of foraminifera and other microfossil groups occur at times other than the impact horizon, and that the impact in fact had little to do with the demise of various life forms. This rather strains credulity, but the conflicts between different biostratigraphers ought to be resolvable.

So, barring a small number of persistent critics, the impact model is accepted by a majority of earth scientists. But did this cause the extinction of the dinosaurs and, if so, how? Again, it would seem incredible if there were no linkage between the impact and the extinction. The coincidence of timing is strongly suggestive. However, there are three outstanding areas for exploration; the pattern of the die-off, quality of the record, and the biotic consequences of impact.

- (1) The pattern of the die-off. It is well documented that two large-scale attempts to document huge numbers of fossils through the Hell Creek Formation in Montana failed to find agreement. Peter Sheehan and colleagues found evidence for catastrophic extinction (*i.e.* survival of most dinosaurian species right to the last inch of the Maastrichtian, and their instant disappearance at one horizon), while David Archibald and colleagues found evidence for longer-term or gradual decline. This dispute might suggest that the question will never be resolved. What geological succession could be more appropriate, and how many more specimens have to be counted in order to provide convincing evidence one way or the other?
- (2) Quality of the record. One issue in the Sheehan vs. Archibald debate was that of quality. How perfect does one expect the fossil record to be, and to what extent can one calculate probability measures and apply correction factors? Studies of ammonite diversity up to the K/T boundary suggest that the more one collects the more one finds. However, intensity of collection effort is also an important factor in avoiding the mistake of failing to identify a decline in abundance, if not of diversity. Patchy collecting and gaps in the rock record can either make a catastrophic extinction pattern seem gradual or a gradual pattern seem catastrophic respectively.
- (3) Biotic consequences of impact. Very little attention has been given to killing models. How can an impact, and its physical environmental consequences, cause mass dying? All we have for comparison are volcanic eruptions and other essentially local-scale phenomena. Many K/T researchers believe it was enough to establish that impact had occurred, and to determine the consequences. However, it is hard to kill many species worldwide. The killing models have yet to be developed.

## Dinosaur eggs and babies: facts versus fiction

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Dinosaur eggs were first discovered in the Upper Cretaceous of southern France in the mid-nineteenth century by Philippe Matheron and Jean-Jacques Pouech, and an initial study of eggshell microstructure was published by Paul Gervais in 1877. However, dinosaur eggs first attracted widespread attention in the 1920s with the much publicised discoveries of the American Museum of Natural History expeditions to the Gobi Desert. Starting in the 1960s, systematic investigations in the field and laboratory have shown that fossil eggs are extremely common in some Mesozoic formations, ranging in age from Triassic to terminal Cretaceous.

A major difficulty faced by studies on fossil eggs is that the identity of the egg-layer can be strictly ascertained only when an identifiable embryo is present within the egg. Although a number of fossil embryos have been reported from various parts of the world, the vast majority of fossil eggs are not associated with embryonic remains. A detailed parataxonomy of fossil eggs was established in the 1980s and 1990s, but many “ootaxa” are still insufficiently linked to taxa based on skeletal remains. This problem has been compounded by misidentifications of embryos or purported egg-layers, the best known example being that of the supposed *Protoceratops* eggs from the Gobi which turned out to be those of the theropod *Oviraptor*. Similarly, embryos long referred to the ornithomimid *Orodromeus* were shown to belong to the theropod *Troodon*. An enduring problem is that of megaloolithid eggs, which are clearly associated with titanosaurid sauropods in Argentina, but may be associated with hadrosaurids in Romania.

Nesting behaviour in dinosaurs is still incompletely known, despite several well-publicised studies, as egg-laying patterns are not always easily discernible. Clutches arranged in circles have been reported from southern France, but are probably an artefact of excavation. Most dinosaurs seem to have laid their eggs in tightly assembled clutches, and in some cases these may have been buried. Brooding is well documented in oviraptorosaurs (which some authors suggest may have been birds rather than dinosaurs). Histological evidence suggests that hatchlings of some dinosaurs were precocial, while others may have been altricial. Hatchlings and babies are known from various dinosaur groups and provide interesting evidence about growth rates (which appear to have been fast) and patterns.

Purported evidence of dinosaur decline prior to extinction based on a supposed increase of pathological eggshells in latest Cretaceous formations in southern France has been shown to be erroneous. Attempts to use dinosaur eggshells as stratigraphic markers in southern France have been only moderately convincing, as the reported succession of eggshell types bears little resemblance to evidence based on skeletal elements.

## Stability and Agility in Dinosaurs

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The combination of large size and large mass in most dinosaurs would have exerted a strong effect on what they were capable of as living, moving organisms. Lacking living examples of animals with sizes equal to those of dinosaurs, investigating aspects of stability and agility in dinosaurian locomotion can be done using ideas and techniques from physics and engineering.

A basic requirement for any animal is that it be able to balance and remain stable while standing still or walking, and determining the centre of mass (CM) of a dinosaur is a key component in understanding how they did this. Knowing the position of the CM can also lead to the testing of restorations of dinosaurs to see if a proposed restoration would have permitted the animal to have walked without becoming unstable. Examining the stance of a dinosaur and the position of its CM relative to its limb sockets can also reveal whether the animal was a biped, a quadruped, or something in between.

Given that dinosaurian body masses span at least five orders of magnitude, a study of the patterns of phylogenetic increases in body size reveals allometric changes in body shape that suggest strategies for maintaining levels of agility that would be impossible if growth was isometric. These changes are especially marked in the bipedal dinosaurs such as the carnivorous theropods and the herbivorous ornithomimids where bodies become deeper and wider, and tails become relatively shorter with increasing body size. This has the effect that body mass becomes concentrated towards the hips and trunk region, and results in relatively lower rotational inertia about a vertical axis. A reduced rotational inertia for an animal enables it to pivot and change direction much more quickly, which has implications for both predators and their prey.

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## The dinosaurian origin of birds – a state-of-the-art review.

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*Archaeopteryx*, from the latest Jurassic of Germany, is the earliest known bird. It has long been regarded as an example of evolution in action by virtue of a suite of skeletal features shared with maniraptoran theropod dinosaurs, yet it possesses impressions of modern asymmetrical flight feathers. The wing feathers have a configuration of primary and secondary flight feathers identical to those of modern birds, suggesting that *Archaeopteryx* had some powered flight capability. It is thus a key taxon in the investigation of the dinosaurian origin of birds and the origin of flight. However, it provides no clues as to how feathers evolved, although they must, logically, have been present in the dinosaur lineage that gave rise to birds. That has now been demonstrated by a series of spectacular discoveries in the last ten years from an Early Cretaceous lagerstätten in Liaoning Province, China. Several taxa of feathered dinosaurs have provided the ‘missing’ feather

evidence and stimulated debate about feather origins, feather development and feather function. Representatives of several lineages of small coelurosaurian dinosaurs are present in the Liaoning assemblage and allow the evolution of feathers to be mapped onto theropod phylogeny.

Most of the feathered dinosaurs from Liaoning were not capable of flight. However, a small arboreal form, *Microraptor*, adds new fuel to the controversial debate over whether flight began from the ground up or the trees down, and recent studies on ground living modern birds have generated new ideas on how birds became airborne. The Liaoning assemblage also includes a range of primitive true flying birds that show how elaboration of the flight apparatus developed beyond the *Archaeopteryx* stage.

The Liaoning discoveries have demonstrated that that most obvious defining character of birds – feathers – is no longer an avian exclusive. So what makes a bird a bird? Recent computed tomography and three-dimensional reconstruction of the braincase and brain of *Archaeopteryx* may provide some new characters by which birds can be distinguished from feathered dinosaurs.

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### The evolution of the Dinosauria

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It is very probable that the first dinosaurs appeared on Earth during the Late Triassic. The actual fossil record of dinosaurs begins in the latest part of the Carnian stage (c. 225 Ma) of the Late Triassic, at which time they had already differentiated into the two major clades: Ornithischia and Saurischia.

Early representatives of the Dinosauria are, generally speaking, medium-sized animals (1-3 m long) characterised by being bipedal and possessing elongate hindlimbs that were moved vertically beneath the body on either side of the midline (in what is described as parasagittal motion). This style of motion permitted these animals to move their limbs very effectively: giving them a long stride and thus the ability to move very quickly over the ground, as well as offering the alternative strategy of allowing the hindlimbs to act as vertical pillars that were capable of supporting great body weight.

The characteristically dinosaurian limb posture is linked directly with a number of diagnostic dinosaurian features: the feet are narrow and the toes, which point forward, tend to be symmetrically arranged about a midline axis; the feet are digitigrade (dinosaurs walk by balancing on their toes alone, rather than using the entire length of the foot as in the case of the human foot); the ankle and knee joints form simple uni-axial hinges; and the upper end of the femur (thigh bone), possesses an in-turned articular head. The in-turned femoral head fits into a deep (open-backed) cup-shaped socket (acetabulum) on the pelvis, above which is found a prominent, curved shelf of bone (the supracetabular crest) which buttresses the hip socket against the vertical forces exerted by the head of the femur. Related to these features, the attachment of the pelvis to the vertebral column is reinforced through an increased number of sacral ribs, and the lower pelvic bones (ischium and pubis) are generally narrow and elongated primarily to maintain the mechanical advantage of their associated hindlimb-moving muscles.

The significance of the highly distinctive saurischian and ornithischian pelvic constructions will be discussed briefly. This will be followed by an overview of the patterns of appearance, diversification and subsequent extinction, of many of the principal dinosaurian clades (phylogenetic lineages) throughout the remainder of the Mesozoic Era and the subtle, but overarching, influence of the tectonic evolution of the Earth during this, primarily dinosaurian, Era.

In summary, the Late Triassic is dominated primarily by medium-sized, bipedal, carnivorous saurischians (theropods), abundant, facultatively bipedal, herbivorous saurischians (sauropodomorphs) and relatively rare bipedal ornithischians. The Jurassic records a significant diversification of sauropodomorphs and some ornithischians, while the Cretaceous Period is notable for the relative decline in overall sauropodomorph diversity (although this is a decidedly geographically variable phenomenon), and a comparatively spectacular diversification of theropod and ornithischian dinosaurs right through to the end of the Cretaceous. The abrupt termination of an ecologically dominant and clearly vigorously evolving set of lineages, represented by the non-avian dinosaurs, by the event at the close of the Cretaceous Period represents one of the most stark examples of a punctuation mark in the story of life on Earth.

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### Biomechanical approaches to feeding, skull form and function in carnivorous dinosaurs

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Theropod dinosaur feeding habits are traditionally viewed as conservative in comparison to the range of unique cranial and dental adaptations utilized by ornithischian dinosaurs. Recent research, particularly using biomechanical analysis, is however currently uncovering a range of dietary specialisations in the arguably less morphologically diverse non-avian theropods. Here, I present an overview of recent biomechanical research into form, function and feeding in carnivorous Theropoda. Such analysis offers insight not only into the feeding behaviour of specific theropod taxa, but also the evolutionary pressures driving cranial design across the group as a whole.

Primary fossil evidence provides us with our most direct inferences of feeding: cannibalism, coprolites and bite marks are discussed in the context of prey preference and feeding behaviour. Comparative studies offer tantalising insights into the nature of feeding in particular taxa. For example, the cranial morphology of the so-called 'crocodile-mimic' spinosaurids alludes to a piscivorous lifestyle. Such hypotheses demand to be tested by further biomechanical means in the future.

'Traditional' biomechanical approaches such as adductor muscle reconstruction, lever-arm mechanics and bending strength analysis have proved immensely valuable in estimating and elucidating theropod bite forces, cranial strength and construction parameters, such as orbit and fenestration dimensions and also mandibular adaptation. Morphometrics has offered insight into cranium-specific niche partitioning and dimensional shifts in skull evolution.

The engineering/orthopaedic technique Finite Element Analysis (FEA) permits an assessment of cranial stress, strain and strength in response to external loads, such as bite and muscular forces.

FEA has been used to infer cranial mechanical performance and possible feeding behaviour in the skulls of *Allosaurus fragilis* and *Tyrannosaurus rex*, and these results are discussed here. Such FE-models allow the adaptive significance of particular cranial features to be identified, and have implications for the significance of patent (open) sutures in the crania of large theropods.

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### The biogeographic history of dinosaurs

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The biogeographic history of dinosaurs has received considerable attention but remains controversial. Few studies have applied a rigorous biogeographic method to a large data-set or evaluated the statistical significance of their results. Nevertheless, the recent influx of data on dinosaur distributions and phylogeny makes a review of dinosaur biogeography feasible and timely.

Several dinosaur groups became widespread during their Late Triassic radiations. This is consistent with the existence of Pangaea at this time. However, we do not see a cosmopolitan fauna at the generic or specific level across Pangaea: this suggests that, after an initial “global” dispersal some vicariance occurred. During the Early and Middle Jurassic, eustatic and tectonic events led to the isolation of Asia, and then the separation of North America from Gondwana, resulting in statistically significant levels of vicariance. This explains why many Asian dinosaurs are the most basal forms in their clades. Furthermore, similarities between the Late Jurassic faunas of North America and Africa, which have previously been explained in terms of dispersal, are more plausibly interpreted as vicariance. Vicariance events also occurred during the Late Jurassic and Early Cretaceous as Gondwana fragmented, first into western and eastern portions and then the separate continents we know today. Thus, there is a consistently closer relationship between South American and African forms relative to organisms elsewhere in Gondwana. Marine regression during the Aptian-Albian created a connection between Europe and Asia allowing the geodispersal of many dinosaur groups. The Late Cretaceous has not yet produced a statistically significant level of pattern repetition, so biogeographic interpretation remains preliminary. Nevertheless, the strong similarities between North America and Asia are consistent with the formation of a land connection across the north Pacific during the early Late Cretaceous. There is also growing evidence that South America formed a new connection with eastern Gondwana via Antarctica at this time.

These results have several implications for our understanding of dinosaur evolution. First, the presence of vicariance signals contradicts many hypotheses for dinosaur distributions based on dispersal, and thus resolves many conflicts between biogeography and palaeogeography. Second, biogeographic patterns can make predictions about the distribution histories of individual clades, such as the proposal that diplodocid sauropods are an endemic radiation restricted to the Late Jurassic of North America. Finally, the presence of vicariance patterns that match the sequence and timing of Pangaeon fragmentation indicates that many dinosaur clades had diversified by the late Early Jurassic, somewhat earlier than the fossil record indicates directly.

dinosaurs

dinosaurs